

Annex R

A Full Description of the Standard BALEEN II Model and Some Variants Thereof

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ABSTRACT

A full mathematical description of the BALEEN II population dynamics model is provided. The specifications required for alternative parameterisations of this model and to initiate projections when the population is not at its pre-exploitation equilibrium are also listed. Some new insights into the implications of different definitions for the yield curve are provided.

INTRODUCTION

The Hitter-Fitter package (de la Mare, 1989; Punt and Butterworth, 1991; de la Mare and Cooke, 1992; Punt, 1996) has been used in the assessments of a number of whale stocks (e.g. IWC, 1991a; b; Butterworth and Punt, 1992a). The BALEEN II population dynamics model underlying this package is age- and sex-structured, and can take age-specific recruitment and maturation ogives into account. Both maximum likelihood (e.g. Butterworth and Punt, 1992a) and Bayesian estimators (e.g. Givens *et al.*, 1993; 1995) have been used to estimate the parameters of this population model.

This paper provides a full description of the BALEEN II population dynamics model¹. It also describes the implementation details of a subset of the various possible parameterisations of the model (primarily those related to the assessment of the Bering-Chukchi-Beaufort (B-C-B) Seas stock of bowhead whales), provides full specifications for the case in which the population projection does not start at pre-exploitation equilibrium, lists the specifications of the output from the model, and contrasts a variety of ways of defining *MSYL* and *MSYR* in terms of population components other than that from which harvests are removed (i.e. other than the 'recruited'² component of the population as modelled).

THE BALEEN II POPULATION DYNAMICS MODEL

Basic dynamics

BALEEN II is age- and sex-structured, and considers animals as being either 'recruited' or 'unrecruited'. It assumes that all whaling takes place at the start of the year, and that all animals are 'recruited' (and have reached the age at first parturition) by age $x - 1$. The dynamics of the population are assumed to be governed by the equations:

¹ W.K. de la Mare wrote the core code for BALEEN II for the Hitter-Fitter package.

² 'Recruited' and 'unrecruited' are placed in quotes because there are cases in which some of the catch is taken from the 'unrecruited' component of the population because the catch exceeds the size of the 'recruited' component of the population.

$$N_{t+1,a}^s = \begin{cases} 0.5 \alpha_0^s P_{t+1}^{M,f} f_{t+1} & \text{if } a = 0 \\ N_{t,a-1}^s (1 - F_{r,t,a-1}^s) S_{a-1}^s \\ \quad + U_{t,a-1}^s (1 - F_{u,t}^s) S_{a-1}^s \delta_a^s & \text{if } 1 \leq a \leq x-1 \\ N_{t,x}^s (1 - F_{r,t,x}^s) S_x^s \\ \quad + N_{t,x-1}^s (1 - F_{r,t,x-1}^s) S_{x-1}^s & \text{if } a = x \end{cases} \quad (1)$$

$$U_{t+1,a}^s = \begin{cases} 0.5 (1 - \alpha_0^s) P_{t+1}^{M,f} f_{t+1} & \text{if } a = 0 \\ U_{t,a-1}^s (1 - F_{u,t}^s) S_{a-1}^s (1 - \delta_a^s) & \text{if } 1 \leq a \leq x-2 \end{cases} \quad (2)$$

where

$N_{t,a}^s$ is the number of 'recruited' animals of age a and sex s (m/f) at the start of year t ,

$U_{t,a}^s$ is the number of 'unrecruited' animals of age a and sex s at the start of year t ,

δ_a^s is the proportion of 'unrecruited' animals of sex s and age $a-1$ which recruit at age a ,

S_a^s is the annual survival rate of animals of sex s and age a , and is equal to $\exp(-M_a^s)$

where M_a^s is the instantaneous rate of natural mortality on animals of sex s and age a ,

$F_{r,t,a}^s$ is the exploitation rate on 'recruited' animals of sex s and age a during year t ,

$F_{u,t}^s$ is the exploitation rate (uniform over age) on 'unrecruited' animals of sex s during year t ,

α_a^s is the proportion of animals of sex s and age a which would be 'recruited' if the population were at pre-exploitation equilibrium,

$P_t^{M,f}$ is the number of females that have reached the age at first parturition by the start of year t ,

f_t is pregnancy rate (number of calves per 'mature' female) during year t (note that Equations (1) and (2) assume an equal male : female sex ratio at birth), and

x is the maximum (lumped) age-class.

Note that in the interests of generalisation, f_t is defined as in Punt (1996), which differs from convention in some earlier papers (de la Mare, 1989; Punt and Butterworth, 1991; de la

Mare and Cooke, 1992) in that it applies to both sexes born rather than to females only. Note also that the convention of referring to $P_t^{M,f}$ as the 'mature' female component of the population is used here, although it actually refers to animals no younger than their true age-at-maturity plus the gestation period, which is assumed to be one year. The survival rate S is assumed to depend on sex and age but to be independent of time. Punt (1996) provides a description of an extension to the BALEEN II model that allows for the possibility of density-dependent natural mortality and Punt and Butterworth (1996) include assessments of the B-C-B bowhead stock under the assumption that density-dependence impacts natural mortality rather than fecundity.

The possibility that age 0 animals (calves) are 'recruited' is allowed. However, for most applications (including the assessment of the B-C-B bowhead stock), the value of α_0^s is set equal to zero³. The values of $U_{t,x-1}^s$ and $U_{t,x}^s$ are not defined by Equation (2) because it is assumed that all animals of ages $x-1$ and x are 'recruited' (i.e. $\alpha_{x-1}^s = \alpha_x^s = 1$).

Density dependence

Density dependence on fecundity can be modelled by writing the pregnancy rate, f_t , as follows:

$$f_t = \max\left(f_{eq}\left[1 + A\left\{1 - \left(P_t^D / K_t^D\right)^z\right\}\right], 0\right) \quad (3)$$

where f_{eq} is the pregnancy rate at the pre-exploitation equilibrium, $f(0)$ ⁴:

$$f(F) = 2\left\{\sum_{a=\text{mat}_{\min}}^x \beta_a \left[\tilde{N}_a^t(F) + \tilde{U}_a^t(F)\right]\right\}^{-1} \quad (4)$$

A is the resilience parameter:

$$A = \frac{f_{\max} - f_{eq}}{f_{eq}} \quad (5)$$

f_{\max} is the maximum (theoretical) pregnancy rate,
 z is the degree of compensation,
 P_t^D is the size, at the start of year t , of the component of the population to which density dependence is functionally related (either total (1+) population size, P_t^{1+} , 'recruited' population size⁵, $P_t^{E,s}$, or the number of females that have reached the age at first parturition $P_t^{M,f}$):

$$P_t^{1+} = \sum_s \sum_{a=1}^x (N_{t,a}^s + U_{t,a}^s) \quad (6a)$$

$$P_t^E = \sum_s \sum_{a=1}^x N_{t,a}^s \quad (6b)$$

$$P_t^{M,s} = \sum_{a=\text{mat}_{\min}}^x \beta_a (N_{t,a}^s + U_{t,a}^s) \quad (6c)$$

mat_{\min} is the lowest age that a female can reach first parturition (constrained to be at least 2),

³ The current Baleen II software actually prohibits age 0 animals from being 'recruited'.

