# Further analyses of the effects of environmental variability on the estimation of MSY rates

Justin G. Cooke[1]

ABSTRACT

Further simulation trials of the properties of the estimation of *MSYR* (exploitation rate at the MSY population level) from time series of abundance data in the presence of environmental variation were conducted as recommended in SC/61/Rep 6 (Report of the Workshop on *MSYR* for Baleen Whales). The results confirm that *MSYR* (the sustainable exploitation rate at the optimal population level) can be substantially overestimated when the true *MSYR* is low. When the true *MSYR* is 1%, the median *MSYR* estimates can be up to 5% in scenarios with high environmental variability. Furthermore, there is a high probability (which exceeds 50% in some scenarios) that a model with the conventional assumption that the population is at is carrying capacity *K* at the start of exploitation will fail to fit the observed time series. Paradoxically, the overestimation of *MSYR* rates is less severe if the assumption that the population is at *K* at the start of exploitation is retained, even when the data are incompatible with this assumption. If the true *MSYR* rate is defined as the long-term constant exploitation rate that results in the highest average yield, then the median realised stochastic *MSYR* in the presence of environmental variability is found to be close to the nominal *MSYR* of the model.

## INTRODUCTION

Since the first attempts to place the management of whaling on a scientific basis in the mid-20th century, the conceptual model for management has been based on the notion of deterministic density-dependent dynamics under which an unexploited whale population is assumed to be in deterministic equilibrium at the population level corresponding to the carrying capacity (*K*) (Allen, 1980). The population level at which the maximum sustainable yield is obtained (*MSYL*) is assumed to be a fixed fraction of *K,* and it is assumed that a population at this level can be sustainably exploited under a constant exploitation rate, provided that this does not exceed the Maximum Sustainable Yield rate (*MSYR*). The maximum sustainable yield rate and level played an explicit role in the so-called New Management Procedure which the IWC adopted in 1974, and which is still nominally in force in the IWC Schedule. In the absence of a means to determine these quantities directly for most baleen whale stocks, the practice of the Scientific Committee in the operation of the NMP was to assume that the *MSYL* occurred at 60% of carrying capacity, *K* (the notional population level in the absence of exploitation), and that, in the absence of evidence to the contrary, the MSY rate was 4% of the *MSYL* population level.

A framework was developed by Cooke (2007) for incorporating environmental variation into models of the net recruitment rate of baleen whales. Simulation studies by Cooke (2007) showed that in the presence of environmental variability, fitting the conventional deterministic density-dependent model to time series of abundance data can result in substantial positive median bias in the estimates of *MSYR* when the true *MSYR* is low. Cooke (2009a) further showed that there can be a high probability that the deterministic model will fail to fit the time series of abundance data, and that the overestimation of *MSYR* is greater when the model assumptions are relaxed to allow a better fit to the data.

This paper reports results for the addition simulation scenarios recommended by IWC (2009) for the examination of the implications of environmental variability for *MSYR* estimation.

[1] CEMS, Höllenbergstraße 7, 79312 Windenreute, Germany Email: jgc@cems.de

## METHODS

### Incorporation of environment variability into models of the net recruitment rate

Traditional deterministic population models used to model baleen whale populations relate the *per capita* rate of increase (net recruitment rate) to the population size relative to carrying capacity, $K$, e.g.

$$r = \frac{1}{N}\frac{dN}{dt} = r_0\left(1 - \left(\frac{N}{K}\right)^z\right) \qquad (1)$$

The model is usually extended to include age and sex structure, but for simplicity this is not introduced here. The parameter $r_0$ is usually called the intrinsic or maximum rate of increase. Because it represents the assumed maximum possible rate of increase for the population, it is alternatively denoted $r_{\max}$. Traditionally these quantities are regarded as synonymous.

