

# An age-structured model with leading management parameters, incorporating age-specific selectivity and maturity

Robyn E. Forrest, Steven J.D. Martell, Michael C. Melnychuk, and Carl J. Walters

**Abstract:** Previous authors have shown analytically that the optimal equilibrium harvest rate ( $U_{MSY}$ ) for an iteroparous fish stock is a function of the slope of the stock–recruitment curve at low stock size ( $\alpha$ ) and that  $U_{MSY}$  can therefore be considered a direct measure of stock productivity. As such, it can be used as a leading parameter in stock assessment models and directly estimated using Bayesian or similar techniques. Here we present an alternative method for deriving  $\alpha$  from  $U_{MSY}$  that incorporates age-specific selectivity and fecundity, avoiding assumptions of knife-edged recruitment and maturity. We present an age-structured model with two fisheries reference points ( $U_{MSY}$  and maximum sustainable yield, MSY) as its leading parameters. We show equilibrium properties of the model, chiefly in terms of its ability to show relationships between life history traits, density dependence, and  $U_{MSY}$ . We also demonstrate a simple Bayesian estimation routine to illustrate estimation of  $U_{MSY}$  and MSY directly from data. We compare our results to those from a structurally identical model with leading biological parameters. Using models with leading management parameters can improve communicability of results to managers.

**Résumé :** Des auteurs ont montré précédemment par analyse que le taux optimal de récolte à l'équilibre ( $U_{MSY}$ ) dans un stock de poissons itéropares est fonction de la pente de la courbe de stock–recrutement lorsque la densité du stock ( $\alpha$ ) est faible; dans ce cas,  $U_{MSY}$  peut être considéré comme une mesure directe de la productivité du stock. Cette valeur peut alors être utilisée comme variable principale dans les modèles d'évaluation des stocks et peut être estimée directement par des techniques bayésiennes ou des techniques semblables. Nous présentons ici une méthode de rechange pour dériver  $\alpha$  de  $U_{MSY}$  qui utilise la sélectivité en fonction de l'âge et la fécondité, évitant ainsi de faire les présuppositions associées au recrutement en lame de couteau et à la maturité. Nous présentons un modèle structuré en fonction de l'âge avec deux points de référence halieutiques ( $U_{MSY}$  et le rendement soutenable maximal, MSY) comme variables principales. Nous démontrons les propriétés d'équilibre du modèle, particulièrement en ce qui a trait à sa capacité de montrer les relations entre les caractéristiques démographiques, la densité-dépendance et  $U_{MSY}$ . Nous faisons la démonstration d'une procédure bayésienne simple d'estimation pour évaluer  $U_{MSY}$  et MSY directement à partir des données. Nous comparons nos résultats à un modèle de structure identique qui est basé sur les variables biologiques principales. L'utilisation de modèles basés sur les variables principales de la gestion peut permettre de mieux communiquer les résultats aux gestionnaires.

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## Introduction

Maximum sustainable yield (MSY) has formed the basis of fisheries management strategies since at least the 1950s (e.g., Schaefer 1954). Despite well-documented problems with implementation of MSY policies (Larkin 1977; Punt and Smith 2001), the recent shift towards setting the fishing mortality rate that achieves MSY ( $F_{MSY}$ , or its dimensionless, discrete equivalent  $U_{MSY}$ ) as a limit reference point rather than a target reference point has resulted in renewed interest in MSY as a means of determining precautionary harvest rates in both single species and ecosystem-based management contexts (Mace 2001).

Fisheries stock assessment involves estimating key parameters (leading parameters) by fitting a model to fishery-dependent or -independent data. The leading parameters of a model are those that are of greatest interest in terms of establishing reference points, even though other “nuisance” parameters (e.g., catchability, growth, and selectivity parameters) may be required for a fully specified model (Walters et al. 2006). At the very least, population models require leading parameters that determine the scale and productivity of the population, with the leading parameter describing productivity the main determinant of the behaviour of a fish stock under harvesting and, therefore, its maximum sustainable harvest rate,  $U_{MSY}$ . There are a number of ways that