⁴ The pregnancy rate at the pre-exploitation equilibrium can be considered to be the equilibrium pregnancy rate when the exploitation rate, F , is fixed at zero.

⁵ The contribution of 'recruited' animals of age 0 to Equation (6b) is ignored to avoid the need for solving a non-linear equation for the number of births.

β_a is the fraction of females of age a which have reached the age at first parturition,
 K_t^D is the pre-exploitation equilibrium size (carrying capacity) at the start of year t of the component of the population to which density dependence is functionally related,
 $\tilde{N}_a^s(F)$ is the number of animals of sex s and age a that are 'recruited' when the exploitation rate is fixed at F , expressed as a fraction of the number of calves of the same sex s (see Appendix 1), and
 $\tilde{U}_a^s(F)$ is the number of animals of sex s and age a that are 'unrecruited' when the exploitation rate is fixed at F , expressed as a fraction of the number of calves of the same sex s .

Note that although these equations are written formally as if only the pregnancy rate component of 'fecundity' as defined here is density-dependent, exactly the same equations follow if some or all of this dependence occurs in the infant survival rate. Note that the dependence of K^D on t allows for the possibility that carrying capacity has varied over time. Butterworth *et al.* (1990) examine the implications of changes in carrying capacity for the assessment of the Eastern North Pacific gray whale.

Catches

BALEEN II allows for two series of sex-specific catches. One series of catches is taken uniformly from the 'recruited' component of the population while the other series is taken uniformly from the component of the population that is both 'recruited' and 'mature', which is termed 'mature-recruited' below. The equations which define $F_{r,t,a}^s$ and $F_{u,t}^s$ depend upon which of four cases applies. Of the four cases, Case 1 represents the normal situation; Cases 2 - 4 cover situations in which the catch in a given year exceeds the size of the component of the population from which it is assumed to be taken.

Case 1 - The total catch is less than the total number of 'recruited' animals and the 'mature-recruited' catch is less than the number of 'mature' animals (after the catch of 'recruited' animals is removed) (i.e. $C_t^{E,s} + C_t^{M,s} < P_t^{E,s}$ and $C_t^{M,s} < P_t^{M,s} (1 - C_t^{E,s}/P_t^{E,s})$). For this case, the catch can be taken as desired:

$$F_{r,t,a}^s = C_t^{E,s} / P_t^{E,s} + \beta_a C_t^{M,s} / P_t^{M,s} \\ F_{u,t}^s = 0 \quad (7a)$$

where

$C_t^{E,s}$ is the total catch of animals of sex s during year t taken uniformly from the 'recruited' component of the population,

$C_t^{M,s}$ is the total catch of animals of sex s during year t taken uniformly from the 'mature-recruited' component of the population⁶, and

$P_t^{E,s}$ is the total number of 'recruited' animals of sex s at the start of year t :

$$P_t^{E,s} = \sum_{a=0}^x N_{t,a}^s \quad (8)$$

To understand Equation (7a) further, consider the sum over all age-classes of the product of the number of recruited animals and the exploitation rate:

⁶ The calculation of the exploitation rate assumes that all 'mature' animals are 'recruited'.

$$\sum_{a=0}^x F_{r,t,a}^s N_{t,a}^s = \sum_{a=0}^x (C_t^{E,s} / P_t^{E,s} + \beta_a C_t^{M,s} / P_t^{M,s}) N_{t,a}^s =$$

$$\frac{C_t^{E,s}}{P_t^{E,s}} \sum_{a=0}^x N_{t,a}^s + \frac{C_t^{M,s}}{P_t^{M,s}} \sum_{a=0}^x \beta_a N_{t,a}^s = C_t^{E,s} + C_t^{M,s}$$

Case 2 - The total catch is less than the total number of 'recruited' animals but the 'mature-recruited' catch is greater than the number of 'mature' animals (after the catch of 'recruited' animals is removed) (i.e. $C_t^{E,s} + C_t^{M,s} < P_t^{E,s}$ and $C_t^{M,s} > P_t^{M,s}(1 - C_t^{E,s}/P_t^{E,s})$). For this case, the total catch is assumed to be removed uniformly from the 'recruited' component of the population:

$$F_{r,t,a}^s = (C_t^{E,s} + C_t^{M,s}) / P_t^{E,s}$$

$$F_{u,t}^s = 0 \tag{7b}$$

Case 3 - The total catch is greater than the total number of 'recruited' animals but is less than the total (0+) population size (i.e. $C_t^{E,s} + C_t^{M,s} > P_t^{E,s}$ and $C_t^{E,s} + C_t^{M,s} < P_t^{T,s}$). For this case, the 'recruited' component is extirpated and the difference between the total catch and the size of 'recruited' component of the population is removed with uniform selectivity from the 'unrecruited' component of the population:

$$F_{r,t,a}^s = 1$$

$$F_{u,t}^s = (C_t^{E,s} + C_t^{M,s} - P_t^{E,s}) / (P_t^{T,s} - P_t^{E,s}) \tag{7c}$$

where $P_t^{T,s}$ is the size of the total (0+) component of the population for sex s :

$$P_t^{T,s} = \sum_{a=0}^x (N_{t,a}^s + U_{t,a}^s) \tag{9}$$

Case 4 - The total catch is greater than the total (0+) population size (i.e. $C_t^{E,s} + C_t^{M,s} > P_t^{T,s}$). For this case, the entire population (both 'recruited' and 'unrecruited' components) is extirpated:

$$F_{r,t,a}^s = 1$$

$$F_{u,t}^s = 1 \tag{7d}$$

These equations are based on the assumption that the harvest occurs in a pulse at the start of the year (before natural mortality). It would be straightforward to generalise Equation (7) to allow the harvest to occur at any time during the year.

Recruitment and maturity

The fraction of 'unrecruited' animals of sex s and age a which 'recruit' at age $a+1$, α_{a+1}^s , is given by:

$$\alpha_{a+1}^s = \begin{cases} (\alpha_{a+1}^s - \alpha_a^s) / (1 - \alpha_a^s) & \text{if } \alpha_a^s < 1 \\ 1 & \text{if } \alpha_a^s = 1 \end{cases} \tag{10}$$

where α_a^s is the proportion of animals of sex s and age a which would be 'recruited' if the population were at pre-exploitation equilibrium:

$$\alpha_a^s = \begin{cases} 0 & \text{if } a < \text{rec}_{\min} \\ [1 + \exp\{-(a - r_{50}^s) / \sigma_r^s\}]^{-1} & \text{if } \text{rec}_{\min} \leq a \leq x-2 \\ 1 & \text{if } a \geq x-1 \end{cases} \tag{11}$$

r_{50}^s is the age at 50% recruitment for animals of sex s ,

σ_r^s is the parameter which determines the width of the recruitment ogive for animals of sex s ⁷, and

⁷ BALEEN II allows for the possibility that recruitment (and maturity) are knife-edged functions of age (i.e. $\sigma_r^s \rightarrow 0(\sigma_p \rightarrow 0)$).

rec_{\min} is the lowest age at which an animal may be 'recruited'.