In the framework developed by Cooke (2007), a distinction is made between $r_{\max}$, the biologically determined maximum rate of increase that can occur in an ideal habitat, and $r_0$, the average rate of increase at low population levels for a given stock in a given habitat. $r_0$ is related to habitat quality, and $r_0 \leq r_{\max}$, with equality only in ideal habitats. The habitat quality is presumed to be subject to random inter-annual variability. The model results in the following expression for the net recruitment rate:

$$r(x,t) = r_{\max}\left(1 - e^{-\left(\sigma v_t + \frac{1}{2}\sigma^2\right)}\left(1 - q + q\left(x/K\right)\right)^z\right) \qquad (2)$$

Where:
$x$ is the current population size
$q$ is a measure of habitat quality, ranging from zero in marginal habitats (where the species can barely persist) to unity in ideal habitats (where the species can increase at its biological maximum rate).
$K$ is the mean carrying capacity
$\sigma$ is a measure of environmental variability
$v_t$ are standard normal random variables (possibly exhibiting serial correlation).
$z$ density-dependent exponent

The *MSYR* depends on $r_{\max}$, $q$ and $z$. The MSY population level as a fraction of $K$ (*MSYL*) depends on $q$ and $z$.

Empirical information of the level of variability in baleen whale demography is limited, but Cooke (2007) discusses the data on gray and southern right whales and finds they are consistent with quite high levels of variability.

### Scenarios examined

IWC (2009, Table 2) recommended generation of scenarios incorporating the following range of factors and parameter values:

*Parameters relation to past exploitation and current monitoring:*
Years of exploitation: 50
Depletion level: 0.05 and 0.25 of pre-exploitation level
Gap between end of exploitation and start of monitoring: 0 and 20 years
Length of time series of abundance data: 10 and 30 years
Intervals between abundance estimates: 2 and 5 years
CV of abundance estimates: 0.0 and 0.2 (assumed CV = 0.2)

*Biological parameters*
$\sigma$ *:* Environmental variation in net recruitment rate (equation 2): values from 0.0, 0.5 and 1.0
$\rho$: serial correlation in environmental variability: 0.0, 0.5 and 0.9.
$r_{max}$ : max rate of increase in ideal habitat: 0.10.
$q$ : habitat quality: 0.1, 0.4 and 0.9 (with $z = 2.39$)
(Corresponds to *MSYR* = 0.011, 0.039 and 0.067 and *MSYL* = 0.509, 0.538 and 0.589).
Also: $q = 0.2$ and 0.8 with $z = 1$ (*MSYR* = 0.01 and 0.04, *MSYL* = 0.5).

The full list of scenarios examined is given in Table 1 (as recommended by IWC 2009). The specifications of the simulation model are given by Cooke (2009b). 400 replicates of each scenario were run (except for the A scenarios, which are deterministic).

For most scenarios, the assumed *MSYL* was fixed at the conventional value of 0.6K when fitting the model. For some scenarios the assumed *MSYL* was set to the true *MSYL*. The latter assumption is somewhat artificial (because in reality the true *MSYL* is not known), but was examined, according to IWC (2009), in order to separate out the effects of miss-specification of the *MSYL* from other potential sources of bias in the estimate of *MSYR*.

The O scenarios (involving explicitly varying calving intervals) recommended by IWC (2009) were not run because it was not clear what additional assumptions should be made to implement them.

**Fitting the model**
For each scenario, the model was fitted in three alternative ways:
(i) Assuming population at *K* at start of exploitation
(ii) Allowing an arbitrary population level at the start of exploitation (as a free parameter)
(iii) Assume population at *K* at start of exploitation unless rejected at 5% significance level in favour of option (ii) based on a likelihood ratio test.

**Comparing nominal and realised MSYR**
For each scenario, the "realised stochastic" *MSYR* and *MSYL* were estimated by simulation. The realised stochastic *MSYR* is defined as proposed by Punt (in press) in terms of the fixed annual exploitation rate that results in the highest long-term average yield. The *MSYL* is the corresponding mean population level as a fraction of the mean unexploited population level. For each scenario, the population was simulated for 11,000 years under a fixed exploitation rate, and the first 1,000 years were discarded to ensure that equilibrium had been reached. 400 replicate simulations were conducted for each scenario. The median, 5$^{th}$ and 95$^{th}$ percentiles of the "realised stochastic" *MSYR* and *MSYL* were recorded.