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productivity can be represented in population models, the simplest being the logistic model's intrinsic rate of growth,  $r$  (e.g., Schaefer 1954). Alternatively, some models use the slope of a stock–recruitment function near the origin,  $\alpha$  (e.g., Ricker 1954; Beverton and Holt 1957). Goodyear (1977) expressed productivity in terms of the recruitment compensation ratio (CR), which is the relative improvement in juvenile survival as spawning stock abundance is reduced towards zero. In common use is a reparameterised version of the Beverton–Holt recruitment function, which uses the steepness parameter,  $h$ , defined as the proportion of recruits that are produced when egg production (i.e., spawner abundance) is at 20% of unfished egg production (Mace and Doonan 1988; Hilborn and Walters 1992). Myers et al. (1999) expressed  $h$  (called  $z$  in their paper) as a function of lifetime spawners per spawner at low abundance,  $\hat{\alpha}$ . Their meta-analysis, based on stock–recruitment data for more than 700 fish stocks, suggested that the magnitude of compensation in recruitment is a relatively conservative property of fish stocks, with the maximum lifetime production of spawners per spawner rarely exceeding 50. Mathematically,  $\hat{\alpha}$  is the equivalent of CR under certain assumptions about fecundity (see section below). Goodwin et al. (2006) reported CR for 54 Atlantic fish stocks, again reporting CR < 50 for the majority of stocks. The finding that CR tends to be confined within certain bounds across multiple species and life histories makes CR a useful productivity parameter for modellers, especially given its analytical relationship to the more familiar  $h$ .

Biological productivity parameters are usually of secondary interest to managers, who tend to be more concerned with measures such as total allowable catch or maximum sustainable harvest rate. Management parameters must therefore be derived from models, using either analytical or numerical relationships. Simple surplus production models (e.g., Schaefer 1954), which do not explicitly incorporate recruitment, provide a direct analytical relationship between  $r$  and  $U_{MSY}$  ( $U_{MSY} = r/2$ ). For semelparous species,  $U_{MSY}$  can be expressed as a function of  $\alpha$ , using Ricker (1954) or Beverton and Holt (1957) recruitment functions (Hilborn and Walters 1992). Schnute and Kronlund (1996) derived analytical relationships between biological and management parameters using a generalised recruitment function for semelparous species. The resulting stock–recruitment function was parameterised in terms of two leading management parameters,  $U_{MSY}$  and MSY, which could be estimated directly using established stock assessment fitting procedures. Schnute and Richards (1998) extended the approach and developed a generalised age-structured model that could be used for iteroparous species that incorporated a reparameterised stock–recruitment function in terms of  $U_{MSY}$  and MSY. It assumed knife-edged selectivity and maturity and that natural and fishing mortality occurred separately. Despite these limiting assumptions, their approach enabled direct estimation of  $U_{MSY}$  from data for a much broader range of species than had been previously possible.

We extend the approach of Schnute and Richards (1998) by presenting an alternative formulation of the derivation of  $\alpha$  from  $U_{MSY}$  that incorporates age-specific selectivity and maturity. We use an age-structured population model that

utilises Botsford “incidence” functions (Botsford 1981; see Walters and Martell 2004) to calculate equilibrium eggs per recruit and vulnerable biomass per recruit, which simultaneously capture the effects of fishing and natural mortality on fish as they age. Our method avoids the assumption of knife-edged selectivity and maturity and is flexible to a wide range of selectivity and maturity schedules. These developments broaden the range of fisheries for which  $U_{MSY}$  can be estimated directly.

### Links between life history and productivity

There is currently much interest in the link between life history traits and productivity, especially for species that are data-limited (Reynolds et al. 2001). Although certain life history traits (e.g., late maturity, slow growth, low natural mortality) tend to predispose species towards low values of  $U_{MSY}$ , density dependence in recruitment is also an important determinant. Density dependence principally refers to the improvement in juvenile survival rate as spawning stock size is reduced. Density-dependent mortality may occur at a number of life history stages but probably occurs principally in juvenile demersal stages for coastal species (Myers 2002). Mechanisms include increased territorial behaviour and greater competition for food as juvenile density increases, which lead to increased time taken to reach sizes less vulnerable to predation (see Hilborn and Walters 1992; Rose et al. 2001; Myers 2002). Foraging arena theory (Walters and Juanes 1993; Walters and Korman 1999; Walters and Martell 2004) has recently been introduced as an overarching explanation for density dependence in juvenile survival rates and predicts that density dependence is an emergent consequence of the trade-off between time spent feeding and risk of predation.