The component of the population which may reproduce in a given year is the females that have reached the age at first parturition; this is the age at sexual maturity plus the gestation period (taken in BALEEN II to be one year). The proportion of females of age a which have reached the age at first parturition is given by:

$$\beta_a = \begin{cases} 0 & \text{if } a < \text{mat}_{\min} \\ [1 + \exp\{-(a - p_{50}) / \sigma_p\}]^{-1} & \text{if } \text{mat}_{\min} \leq a \leq x-2 \\ 1 & \text{if } a \geq x-1 \end{cases} \tag{12}$$

where p_{50} is the age at 50% maturity plus one year, and σ_p is the parameter which determines the width of the maturation ogive.

Initial conditions

The population is assumed either to be at pre-exploitation equilibrium or to have a stable age-structure at the start of the projection period (year t_{INIT}). For the former case, a value for $K_{t_{INIT}}^E$, the pre-exploitation equilibrium size of the 'recruited' component of the population at the start of year t_{INIT} , is used to calculate the numbers at each age⁸:

$$U_{t_{INIT},a}^s = K_{t_{INIT}}^E \tilde{U}_a^s(0) / \sum_{s'} \sum_{a'=0}^x \tilde{N}_{a'}^{s'}(0)$$

$$N_{t_{INIT},a}^s = K_{t_{INIT}}^E \tilde{N}_a^s(0) / \sum_{s'} \sum_{a'=0}^x \tilde{N}_{a'}^{s'}(0) \tag{13}$$

For the case in which the population is assumed to have a stable age structure (corresponding to uniform harvesting on the 0+ population⁹) at the start of year t_{INIT} , the numbers at each age are given by:

$$U_{t_{INIT},a}^s = N_{t_{INIT}}^E \tilde{U}_a^s(F_{INIT}) / \sum_{s'} \sum_{a'=0}^x \tilde{N}_{a'}^{s'}(F_{INIT})$$

$$N_{t_{INIT},a}^s = N_{t_{INIT}}^E \tilde{N}_a^s(F_{INIT}) / \sum_{s'} \sum_{a'=0}^x \tilde{N}_{a'}^{s'}(F_{INIT}) \tag{14}$$

where $N_{t_{INIT}}^E$ is the size of the 'recruited' component of the population at the start of year t_{INIT} .

The value of F_{INIT} is selected numerically so that:

$$N_{t_{INIT}}^E = 0.5 N_0(F_{INIT}) \sum_{s'} \sum_{a=0}^x \tilde{N}_a^s(F_{INIT})^{10} \tag{15}$$

where $N_0(F_{INIT})$ is the number of calves (of both sexes) at the start of the year when $F = F_{INIT}$ (Appendix 2 for a derivation):

$$N_0(F_{INIT}) = \left(1 - \frac{1}{A} \left[\frac{f(F_{INIT})}{f_{eq}} - 1 \right] \right)^{1/z} \frac{K_{t_{INIT}}^D}{\tilde{P}^D(F_{INIT})} \tag{16}$$

$\tilde{P}^D(F)$ is the size of the component of the population to which density dependence is functionally related as a function of F (either the total (1+) population size, the 'recruited'

⁸ Equation (13) is based on $K_{t_{INIT}}^E$, rather than, say, the pre-exploitation equilibrium size of the total population because $K_{t_{INIT}}^E$ is the parameter which for which a value is specified/estimated in the Hitter-Fitter package.

⁹ The stable age-structure applies to the 0+ component of the population because F_{INIT} should be considered to be an increase rate rather than an exploitation rate.

¹⁰ The 0.5 is needed to correct for the equations in Appendix 1 being defined in terms of one animal of each sex at birth.

population size, or the number of females that have reached the age at first parturition), expressed as a fraction of the number of calves (of both sexes).

The value for K_{imm}^D needed to apply Equation (16) is computed straightforwardly from K_{imm}^E . This calculation does not involve the values for the parameters that determine the extent of density dependence (A and z).

Determination of the resilience and degree of compensation parameters

The values of the parameters A and z are obtained by assigning values to the quantities $MSYL$ and $MSYR$, and then solving the set of equations relating these quantities to z and A . $MSYL$ and $MSYR$ may be chosen to refer either to the 'recruited' component of the population, that component which has reached the age at first parturition (the 'mature' component), or the 1+ population with uniform selectivity harvesting. Sex-structure is ignored when calculating the resilience and degree of compensation from $MSYR$ and $MSYL$. The recruitment ogive and the age-specific natural mortality rates for females are thus assumed to apply to both sexes for the purposes of this calculation. In reality, male and female recruitment ogives will not always be identical which will lead to some error in evaluating A and z (and hence MSY).

The (normalised) sustainable yield as a function of the exploitation rate, $C(F)$, is given by:

$$C(F) = F P(F) = F B(F) \tilde{P}(F) \quad (17)$$

where $P(F)$ is the equilibrium number of 'recruited' animals when the exploitation rate is fixed at F (either the number of animals defined by the female recruitment ogive, the number which have reached the age at first parturition, or the number of age 1+ animals),

$B(F)$ is the normalised number of births when the exploitation rate is fixed at F , and

$\tilde{P}(F)$ is the number of 'recruited' animals per birth when the exploitation rate is fixed at F .

The normalisation is provided by dividing by the number of births at pre-exploitation equilibrium.

For MSY :

$$\frac{dC}{dF} \Big|_{F=F_{MSY}} = \frac{d\{F B(F) \tilde{P}(F)\}}{dF} \Big|_{F=F_{MSY}} = 0 \quad (18)$$

$$\text{i.e.: } P(F_{MSY}) + F_{MSY} \left\{ \begin{array}{l} B(F_{MSY}) \frac{d\tilde{P}(F)}{dF} \Big|_{F=F_{MSY}} \\ + \tilde{P}(F_{MSY}) \frac{dB(F)}{dF} \Big|_{F=F_{MSY}} \end{array} \right\} = 0 \quad (19)$$

The values for the resilience and degree of compensation parameters are obtained by solving Equation (19) given a value for $MSYR$ ($= F_{MSY}$ - see Equation (17)) subject to the constraint that $MSYL$ is equal to a pre-specified value.