## RESULTS

The results of the simulation trials are shown in Tables 2 for each scenario for the 3 alternative fitting methods, in terms of the median, 5$^{th}$ and 95$^{th}$ percentile of the *MSYR* estimates. Also shown is the proportion of replicates for which the model with the population assumed to be at *K* at the start of exploitation is rejected in favour of the alternative.

Table 3 shows the 5$^{th}$, 50$^{th}$ and 95$^{th}$ percentiles of the estimates of "true stochastic" *MSYR* and *MSYL* for each scenario along with the assumed deterministic values of these quantities.

## DISCUSSION

Estimation of *MSYR* is relatively median unbiassed for the higher true *MSYR* values, but the estimated *MSYR* is positively median biassed when the true *MSYR* is low. When the true *MSYR* is 0.011, the median of the estimated *MSYR* ranges up to 0.050 in scenarios with high variability.

Fitting the abundance data with the assumption that the population is at *K* at the start of exploitation reduces the positive bias in *MSYR* somewhat. However, the assumption that the population starts at *K* is rejected with a high probability, which exceeds 50% in some scenarios. Indeed, in terms of reducing bias in the estimate of *MSYR*, it can preferable to assume that the population starts at *K* even when this assumption is rejected by the data. For example, in scenario N1 where the true *MSYR* is 0.011, the median *MSYR* estimate is 0.044 when the hypothesis that the initial population is at *K* can be rejected (depending on the data) but the median MSYR estimate is "only" 0.023 when the population is assumed to start at *K* regardless of the data.

This somewhat counter-intuitive result has implications for the estimation of *MSYR* for recovering whale stocks where it has been found that the data cannot fit a simple density-dependent recovery from past exploitation. Population modelling exercises for North Atlantic humpback whales (Punt *et al* 2006) and eastern North Pacific gray whales (Wade *et al* 2002; Butterworth *et al* 2002) found that the time series data were not consistent with the assumption of populations at *K* at the start of exploitation. The results of this paper suggest that: (i) this phenomenon is not necessarily an anomaly, but may be *a priori* quite probable, if there is environmental variability; (ii) estimates of *MSYR* may be less positively biassed if the population is assumed to start at *K*, even in cases such as these where the assumption cannot be reconciled with the data.

The median "realised stochastic" *MSYR* and *MSYL* are close to the nominal values of the corresponding model is all scenarios. The conjecture expressed by IWC (2009) that this factor may be contributing to the positive bias in estimates of *MSYR* is, therefore, not confirmed. However, in the N1 scenario there is noticeable stochastic deviation around the median despite 10,000 years of simulation.

In conclusion, the results of this paper and that of Cooke (2009a) lend further support to the notion that explicit consideration of environmental variability is important in the interpretation of historic trends in baleen whales populations, and in the derivation of suitable ranges of parameter values for the simulation testing of management procedures.

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Table 1. List of scenarios for testing MSYR estimation with environmental stochasticity