Mechanisms leading to density dependence are complex and subject to considerable interannual variability. On average, however, some species show a stronger response to changes in spawning stock size than others. All other things equal, stronger density dependence implies greater resilience to fishing due to the stock's ability to respond positively to reductions in adult biomass (e.g., Goodyear 1977). Density dependence is difficult to measure in nature because of problems with observing juvenile fish, although the meta-analyses of Myers et al. (1999) and Goodwin et al. (2006) have improved understanding of the likely range of magnitude of these effects. Quantifying interactions among life history parameters, density dependence, and sustainable harvest rates could aid in understanding the mechanisms that lead to overfishing and could be useful in design of sustainable fishing strategies. The structure of our model, with an analytical relationship between productivity and  $U_{MSY}$ , allows these linkages to be considered simultaneously.

### Bayesian estimation

Bayesian inference is now in mainstream use in fisheries stock assessment (e.g., Punt and Hilborn 1997; Chen et al. 2003) and has facilitated a general move towards consideration of population and management parameters as probability distributions, rather than point estimates. Once distributions of a model's leading parameters have been estimated, the past and current state of the fishery, in terms of

population size or harvest rates, can also be estimated to determine the probability of exceeding reference points. Combining direct estimation of fishery reference points, such as MSY and  $U_{MSY}$ , with a Bayesian approach can improve communication of scientific results considerably (Schnute and Kronlund 1996; Schnute and Richards 1998). Managers are more familiar with the parameters MSY and  $U_{MSY}$  than their more abstract biological analogues, and in fully developed fisheries, it is likely that MSY and  $U_{MSY}$  lie within management experience. Dialogue between managers and scientists about the range of uncertainty to admit in stock assessments is likely to be more transparent if all parties are discussing parameters with which they are familiar.

This paper proceeds as follows. First we describe an age-structured population model that uses MSY and  $U_{MSY}$  as leading parameters. Then we briefly describe some properties of the model, chiefly in terms of its ability to show relationships between life history, density dependence, and  $U_{MSY}$ . Finally, we implement a simple Bayesian estimation routine to illustrate estimation of  $U_{MSY}$  directly.

### Population model with MSY and $U_{MSY}$ as leading parameters

The model is an age-structured population model with leading parameters MSY and  $U_{MSY}$  describing scale and productivity of the population, respectively. First, we describe the equilibrium structure of the model and then incorporate time dynamics. The key difference between this model and other age-structured models is the analytical linkage between the leading management parameters and recruitment parameters.

Equilibrium recruitment ( $R$ ) under a given constant harvest rate is a function of stock size (expressed in terms of eggs,  $E$ ) and the leading parameters of the model. Here it is described by the Beverton and Holt (1957) recruitment function, i.e.,

$$(1) \quad R = \frac{\alpha E}{1 + \beta E}$$

where we define a recruit as a fish of age 1. Equilibrium eggs per recruit ( $\phi_E$ ) can be obtained using an ‘‘incidence’’ function (Botsford 1981; Walters and Martell 2004), which captures the effects of natural mortality and fishing mortality over the lifetime of individuals assuming equilibrium conditions, i.e.,

$$(2) \quad \phi_E = \sum_a l_a f_a$$

where  $f_a$  is relative fecundity-at-age (we assumed fecundity based on weight and a logistic maturity function; Appendix B). Survivorship-at-age,  $l_a$  (the proportion of fish that survive to age  $a$  under a given constant equilibrium harvest rate  $U$ ), is given by

$$(3) \quad l_a = \begin{cases} 1 & \text{if } a = 1 \\ l_{a-1} s_{a-1} (1 - v_{a-1} U) & \text{if } a > 1 \end{cases}$$

where  $s_a$  is natural survival-at-age. We assumed  $s_a$  to be constant and proportional to the von Bertalanffy growth rate,  $\kappa$ , via the relationship  $s_a = e^{-M}$ , where  $M$  is the instantaneous natural mortality rate, with the simplifying assumption that

$M = 1.5\kappa$  (Beverton and Holt 1959). The term  $s_a(1 - v_a U)$  represents the survival rate under fishing,  $s_{a\_fished}$ . Equation 3 represents equilibrium survivorship under a particular constant harvesting regime and enables calculation of useful equilibrium per recruit quantities under different harvesting regimes. Note that unfished survivorship is obtained by setting  $U = 0$ .