Now, the population component (H) chosen for defining $MSYL$ will not necessarily be the same as that to which density dependence is functionally related (D). For the calculations that follow, the value of $MSYL^D = P^D(F_{MSY})/K^D$ is required. This is obtained from the formula (Punt and Butterworth, 1991):

$$MSYL^D = [MSYL^H \tilde{K}^H \tilde{P}^D(F_{MSY})] / [\tilde{P}^H(F_{MSY}) \tilde{K}^D] \quad (20)$$

where \tilde{K} is defined as $\tilde{P}(0)$ for the relevant component of the population.

The left-hand side of Equation (19) can be simplified to a form that does not involve the parameter (see Appendix 3):

$$1 + F_{MSY} \left(\frac{1}{\tilde{P}(F_{MSY})} \frac{d\tilde{P}(F)}{dF} \Big|_{F=F_{MSY}} - \frac{1}{\tilde{P}^D(F_{MSY})} \frac{d\tilde{P}^D(F)}{dF} \Big|_{F=F_{MSY}} \right) - \frac{1}{z} \frac{(MSYL^D)^{-z} - 1}{f(F_{MSY}) - f_{eq}} \frac{df(F)}{dF} \Big|_{F=F_{MSY}} \quad (21)$$

where the required derivatives are determined by taking finite differences. The value of z is determined by solving Equation (21).

To calculate $MSYR$ ($= F_{MSY}$) and $MSYL$ for alternative harvesting patterns (e.g. uniform selectivity harvesting of the 1+ component of the population) than that used when calculating A and z , Equation (21) is solved for F_{MSY} where the alternative harvesting pattern is used to calculate the vectors \tilde{U}^f and \tilde{N}^f and hence the functions $\tilde{P}(F)$, $\tilde{P}^D(F)$ and $f(P)$. The value of $MSYL$ is then calculated using an appropriate modification of Equation (20).

OUTPUT STATISTICS

Population components

BALEEN II stores time-trajectories of the following population components:

- Total (1+) population size, P_t^{1+} .
- Total (0+) population size, P_t^0 .
- Total 'mature' population size, $P_t^{M,f} + P_t^{M,m}$.
- 'Mature' female population size, $P_t^{M,f}$.
- Total 'recruited' population size, $P_t^{E,f} + P_t^{E,m}$.
- 'Recruited' male population size, $P_t^{E,m}$.
- 'Recruited' female population size, $P_t^{E,f}$.
- Calves, $P_t^{M,f} f_t$.

These model outputs can be used to calculate a variety of output statistics, e.g., the depletion in any year, trends in population size over various years, the maximum (realised) pregnancy rate over the projection period, and the fraction of the total (0+) population size in a given year consisting of, for example, calves.

Replacement yield

The replacement yield for year t is defined as the catch, at the start of year t , which will leave the size of the 'recruited' component of the population the same at the start of year $t+1$ as at the start of year t :

$$RY_t = \frac{P_t^E}{\sum_s \sum_{a=0}^s S_a^s N_{t,a}^s} \left[\sum_s \left(N_{t,0}^s + \sum_{a=0}^{s-2} S_a^s U_{t,a}^s \delta_{a+1}^s \right) + \sum_s \sum_{a=0}^s S_a^s N_{t,a}^s - P_t^E \right] \quad (22)$$

The term in square parenthesis is almost¹¹ the difference between the size of the 'recruited' component at the start of year t and the size of this component at the end of year t in

¹¹ Almost, because the $N_{t,0}^s$ term should be replaced by $N_{t+1,0}^s$ - this is not needed here because the computation of RY assumes that population is in steady state and that the harvest will be equal to the replacement yield so that $N_{t+1,0}^s = N_{t,0}^s$. Note that for most applications, calves are not recruited so this complication does not arise.

the absence of harvesting (i.e. accounts for the impact of recruitment and natural mortality). The first term accounts for the fact that the catch is assumed to occur in a pulse at the start of the year, and is equal to $1/S$ if survival is assumed to be independent of age for all 'recruited' animals.

Productivity

The productivity of the resource can be assessed through $MSYR$ and $MSYL$ (defined in terms of harvesting of the 'recruited', total (1+) or 'mature' components of the population). The maximum sustainable yield, MSY , can be calculated as $MSYR.MSYL.K$ where K is the pre-exploitation size of that component of the population in terms of which $MSYR$ and $MSYL$ are defined. Other measures of productivity are the maximum theoretical pregnancy rate, f_{max} , and the maximum steady rate of increase, λ_{max} . The latter is the positive real root of the equation:

$$1 = f_{max} \left[\sum_{a=mat_{min}}^{x-1} \frac{\beta_a}{\lambda_{max}^{a+1}} \prod_{a'=0}^{a-1} S_{a'}^f + \frac{\beta_x \prod_{a'=0}^{x-1} S_{a'}^f}{\lambda_{max}^x (\lambda_{max} - S_x^f)} \right] \quad (23)$$

Equations (1) and (2) of Breiwick *et al.* (1984) can be shown to be special cases of Equation (23).

ALTERNATIVE PARAMETERISATIONS

The most common method for parameterising the BALEEN II model involves providing specifications for the following.

- (a) The historical catches.
- (b) Natural mortality for each combination of sex and age.
- (c) The parameters of the recruitment ogive.
- (d) The parameters of the maturity ogive.
- (e) The pre-exploitation equilibrium size of the 'recruited' component of the population at the start of year, t_{INIT} , $K_{t_{INIT}}^E$.
- (f) The size of the 'recruited' component of the population at the start of year, t_{INIT} , $N_{t_{INIT}}^E$, if it is assumed that the population was not at its pre-exploitation equilibrium size at the start of year t_{INIT} .
- (g) $MSYR$, $MSYL$ and the components to which these quantities apply.
- (h) The component to which density dependence is functionally related.

However, alternative parameterisations are possible. The following three sections outline three alternatives that may be appropriate for an assessment of the B-C-B bowhead stock.

'Forwards' vs. 'Backwards'

The 'backwards' parameterisation of the BALEEN II model is based on the 'Hitting-with-fixed-MSYR' option of the Hitter-Fitter package. It involves specifying the size of some component of the population in some given year, N_{targ} , and selecting the value of $N_{t_{INIT}}^E$ (or $K_{t_{INIT}}^E$ if it is assumed that the population was at its pre-exploitation equilibrium level at the start of year t_{INIT}) so that if the population is projected from year t_{INIT} to the current year, the projected size of that component of the population in the specified year is equal to N_{targ} . Brent's method (Press *et al.*, 1988) is used to solve the non-linear equation relating N_{targ} to $N_{t_{INIT}}^E$. Note that for some

choices of N_{targ} (e.g. $N_{targ} \gg K$) there is no solution to this non-linear equation while for some choices for $MSYR$, there may be multiple solutions (Butterworth and Punt, 1995).