| Scenario | Years of Catches | Gap years | Data years | Survey interval | CV | Depletion | Habitat quality | Env. var. Sigma | Env. corr. Rho | Calving interval | True MSYR | True Z | True MSYL | Assumed MSYL | Remarks |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A1 | 50 | 0 | 30 | 5 | 0 | 0.25 | 0.1 | 0 | | 1 | 0.011 | 2.39 | 0.509 | 0.6 | Deterministic |
| A2 | 50 | 0 | 30 | 5 | 0 | 0.25 | 0.4 | 0 | | 1 | 0.039 | 2.39 | 0.538 | 0.6 | case |
| A3 | 50 | 0 | 30 | 5 | 0 | 0.25 | 0.9 | 0 | | 1 | 0.067 | 2.39 | 0.589 | 0.6 | |
| B1 | 50 | 0 | 30 | 5 | 0.2 | 0.25 | 0.1 | 0.5 | 0.5 | 1 | 0.011 | 2.39 | 0.509 | 0.6 | Reference |
| B2 | 50 | 0 | 30 | 5 | 0.2 | 0.25 | 0.4 | 0.5 | 0.5 | 1 | 0.039 | 2.39 | 0.538 | 0.6 | case |
| B3 | 50 | 0 | 30 | 5 | 0.2 | 0.25 | 0.9 | 0.5 | 0.5 | 1 | 0.067 | 2.39 | 0.589 | 0.6 | |
| C1 | 50 | 0 | 30 | 2 | 0.2 | 0.25 | 0.1 | 0.5 | 0.5 | 1 | 0.011 | 2.39 | 0.509 | 0.6 | Data rich |
| C2 | 50 | 0 | 30 | 2 | 0.2 | 0.25 | 0.4 | 0.5 | 0.5 | 1 | 0.039 | 2.39 | 0.538 | 0.6 | (15 surveys) |
| C3 | 50 | 0 | 30 | 2 | 0.2 | 0.25 | 0.9 | 0.5 | 0.5 | 1 | 0.067 | 2.39 | 0.589 | 0.6 | |
| D1 | 50 | 20 | 10 | 2 | 0.2 | 0.25 | 0.1 | 0.5 | 0.5 | 1 | 0.011 | 2.39 | 0.509 | 0.6 | Data poor |
| D2 | 50 | 20 | 10 | 2 | 0.2 | 0.25 | 0.4 | 0.5 | 0.5 | 1 | 0.039 | 2.39 | 0.538 | 0.6 | (20-year gap) |
| D3 | 50 | 20 | 10 | 2 | 0.2 | 0.25 | 0.9 | 0.5 | 0.5 | 1 | 0.067 | 2.39 | 0.589 | 0.6 | |
| E1 | 50 | 0 | 30 | 5 | 0.2 | 0.05 | 0.1 | 0.5 | 0.5 | 1 | 0.011 | 2.39 | 0.509 | 0.6 | Depletion |
| E2 | 50 | 0 | 30 | 5 | 0.2 | 0.05 | 0.4 | 0.5 | 0.5 | 1 | 0.039 | 2.39 | 0.538 | 0.6 | to 0.05K; |
| E3 | 50 | 0 | 30 | 5 | 0.2 | 0.05 | 0.9 | 0.5 | 0.5 | 1 | 0.067 | 2.39 | 0.589 | 0.6 | standard data |
| F1 | 50 | 0 | 30 | 2 | 0.2 | 0.05 | 0.1 | 0.5 | 0.5 | 1 | 0.011 | 2.39 | 0.509 | 0.6 | Depletion |
| F2 | 50 | 0 | 30 | 2 | 0.2 | 0.05 | 0.4 | 0.5 | 0.5 | 1 | 0.039 | 2.39 | 0.538 | 0.6 | to 0.05K; |
| F3 | 50 | 0 | 30 | 2 | 0.2 | 0.05 | 0.9 | 0.5 | 0.5 | 1 | 0.067 | 2.39 | 0.589 | 0.6 | data rich |