At equilibrium, total egg production is given by  $E = R\phi_E$ . Substituting this into eq. 1 and solving for  $R$  gives

$$(4) \quad R = \frac{\phi_E \alpha - 1}{\beta \phi_E}$$

Using this form of the stock–recruitment function, we show how  $\alpha$  can be derived from the leading productivity parameter  $U_{MSY}$  (Appendix A). The scaling parameter ( $\beta$ ) is more easily obtained from leading parameters  $U_{MSY}$  and MSY. First,

$$VB_{MSY} = \frac{MSY}{U_{MSY}}$$

where  $VB_{MSY}$  is equilibrium vulnerable biomass under  $U_{MSY}$ . Recruitment under  $U_{MSY}$  is therefore given by

$$R_{MSY} = \frac{VB_{MSY}}{\phi_{VB_{MSY}}}$$

where  $\phi_{VB}$  is vulnerable biomass per recruit at  $U_{MSY}$ , calculated as

$$(5) \quad \phi_{VB} = \sum_a l_a w_a v_a$$

with  $l_a$  evaluated at  $U = U_{MSY}$  (eq. 3) and where  $w_a$  is the mean weight-at-age (derived from the von Bertalanffy (1938) growth function; see Appendix B) and  $v_a$  is the mean vulnerability-at-age, defined as the proportion of fish of a given age  $a$  vulnerable to the fishing gear. Asymptotic vulnerability can be represented using a simple logistic function (see Appendix B). Specification of the recruitment function can then be completed by solving eq. 4 for  $\beta$  (with  $R$  and  $\phi_E$  evaluated at  $U_{MSY}$ ), i.e.,

$$\beta = \frac{\phi_{E_{MSY}} \alpha - 1}{R_{MSY} \phi_{E_{MSY}}}$$

Once  $\alpha$  and  $\beta$  are known, other important biological properties can be derived. Unfished recruitment,  $R_0$ , is obtained using  $\phi_{E_0}$  in eq. 4. Unfished biomass,  $B_0$ , is then simply a function of  $R_0$  and unfished biomass per recruit, i.e.,  $B_0 = R_0 \phi_{B_0}$ , where

$$\phi_{B_0} = \sum_a l_a w_a$$

with  $l_a$  evaluated at  $U = 0$ .

Another productivity parameter of interest is the recruitment compensation ratio, CR (Goodyear 1977), which represents the maximum possible compensatory improvement in juvenile survival as stock size is decreased by fishing. It is easily derived from  $\alpha$ , i.e., unfished juvenile survival rate is

**Table 1.** Life history and selectivity parameters used in the model.

| Parameter        | Hypothetical fish       | Namibian Cape hake                   |
|------------------|-------------------------|--------------------------------------|
| $L_\infty$       | 60 cm                   | 111 cm <sup>a</sup>                  |
| $\kappa$         | 0.12·year <sup>-1</sup> | 0.14·year <sup>-1</sup> <sup>a</sup> |
| $a_0$            | -0.5                    | 0                                    |
| $lwa$            | 0.0001                  | 0.00001 <sup>b</sup>                 |
| $lwb$            | 3                       | 3 <sup>b</sup>                       |
| $a_{\max}$       | 15 years                | 25 years <sup>b</sup>                |
| $a_{\text{mat}}$ | 2 years                 | 4 years <sup>c</sup>                 |
| $a_h$            | 3 years                 | 3 years <sup>d</sup>                 |

**Note:**  $L_\infty$ , theoretical maximum length of the fish;  $\kappa$ , instantaneous growth rate;  $a_0$ , theoretical age at which the fish has zero length;  $a_{\text{mat}}$ , age at 50% maturity;  $a_{\max}$ , maximum age;  $a_h$ , age at 50% first harvest. Length is converted to weight using the conversion factors  $lwa$  and  $lwb$ , i.e.,  $w_a = lwa \cdot L_a^{lwb}$ , where  $L_a$  is the length at age  $a$ .

<sup>a</sup>Jones 1974 (cited in FishBase, www.fishbase.org).

<sup>b</sup>These parameters produced the approximate mean maximum weight cited in FishBase (www.fishbase.org).

<sup>c</sup>Hilborn and Mangel 1997.

<sup>d</sup>Arbitrarily assigned.