Using the maximum theoretical pregnancy rate

Equation (5) shows that the maximum theoretical pregnancy rate, f_{max} , is closely related to the resilience parameter A . Therefore, instead of specifying a value for $MSYR$ it is possible to specify a value for f_{max} instead. Within BALEEN II, this involves solving the non-linear equation $f_{max} = f_{max}(MSYR, MSYL)$, i.e. $MSYR$ is chosen so that the implied value for f_{max} is equal to the specified value.

Another possible use for introducing the parameter f_{max} is to eliminate the juvenile natural mortality rate, M_J . M_J may apply solely to calves (e.g. Wade, 1996). However, for the B-C-B bowhead case, M_J has been assumed to apply from age 0 to a transition age (Givens *et al.*, 1995; IWC, 1995). Given values for $MSYR$, $MSYL$ and f_{max} , it is possible, using the following algorithm, to solve for A , z and M_J .

- (a) Guess a value for M_J .
- (b) Calculate $\tilde{U}(0)$, $\tilde{N}(0)$, $\tilde{U}(F_{MSY})$ and $\tilde{N}(F_{MSY})$.
- (c) Calculate f_{eq} using Equation (4).
- (d) Calculate A and z from $MSYL$ and $MSYR$ as described above.
- (e) Calculate f_{max} using Equation (5).
- (f) Compare this value of f_{max} with the input value and repeat steps (a) - (f) until convergence is achieved.

When solving for M_J , it is common to impose biologically sensible bounds such as that M_J is greater than the natural mortality rate for adults. Punt and Butterworth (1997) note that it is possible to use this approach to eliminate any of the other 'biological' parameters (age-at-maturity, adult natural mortality rate, etc.), but it seems most sensible to eliminate M_J because direct information about this parameter is seldom (if ever) available.

Using the maximum increase rate

The parameter λ_{max} can be used to replace $MSYR$ ¹². For the case in which f_{max} is also used to specify M_J , the calculation procedure is as follows:

- (a) Solve Equation (23) for M_J given f_{max} , λ_{max} and the remaining biological parameters.
- (b) Calculate $\tilde{U}(0)$ and $\tilde{N}(0)$, and hence f_{eq} (see Equation (4)).
- (c) Guess a value for F_{MSY} .
- (d) Calculate $\tilde{U}(F_{MSY})$ and $\tilde{N}(F_{MSY})$.
- (e) Calculate A and z from $MSYL$ and $MSYR (=F_{MSY})$ as described above.
- (f) Calculate f_{max} using Equation (5).
- (g) Compare this value of f_{max} with the input value and repeat steps (c) - (g) until convergence is achieved.

IMPLICATIONS FOR DEFINING MSYR AND MSYL IN TERMS OF OTHER POPULATION COMPONENTS

There has been considerable debate in the Scientific Committee regarding the appropriate component to which the assumption $MSYL = 0.6$ should be assumed to apply (e.g. Butterworth and Punt, 1992b; Cooke and de la Mare, 1994; IWC, 1994; 1998). To examine this issue further, yield curves have been produced for representative choices for the biological parameters for the East Greenland-Iceland fin

¹² In principle, λ_{max} can replace f_{max} but this option is ignored here.

whales and the B-C-B bowhead whales (see Table 1)¹³. Fig. 1(a) show plots of sustainable yield against 'mature' female and total (1+) depletion for the B-C-B bowhead stock when harvesting is assumed to be uniform on the 'mature' component of the population, $MSYL_{mat}=0.6$ and $MSYR_{mat}=3/5/7\%$. Fig. 1(b) shows the same quantities except that harvesting is assumed to be uniform on the 1+ component of the population (the values for the parameters A and z for Fig. 1(b) are computed using the specifications for Fig. 1(a)). Fig. 2 shows the same quantities as Fig. 1 except that A and z are computed for the case $MSYL_{1+}=0.6$. Fig. 3 shows the same quantities as Fig. 1, except that the results pertain to the East Greenland-Iceland fin whales.

The most notable feature of Fig. 1(a) is that, for some choices for $MSYR$, if $MSYL$ is defined in terms of the 'mature' component of the population, the size of the 1+ component at $MSYL$ can be above K . This occurs because the stock-recruitment relationship exhibits strong super-compensation (i.e. the number of births drops as the population approaches carrying capacity - Holt, 1985; Butterworth and Best, 1990; Fig. 4) and so that the age-structure of the population at MSY is markedly skewed towards animals younger than the age at first parturition. The same qualitative result (quantitatively less marked) occurs if harvesting occurs on 1+ component of the population (Fig. 1b) or if the biological parameters for the East Greenland-Iceland fin whales are assumed instead (Fig. 3). The difference between the depletion of the 'mature' and 1+ components at $MSYL$ is also reduced if density dependence

¹³ For simplicity, density dependence is assumed to act on the mature female component of the population in all of the calculations of this section.

is assumed to be functionally related to the 1+ rather than the 'mature' component of the population. As expected, defining $MSYL$ in terms of the 1+ component of the population leads to $MSYL$ for the 'mature' component of the population occurring at sizes well below 0.6 (Fig. 2). The

Table 1

Values for the biological and technological parameters for the East Greenland-Iceland stock of fin whales and the Bering-Chukchi-Beaufort Seas stock of bowhead whales used as inputs for the BALEEN II computations for Figures 1-4.

Parameter	East Greenland-Iceland fin whales ¹	Bering-Chukchi-Beaufort Seas bowhead whales ²
Natural mortality (yr ⁻¹)	0.04 for all ages	0.04 ($a=0, \dots, 4$); 0.02 ($a=5+$)
Age at 50% recruitment (males) (yr)	5	1
Age at 95% recruitment (males) (yr)	7	1
Age at 50% recruitment (females) (yr)	4	1
Age at 95% recruitment (females) (yr)	5	1
Age at 50% maturity ³ (yr)	8.5	20
Age at 95% maturity ³ (yr)	9.5	20

¹ Source: Butterworth and Punt (1992a).

² The adult natural mortality rate and the ages defining the parturition ('maturity') ogive are chosen to lie close to the medians of priors selected by IWC (1995).

³ The corresponding age at first parturition is taken to be one year older than this.