| G1 | 50 | 20 | 10 | 2 | 0.2 | 0.05 | 0.1 | 0.5 | 0.5 | 1 | 0.011 | 2.39 | 0.509 | 0.6 | Depletion |
| G2 | 50 | 20 | 10 | 2 | 0.2 | 0.05 | 0.4 | 0.5 | 0.5 | 1 | 0.039 | 2.39 | 0.538 | 0.6 | to 0.05K; |
| G3 | 50 | 20 | 10 | 2 | 0.2 | 0.05 | 0.9 | 0.5 | 0.5 | 1 | 0.067 | 2.39 | 0.589 | 0.6 | data poor |
| H1 | 50 | 0 | 30 | 5 | 0.2 | 0.25 | 0.2 | 0.5 | 0.5 | 1 | 0.010 | 1 | 0.500 | 0.5 | MSYL=0.5K |
| H2 | 50 | 0 | 30 | 5 | 0.2 | 0.25 | 0.8 | 0.5 | 0.5 | 1 | 0.040 | 1 | 0.500 | 0.5 | symmetrical |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| J1 | 50 | 0 | 30 | 5 | 0.2 | 0.05 | 0.1 | 0.5 | 0.5 | 1 | 0.011 | 2.39 | 0.509 | 0.509 | MSYL |
| J2 | 50 | 0 | 30 | 5 | 0.2 | 0.05 | 0.4 | 0.5 | 0.5 | 1 | 0.039 | 2.39 | 0.538 | 0.538 | known |
| J3 | 50 | 0 | 30 | 5 | 0.2 | 0.05 | 0.9 | 0.5 | 0.5 | 1 | 0.067 | 2.39 | 0.589 | 0.589 | |
| K1 | 50 | 0 | 30 | 5 | 0.2 | 0.25 | 0.1 | 0.0 | | 1 | 0.011 | 2.39 | 0.509 | 0.6 | No |
| K2 | 50 | 0 | 30 | 5 | 0.2 | 0.25 | 0.4 | 0.0 | | 1 | 0.039 | 2.39 | 0.538 | 0.6 | environmental |
| K3 | 50 | 0 | 30 | 5 | 0.2 | 0.25 | 0.9 | 0.0 | | 1 | 0.067 | 2.39 | 0.589 | 0.6 | variability |
| L1 | 50 | 0 | 30 | 5 | 0.2 | 0.05 | 0.1 | 1.0 | 0.5 | 1 | 0.011 | 2.39 | 0.509 | 0.509 | High |
| L2 | 50 | 0 | 30 | 5 | 0.2 | 0.05 | 0.4 | 1.0 | 0.5 | 1 | 0.039 | 2.39 | 0.538 | 0.538 | environmental |
| L3 | 50 | 0 | 30 | 5 | 0.2 | 0.05 | 0.9 | 1.0 | 0.5 | 1 | 0.067 | 2.39 | 0.589 | 0.589 | variability |
| M1 | 50 | 0 | 30 | 5 | 0.2 | 0.25 | 0.1 | 0.5 | 0.9 | 1 | 0.011 | 2.39 | 0.509 | 0.6 | High |
| M2 | 50 | 0 | 30 | 5 | 0.2 | 0.25 | 0.4 | 0.5 | 0.9 | 1 | 0.039 | 2.39 | 0.538 | 0.6 | environmental |
| M3 | 50 | 0 | 30 | 5 | 0.2 | 0.25 | 0.9 | 0.5 | 0.9 | 1 | 0.067 | 2.39 | 0.589 | 0.6 | correlation |
| N1 | 50 | 0 | 30 | 5 | 0.2 | 0.25 | 0.1 | 1.0 | 0.9 | 1 | 0.011 | 2.39 | 0.509 | 0.6 | High variability |
| N2 | 50 | 0 | 30 | 5 | 0.2 | 0.25 | 0.4 | 1.0 | 0.9 | 1 | 0.039 | 2.39 | 0.538 | 0.6 | and |
| N3 | 50 | 0 | 30 | 5 | 0.2 | 0.25 | 0.9 | 1.0 | 0.9 | 1 | 0.067 | 2.39 | 0.589 | 0.6 | correlation |