$R_0/E_0$ , but,  $\phi_{E_0} = E_0/R_0$ , so unfished survival is simply  $\phi_{E_0}^{-1}$ . As juvenile survival at very low stock size is  $\alpha$ , CR is just the ratio of these two survival rates (Goodyear 1977), i.e.,

$$(6) \quad CR = \alpha \phi_{E_0}$$

When relative fecundity is described as the product of mean weight-at-age and maturity-at-age (Appendix B),  $\phi_{E_0}$  is the same as unfished spawning biomass per recruit ( $SPR_{F=0}$ ; Gabriel et al. 1989). Myers et al. (1999) defined maximum lifetime spawners per spawner ( $\hat{\alpha}$ ) as the product of  $\alpha$  and  $SPR_{F=0}$  and, therefore, the same as CR. When Beverton–Holt recruitment is assumed, the steepness parameter,  $h$ , of Mace and Doonan (1988) is related to  $\hat{\alpha}$  (i.e., CR) by  $h = \hat{\alpha}/(4 + \hat{\alpha})$  (Myers et al. 1999).

The model is made dynamic by simulating changes in numbers  $N$  at age  $a$  and years  $t$  via the equation

$$(7) \quad N_{a+1,t+1} = N_{a,t} s_a (1 - v_{a,t} U_t) \quad (\text{for } a > 1 \text{ and } t > 1)$$

Annual harvest rate,  $U_t$ , is calculated from annual catch,  $C_t$ :

$$(8) \quad U_t = \frac{C_t}{VB_t}$$

where  $VB_t$  is the biomass of fish vulnerable to the fishing gear,

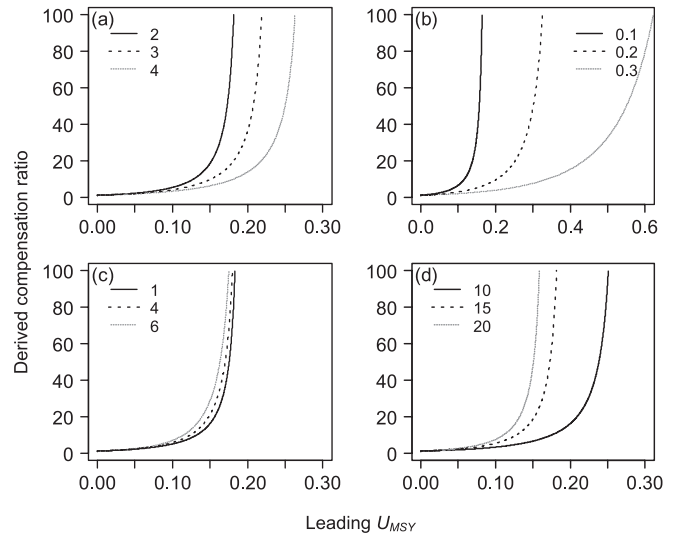
$$(9) \quad VB_t = \sum_a N_{a,t} v_{a,t} w_a$$

Recruits ( $R_t$ , i.e.,  $N_{1,t}$ ) are added to the population using eq. 1 with number of eggs calculated as

$$E_t = \sum_a f_a N_{a,t}$$

We made the common simplifying assumption that the unfished stock was at equilibrium and initialised the model in the first year of fishing with  $N_{a,1} = R_0 J_a$ .

**Fig. 1.** Effect of different values of (a) age at 50% first harvest,  $a_h$  (years); (b) von Bertalanffy growth rate,  $\kappa$  (year<sup>-1</sup>); (c) age at 50% maturity,  $a_{\text{mat}}$  (years); and (d) maximum age,  $a_{\max}$  (years) on the relationship between leading productivity parameter  $U_{\text{MSY}}$  and the derived compensation ratio (CR) for a hypothetical species. Parameter values are provided in Table 1. Note truncation of the y axis at CR = 100 and different scales on the x axes.



### Equilibrium properties: relationships between life history, density dependence, and $U_{\text{MSY}}$

The equilibrium model can be used to examine the predicted form of the relationship between density dependence (measured by CR) and  $U_{\text{MSY}}$ . The effect of gear selectivity and life history traits (e.g., growth rate, age-at-maturity, maximum age, and natural mortality) on this relationship can also be modelled. Here, we consider a hypothetical fish species with known life history parameters (Table 1) and show the effect of increasing (i) age at first harvest, (ii) von Bertalanffy growth rate, (iii) age-at-maturity, and (iv) maximum age on the relationship between CR and  $U_{\text{MSY}}$ . To do this,  $\alpha$  was calculated over a range of hypothesised values of  $U_{\text{MSY}}$  (0 to 1, step size 0.0001) using eq. A6 and converted to CR (eq. 6).