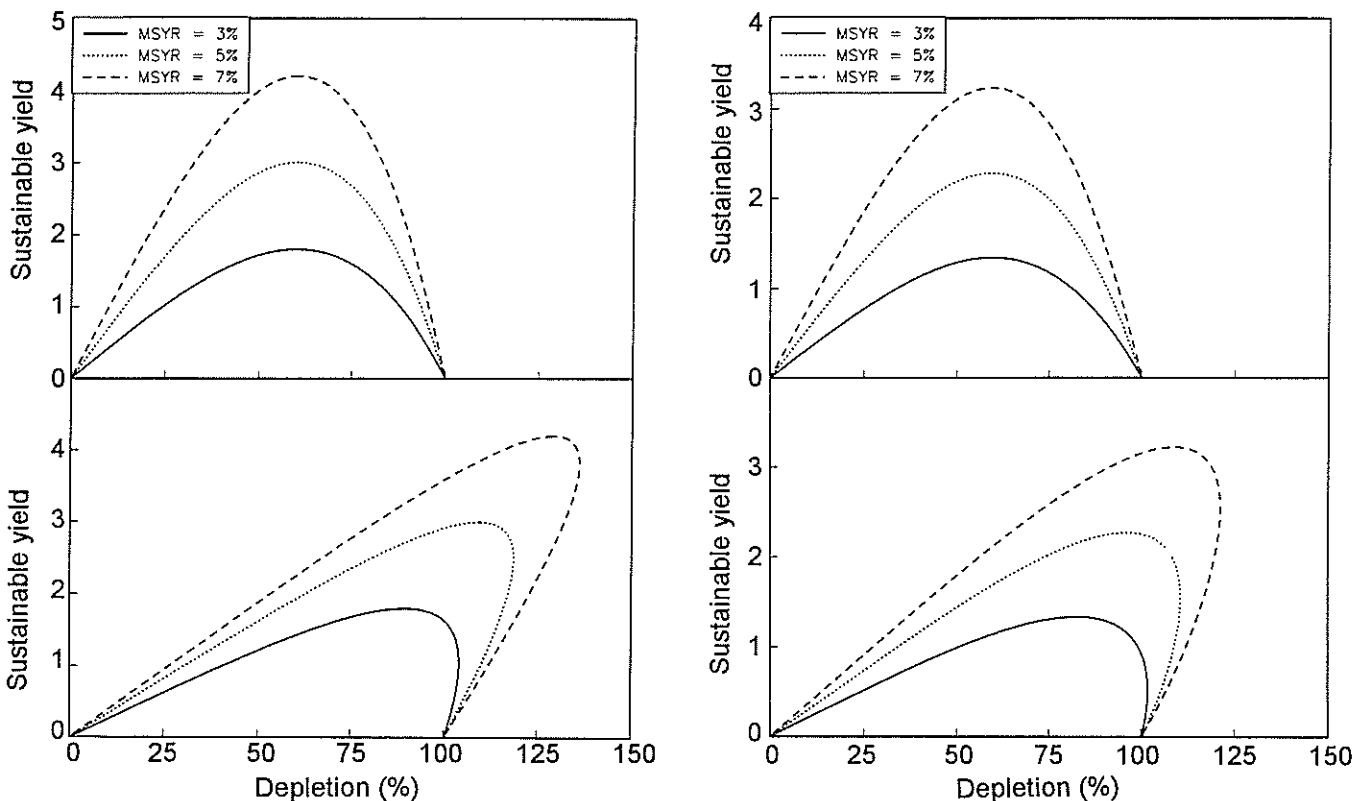


Fig. 1. Yield curves for the Bering-Chukchi-Beaufort Seas stock of bowhead whales. Each plot shows results for $MSYR_{mat} = 3\%, 5\%$, and 7% . The upper panels show yield expressed as a function of the depletion of the 'mature' female component of the population, while the lower panels show yield expressed as a function of the depletion of the 1+ component of the population. Results are shown in (a) for harvesting of the 'mature' component of the population and in (b) for harvesting of the 1+ component of the population. The results in this figure pertain to $MSYL_{mat}=0.6$ and density dependence acting on the 'mature' female component of the population.

results in Figs 1-3 therefore show that the relationship between $MSYL_{1+}$ and $MSYL_{mat}$ does not depend strongly on the exploitation pattern assumed when calculating MSY .

The implications of Figs 1-3 need to be taken into consideration when output statistics are defined for

assessments (e.g. if $MSYL$ for the B-C-B bowhead stock is defined to be 0.6 in terms of the total (1+) component of the population, the 'target level' for the 'mature' component of the population may be 0.4 or less) and performance statistics for simulation trials.

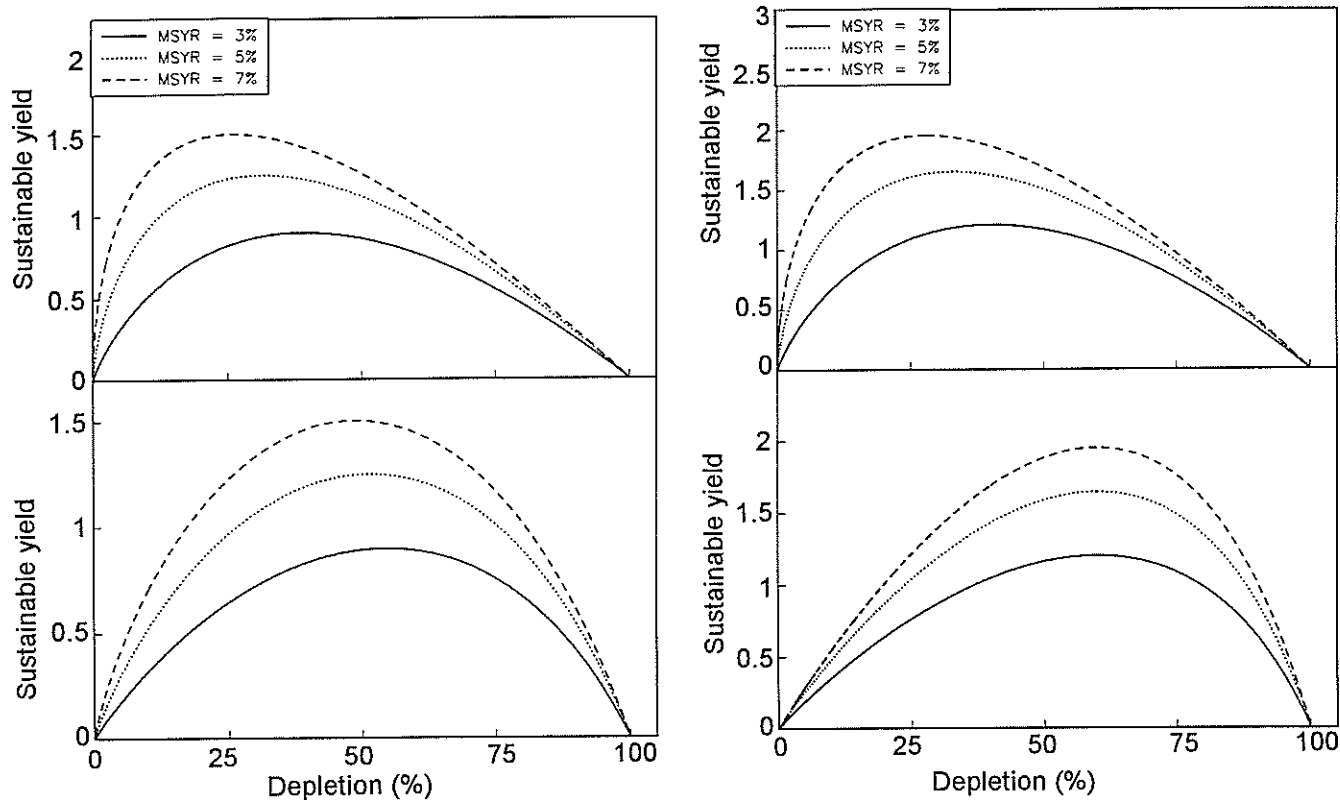


Fig. 2. As for Fig. 1 except that $MSYL_{1+} = 0.6$.