Table 2. Percentiles of estimates of MSYR from simulation scenarios with environmental stochasticity

| Scenario | True MSYR | Estimated MSYR, free initial population 5th | Median | 95th | Estimated MSYR, initial population at K 5th | Median | 95th | % Rejection Initial pop at K | Estimated MSYR, with model selection 5th | Median | 95th |
|---|---|---|---|---|---|---|---|---|---|---|---|
| A1 | 0.011 | | 0.013 | | | 0.012 | | | | 0.012 | |
| A2 | 0.039 | | 0.042 | | | 0.039 | | | | 0.039 | |
| A3 | 0.067 | | 0.070 | | | 0.070 | | | | 0.070 | |
| B1 | 0.011 | 0.003 | 0.030 | 0.114 | 0.000 | 0.015 | 0.105 | 23.0 | 0.000 | 0.019 | 0.114 |
| B2 | 0.039 | 0.024 | 0.044 | 0.114 | 0.020 | 0.041 | 0.104 | 19.8 | 0.020 | 0.041 | 0.104 |
| B3 | 0.067 | 0.039 | 0.072 | 0.114 | 0.037 | 0.069 | 0.114 | 22.5 | 0.037 | 0.070 | 0.114 |
| C1 | 0.011 | 0.003 | 0.026 | 0.114 | 0.000 | 0.016 | 0.100 | 43.0 | 0.000 | 0.020 | 0.114 |
| C2 | 0.039 | 0.022 | 0.043 | 0.084 | 0.020 | 0.041 | 0.093 | 39.3 | 0.020 | 0.042 | 0.096 |
| C3 | 0.067 | 0.043 | 0.070 | 0.106 | 0.039 | 0.069 | 0.114 | 36.8 | 0.041 | 0.069 | 0.107 |
| D1 | 0.011 | 0.003 | 0.061 | 0.114 | 0.000 | 0.021 | 0.080 | 15.8 | 0.000 | 0.025 | 0.114 |
| D2 | 0.039 | 0.014 | 0.073 | 0.114 | 0.000 | 0.040 | 0.076 | 11.5 | 0.001 | 0.043 | 0.094 |
| D3 | 0.067 | 0.037 | 0.098 | 0.114 | 0.028 | 0.055 | 0.090 | 19.3 | 0.029 | 0.057 | 0.114 |
| E1 | 0.011 | 0.000 | 0.023 | 0.114 | 0.010 | 0.018 | 0.034 | 29.0 | 0.006 | 0.019 | 0.050 |
| E2 | 0.039 | 0.036 | 0.054 | 0.088 | 0.033 | 0.048 | 0.061 | 17.8 | 0.035 | 0.049 | 0.068 |
| E3 | 0.067 | 0.061 | 0.077 | 0.097 | 0.058 | 0.067 | 0.090 | 23.3 | 0.058 | 0.070 | 0.090 |
| F1 | 0.011 | 0.000 | 0.023 | 0.080 | 0.009 | 0.017 | 0.031 | 47.5 | 0.004 | 0.020 | 0.061 |
| F2 | 0.039 | 0.039 | 0.051 | 0.069 | 0.037 | 0.046 | 0.056 | 34.0 | 0.037 | 0.048 | 0.063 |
| F3 | 0.067 | 0.064 | 0.074 | 0.087 | 0.060 | 0.067 | 0.081 | 40.5 | 0.061 | 0.070 | 0.085 |
| G1 | 0.011 | 0.000 | 0.022 | 0.114 | 0.011 | 0.019 | 0.046 | 19.0 | 0.009 | 0.020 | 0.066 |
| G2 | 0.039 | 0.013 | 0.057 | 0.114 | 0.016 | 0.038 | 0.066 | 14.8 | 0.016 | 0.038 | 0.079 |
| G3 | 0.067 | 0.034 | 0.078 | 0.114 | 0.031 | 0.044 | 0.068 | 30.5 | 0.031 | 0.052 | 0.107 |
| H1 | 0.010 | 0.003 | 0.032 | 0.114 | 0.000 | 0.016 | 0.098 | 27.3 | 0.000 | 0.020 | 0.114 |
| H2 | 0.040 | 0.023 | 0.045 | 0.114 | 0.022 | 0.043 | 0.114 | 21.8 | 0.022 | 0.044 | 0.114 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| J1 | 0.011 | 0.000 | 0.026 | 0.114 | 0.010 | 0.017 | 0.033 | 25.5 | 0.009 | 0.018 | 0.056 |
| J2 | 0.039 | 0.039 | 0.054 | 0.085 | 0.031 | 0.047 | 0.059 | 19.8 | 0.032 | 0.049 | 0.065 |
| J3 | 0.067 | 0.059 | 0.075 | 0.096 | 0.057 | 0.067 | 0.088 | 22.0 | 0.057 | 0.068 | 0.090 |
| K1 | 0.011 | 0.006 | 0.022 | 0.114 | 0.000 | 0.014 | 0.114 | 12.8 | 0.000 | 0.015 | 0.114 |
| K2 | 0.039 | 0.024 | 0.043 | 0.100 | 0.023 | 0.043 | 0.108 | 10.5 | 0.024 | 0.044 | 0.108 |
| K3 | 0.067 | 0.039 | 0.071 | 0.114 | 0.039 | 0.070 | 0.107 | 17.5 | 0.039 | 0.070 | 0.114 |
| L1 | 0.011 | 0.000 | 0.033 | 0.114 | 0.008 | 0.021 | 0.046 | 41.8 | 0.008 | 0.031 | 0.078 |
| L2 | 0.039 | 0.030 | 0.056 | 0.098 | 0.029 | 0.048 | 0.065 | 24.0 | 0.034 | 0.051 | 0.078 |
| L3 | 0.067 | 0.061 | 0.076 | 0.096 | 0.058 | 0.067 | 0.090 | 26.0 | 0.058 | 0.070 | 0.090 |
| M1 | 0.011 | 0.005 | 0.036 | 0.114 | 0.000 | 0.017 | 0.093 | 43.8 | 0.000 | 0.028 | 0.114 |
| M2 | 0.039 | 0.022 | 0.053 | 0.114 | 0.009 | 0.040 | 0.097 | 33.0 | 0.010 | 0.043 | 0.114 |
| M3 | 0.067 | 0.039 | 0.074 | 0.114 | 0.033 | 0.064 | 0.114 | 26.8 | 0.033 | 0.068 | 0.114 |
| N1 | 0.011 | 0.003 | 0.050 | 0.114 | 0.000 | 0.023 | 0.071 | 56.0 | 0.006 | 0.044 | 0.114 |
| N2 | 0.039 | 0.012 | 0.059 | 0.114 | 0.004 | 0.042 | 0.096 | 51.8 | 0.012 | 0.054 | 0.114 |
| N3 | 0.067 | 0.038 | 0.075 | 0.114 | 0.022 | 0.061 | 0.114 | 44.5 | 0.031 | 0.068 | 0.114 |