We show the form of the relationship between CR and  $U_{\text{MSY}}$  (note that  $U_{\text{MSY}}$  is the independent variable; Fig. 1). The relationship is not dynamic but rather shows the predicted values of CR under a range of hypothesised values of  $U_{\text{MSY}}$  (i.e., the degree of improvement in juvenile survival that would be required for each hypothesised value of  $U_{\text{MSY}}$  to be true). As the hypothesised value of  $U_{\text{MSY}}$  increases, the strength of recruitment compensation that would be needed for the hypothesis to be true increases rapidly and tends towards a vertical asymptote. Values of  $U_{\text{MSY}}$  to the right of the asymptote are undefined, representing hypotheses of  $U_{\text{MSY}}$  for which  $\alpha$  was predicted to be negative (therefore impossible). We have truncated the y axis in Fig. 1 at CR = 100 because as  $U_{\text{MSY}}$  approached its maximum possible value, CR tended rapidly towards very large values, making comparison of the curves difficult. Because most of the

curves become almost vertical by the truncation point, the maximum possible value of  $U_{MSY}$  can still be seen. As values of CR > 100 seem to be rare (Myers et al. 1999; Goodwin et al. 2006), the region of management interest is shown (Fig. 1).

The relationship between CR and  $U_{MSY}$  at different values of age at 50% first harvest,  $a_h$ , is shown (Fig. 1a). Increasing  $a_h$  causes the curve to shift to the right, increasing the range of values of  $U_{MSY}$  that can be considered possible. Increasing  $\kappa$  (von Bertalanffy growth rate and proxy for natural mortality) causes the curve to shift to the right, implying a greater range of possible values of  $U_{MSY}$  for faster-growing species (Fig. 1b). Increasing age at 50% maturity,  $a_{mat}$  (Fig. 1c), or maximum age,  $a_{max}$  (Fig. 1d), however, causes the curve to shift to the left, implying a smaller range and lower possible values of  $U_{MSY}$  for later-maturing or longer-lived species (although the effect of age-at-maturity is small). Importantly, Figure 1 suggests that, for some species for which Beverton–Holt recruitment can be assumed, there is a maximum possible value of  $U_{MSY}$  that can be estimated from life history and selectivity data alone.

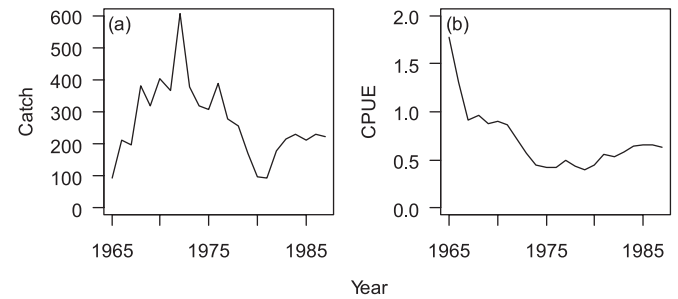
## Bayesian estimation of MSY and $U_{MSY}$

### Methods

In this section, we use our model to show how MSY and  $U_{MSY}$  can be estimated using a Bayesian approach. We used catch and catch per unit effort (CPUE) data (Fig. 2) for Namibian Cape hake (a mixed stock of *Merluccius capensis* and *Merluccius paradoxus*) published in Hilborn and Mangel (1997). We chose this data set because (i) it will be familiar to many readers and (ii) CPUE is considered to be a reasonable index of abundance because the degree of schooling in hake is relatively low. The fishery began in the mid-1960s and was largely unregulated, resulting in a large decline in CPUE in the first 10 years. Following conservation concerns, catches were reduced in the 1970s, which resulted in a slight increase in CPUE (Hilborn and Mangel 1997). Life history and selectivity parameters are provided in Table 1.