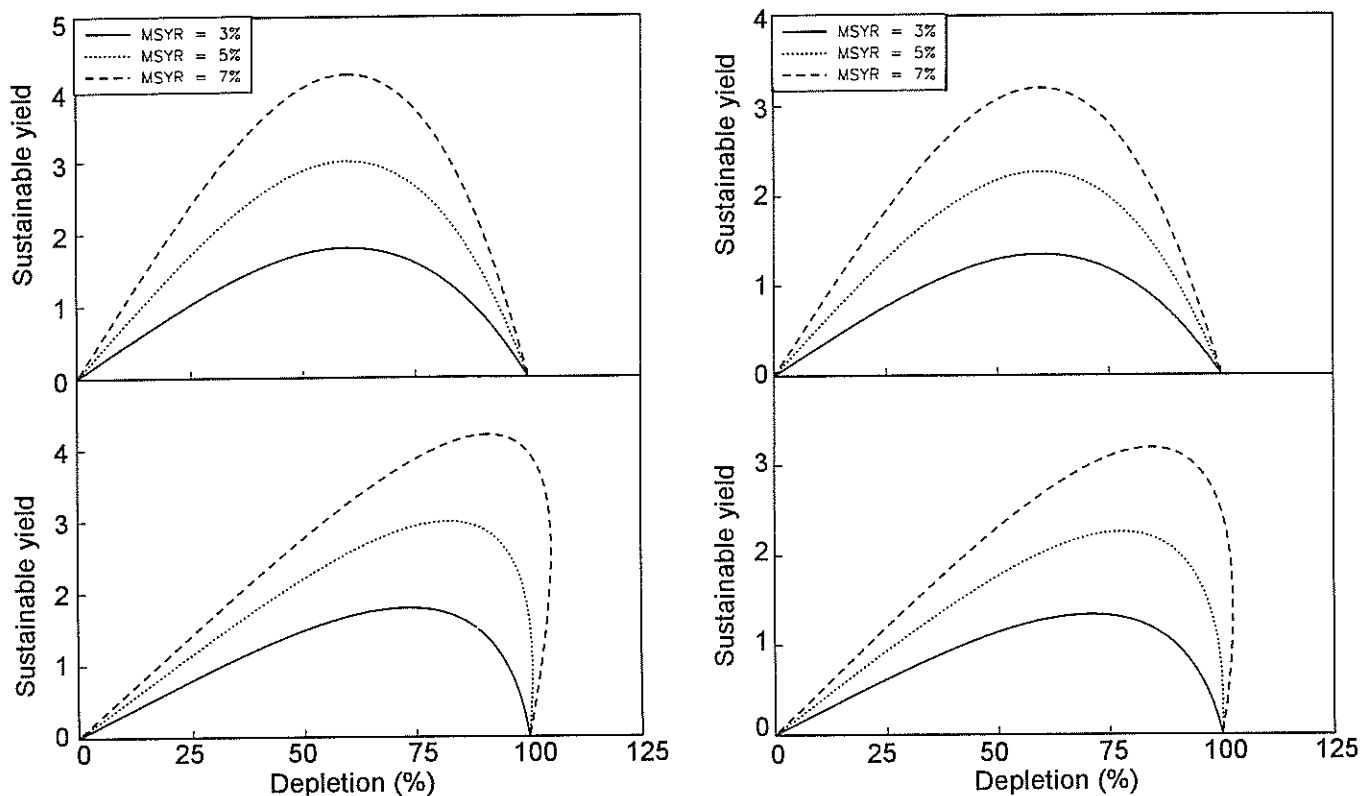


Fig. 3. As for Fig. 1 except that results are shown for the East Greenland-Iceland fin whale stock.

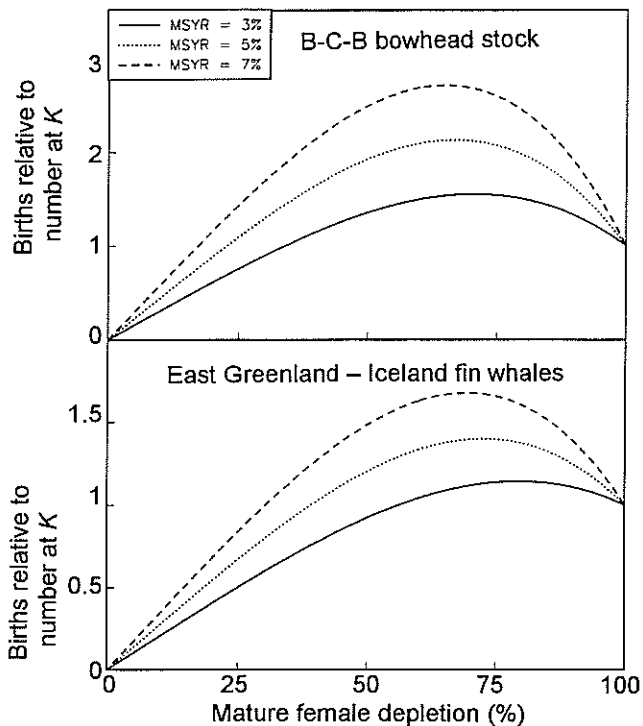


Fig. 4. Stock recruitment relationships for the Bering-Chukchi-Beaufort Seas stock of bowhead whales and the East Greenland-Iceland fin whale stock. Results in this figure pertain to $MSY_{mat} = 0.6$ and density dependence acts on the 'mature' female component of the population. The number of births is shown relative to the number when the resource is at its pre-exploitation equilibrium level.