Table 3. Comparison of realised stochastic MSYR and MSYL with nominal values from model

| Scenario | Nominal MSYR | Nominal MSYL | Realised stochastic MSYR 5th | Realised stochastic MSYR 50th | Realised stochastic MSYR 95th | Realised stochastic MSYL 5th | Realised stochastic MSYL 50th | Realised stochastic MSYL 95th |
|---|---|---|---|---|---|---|---|---|
| A1 | 0.011 | 0.509 | | 0.011 | | | 0.510 | |
| A2 | 0.039 | 0.538 | | 0.038 | | | 0.542 | |
| A3 | 0.067 | 0.589 | | 0.064 | | | 0.596 | |
| B1 | 0.011 | 0.509 | 0.011 | 0.011 | 0.011 | 0.508 | 0.510 | 0.511 |
| B2 | 0.039 | 0.538 | 0.037 | 0.037 | 0.038 | 0.540 | 0.541 | 0.541 |
| B3 | 0.067 | 0.589 | 0.640 | 0.640 | 0.640 | 0.593 | 0.593 | 0.594 |
| H1 | 0.010 | 0.500 | 0.009 | 0.010 | 0.011 | 0.499 | 0.501 | 0.502 |
| H2 | 0.040 | 0.500 | 0.039 | 0.039 | 0.039 | 0.503 | 0.503 | 0.503 |
| L1 | 0.011 | 0.509 | 0.010 | 0.011 | 0.013 | 0.502 | 0.510 | 0.516 |
| L2 | 0.039 | 0.538 | 0.037 | 0.037 | 0.038 | 0.537 | 0.538 | 0.540 |
| L3 | 0.067 | 0.589 | 0.063 | 0.063 | 0.063 | 0.587 | 0.589 | 0.590 |
| M1 | 0.011 | 0.509 | 0.010 | 0.011 | 0.011 | 0.501 | 0.510 | 0.516 |
| M2 | 0.039 | 0.538 | 0.037 | 0.037 | 0.038 | 0.530 | 0.540 | 0.541 |
| M3 | 0.067 | 0.589 | 0.063 | 0.063 | 0.063 | 0.590 | 0.591 | 0.591 |
| N1 | 0.011 | 0.509 | 0.008 | 0.012 | 0.015 | 0.461 | 0.505 | 0.531 |
| N2 | 0.039 | 0.538 | 0.035 | 0.037 | 0.038 | 0.528 | 0.533 | 0.538 |
| N3 | 0.067 | 0.589 | 0.061 | 0.061 | 0.062 | 0.576 | 0.578 | 0.580 |

Note: only scenarios with distinct biological parameters are included