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Appendix 1

EQUILIBRIUM AGE-STRUCTURES

(A) Harvesting of the 'recruited' component of the population

$$\tilde{U}_a^s(F) = \begin{cases} 1 - \alpha_0^s & \text{if } a = 0 \\ S_{a-1}^s \tilde{U}_{a-1}^s(F)(1 - \delta_a^s) & \text{otherwise} \end{cases} \quad (A1.1a)$$

$$\tilde{N}_a^s(F) = \begin{cases} \alpha_0^s & \text{if } a = 0 \\ S_0^s (\alpha_0^s + (1 - \alpha_0^s) \delta_1^s) & \text{if } a = 1 \\ S_{a-1}^s (1 - F) (\tilde{N}_{a-1}^s(F) + \tilde{U}_{a-1}^s(F) \delta_a^s) & \text{if } 2 \leq a < x \\ S_{x-1}^s (1 - F) \tilde{N}_{x-1}^s(F) / (1 - S_x^s (1 - F)) & \text{if } a = x \end{cases} \quad (A1.2b)$$

$$\tilde{N}_a^s(F) = \begin{cases} \alpha_0^s & \text{if } a = 0 \\ S_{a-1}^s (\tilde{N}_{a-1}^s(F)(1 - F) + \tilde{U}_{a-1}^s(F) \delta_a^s) & \text{if } 1 \leq a < x \\ S_{x-1}^s \tilde{N}_{x-1}^s(F)(1 - F) / (1 - S_x^s (1 - F)) & \text{if } a = x \end{cases} \quad (A1.1b)$$

(C) Harvesting of the 'mature' component of the population

$$\tilde{U}_a^s(F) = \begin{cases} 1 - \alpha_0^s & \text{if } a = 0 \\ S_{a-1}^s (1 - F \beta_{a-1}) \tilde{U}_{a-1}^s(F)(1 - \delta_a^s) & \text{otherwise} \end{cases} \quad (A1.3a)$$

(B) Harvesting of the 1+ component of the population

$$\tilde{U}_a^s(F) = \begin{cases} 1 - \alpha_0^s & \text{if } a = 0 \\ S_0^s (1 - \alpha_0^s)(1 - \delta_1^s) & \text{if } a = 1 \\ S_{a-1}^s (1 - F) \tilde{U}_{a-1}^s(F)(1 - \delta_a^s) & \text{otherwise} \end{cases} \quad (A1.2a)$$

$$\tilde{N}_a^s(F) = \begin{cases} \alpha_0^s & \text{if } a = 0 \\ S_{a-1}^s (1 - F \beta_{a-1}) (\tilde{N}_{a-1}^s(F) + \tilde{U}_{a-1}^s(F) \delta_a^s) & \text{if } 1 \leq a < x \\ S_{x-1}^s (1 - F \beta_{a-1}) \tilde{N}_{x-1}^s(F) / (1 - S_x^s (1 - F)) & \text{if } a = x \end{cases} \quad (A1.3b)$$

Appendix 2

THE DERIVATION OF EQUATION (16)

The equation defining fecundity as a function of density is given by:

$$f(F) = f_{eq} [1 + A \{1 - (P^D(F) / K^D)^2\}] \quad (A2.1)$$

Substituting $N_0(F) \tilde{P}^D(F)$ for $P^D(F)$ gives:

$$f(F) = f_{eq} [1 + A \{1 - (N_0(F) \tilde{P}^D(F) / K^D)^2\}] \quad (A2.2)$$

Solving Equation (A2.2) for leads to Equation (16)

Appendix 3

THE DERIVATION OF EQUATION (21)

The equation defining *MSY* is:

$$P(F_{MSY}) + F_{MSY} \left\{ B(F_{MSY}) \frac{d\tilde{P}(F)}{dF} \Big|_{F=F_{MSY}} + \tilde{P}(F_{MSY}) \frac{dB(F)}{dF} \Big|_{F=F_{MSY}} \right\} = 0 \quad (A3.1)$$

Dividing Equation (A3.1) by gives:

$$1 + F_{MSY} \left\{ \frac{1}{\tilde{P}(F_{MSY})} \frac{d\tilde{P}(F)}{dF} \Big|_{F=F_{MSY}} + \frac{1}{B(F_{MSY})} \frac{dB(F)}{dF} \Big|_{F=F_{MSY}} \right\} = 0 \quad (A3.2)$$

Now, differentiating $P^D(F) = B(F)\tilde{P}^D(F)$ with respect to F gives:

$$\frac{dP^D(F)}{dF} = B(F)\frac{d\tilde{P}^D(F)}{dF} + \tilde{P}^D(F)\frac{dB(F)}{dF}$$

Therefore:

$$\frac{dB(F)}{dF} = \frac{1}{\tilde{P}^D(F)} \frac{dP^D(F)}{dF} - \frac{B(F)}{\tilde{P}^D(F)} \frac{d\tilde{P}^D(F)}{dF} \quad (\text{A3.3})$$

Now, $f(F) = f_{eq}[1 + A\{1 - (P^D(F)/K^D)^z\}]$

$$\text{i.e. } \frac{df(F)}{dF} = \frac{-f_{eq}Az}{K^D} [P^D(F)/K^D]^{z-1} \frac{dP^D(F)}{dF} \quad (\text{A3.4})$$

Solving Equation (A3.4) for $\frac{dP^D(F)}{dF}$ then gives:

$$\frac{dP^D(F)}{dF} = \frac{-K^D}{f_{eq}Az} [P^D(F)/K^D]^{1-z} \frac{df(F)}{dF} \quad (\text{A3.5})$$

Substituting Equation (A3.5) into equation (A3.3) then gives:

$$\frac{dB(F)}{dF} = -\frac{B(F)}{\tilde{P}^D(F)} \frac{d\tilde{P}^D(F)}{dF} - \frac{1}{\tilde{P}^D(F)} \frac{K^D}{f_{eq}Az} [P^D(F)/K^D]^{1-z} \frac{df(F)}{dF} \quad (\text{A3.6})$$

Now, $MSYL^D = P^D(F_{MSY})/K^D = B(F_{MSY})\tilde{P}^D(F_{MSY})/K^D$ (A3.7a)

$$\text{or } K^D = B(F_{MSY})\tilde{P}^D(F_{MSY})/MSYL^D \quad (\text{A3.7b})$$

Evaluating Equation (A3.6) at $F = F_{MSY}$, substituting Equation (A3.7) into the resulting equation, dividing by $B(F_{MSY})$, and then simplifying gives:

$$\frac{1}{B(F_{MSY})} \frac{dB(F)}{dF} \Big|_{F=F_{MSY}} = -\frac{1}{\tilde{P}^D(F_{MSY})} \frac{d\tilde{P}^D(F)}{dF} \Big|_{F=F_{MSY}} - \frac{(MSYL^D)^{-z}}{f_{eq}Az} \frac{df(F)}{dF} \Big|_{F=F_{MSY}} \quad (\text{A3.8})$$

Now, from Equation (3), A is related to z and $MSYR^D$ according to the formula:

$$A = \frac{f(F_{MSY})/f_{eq} - 1}{1 - (MSYL^D)^z} \quad (\text{A3.9})$$

Thus, substituting Equation (A3.9) into Equation (A3.8) and simplifying gives:

$$\frac{1}{B(F_{MSY})} \frac{dB(F)}{dF} \Big|_{F=F_{MSY}} = -\frac{1}{\tilde{P}^D(F_{MSY})} \frac{d\tilde{P}^D(F)}{dF} \Big|_{F=F_{MSY}} - \frac{1}{z} \frac{(MSYL^D)^{-z} - 1}{f(F_{MSY}) - f_{eq}} \frac{df(F)}{dF} \Big|_{F=F_{MSY}} \quad (\text{A3.10})$$

Substituting Equation (A3.10) into Equation (A3.2) gives Equation (21) of the main text.