We compare our model with leading management parameters (MSY and  $U_{MSY}$ ; model 1) with one with leading biological parameters ( $R_0$  and CR; model 2) to show that very similar results can be obtained using either approach. Model 2 was identical in structure to model 1, except for the method of calculating the parameters of the recruitment function (i.e., in model 2,  $\alpha$  was obtained from the leading value of CR and eq. 6;  $\beta$  was then obtained from the leading value of  $R_0$  and eq. 4). In both models, in addition to estimating the leading parameters, we also estimated the instantaneous natural mortality rate,  $M$ , and the standard deviation of the observation error anomalies,  $\sigma$ . To obtain the posterior distributions, we used a Metropolis–Hastings algorithm implemented in R, using the function “MCMCmetrop1R” in the MCMC package (Martin and Quinn 2006; R Development Core Team 2006). Markov chain simulation performs a random walk in the parameter space of  $\theta$  (model 1,  $\theta = (MSY, U_{MSY}, M, \sigma)$ ; model 2,  $\theta = (R_0, CR, M, \sigma)$ ), which converges to a distribution that approximates the joint posterior distribution (Gelman et al. 1995). The algorithm was initialised at the maximum likelihood estimates for  $\theta$  and proceeded for 110 000 iterations, the first 10 000 of which were

**Fig. 2.** (a) Catch (thousands of tons) and (b) catch per unit effort (CPUE; tons per standardised trawler hour) used to fit the models for Namibian Cape hake. Data source: Hilborn and Mangel (1997).



discarded to allow for convergence. Convergence was assessed by visually examining trace plots and plotting running medians of length 50 to ensure that the algorithm was sampling from a stable distribution (see Gelman et al. (1995) and Punt and Hilborn (1997) for more details on MCMC methods).

For simplicity we did not try to estimate process error. We assumed lognormal observation error, i.e.,  $CPUE_t = qVB_t e^{v_t}$ , where  $q$  is the constant of proportionality (catchability) and  $v_t \sim N(0, \sigma)$ . We treated  $\sigma$  and  $q$  as uncertain parameters but used the maximum likelihood estimate (MLE) of  $q$  in the joint posterior distribution, using the approach of Walters and Ludwig (1994), i.e., assuming a linear relationship between  $CPUE_t$  and  $VB_t$ , we estimated  $z_t = \ln(CPUE_t) - \ln(VB_t)$  and

$$(10) \quad \bar{z} = \frac{\sum_{t=1}^n z_t}{n}$$

The MLE of  $q$  was then  $e^{\bar{z}}$  and the observation residuals ( $d_t$ ) used in the log-likelihood function were calculated as  $d_t = z_t - \bar{z}$ . The log-likelihood of each observation was thus

$$(11) \quad L_t = \ln(\sigma) + 0.5 \ln(2\pi) + \frac{d_t^2}{2\sigma^2}$$

We assumed uninformative prior probability distributions for  $U_{MSY}$  and MSY in model 1 and for  $R_0$  in model 2. We assumed a normally distributed prior for  $M$ , i.e.,  $M \sim N(0.21, 0.1)$ , with the mean based on the assumption  $M = 1.5\kappa$  (Beverton and Holt 1959). We assumed a weak, lognormally distributed informative prior for CR to penalise negative (i.e., impossible) values of CR. We log-transformed  $R_0$ , CR, and MSY so that the relative scales of parameters in the search routine were similar.  $U_{MSY}$  was logit-transformed to constrain values between 0 and 1.

MSY and  $U_{MSY}$  had to be estimated numerically in model 2. For each  $\theta$ , we used a Newton–Raphson algorithm to search over the derivative of the yield function (eq. A1) with respect to  $U$  to find the value of  $U$  that maximised yield. Note that we may not have used the most current parameters for these hake species and have likely used an incorrect selectivity schedule. Our choice of priors for CR and  $M$  will also influence our results, which should therefore be read as illustrative only.

**Results**

The weak prior placed on CR had the effect of constraining the posterior values of  $U_{MSY}$  and MSY to values that were not associated with impossible recruitment parameters (see life history section). The prior placed on  $M$  constrained this parameter within plausible biological bounds (i.e., close to  $1.5\kappa$ ; Beverton and Holt 1959) and therefore also prevented  $U_{MSY}$  from becoming large. Our choice of  $a_h$  relative to  $a_{mat}$  also affected the results. For fish populations in which most individuals vulnerable to the fishing gear have already had the opportunity to spawn,  $U_{MSY}$  must approach unity. Alternatively, harvesting a population at an age before most individuals have spawned results in lower sustainable harvest rates (this is implicit in Fig. 1a).

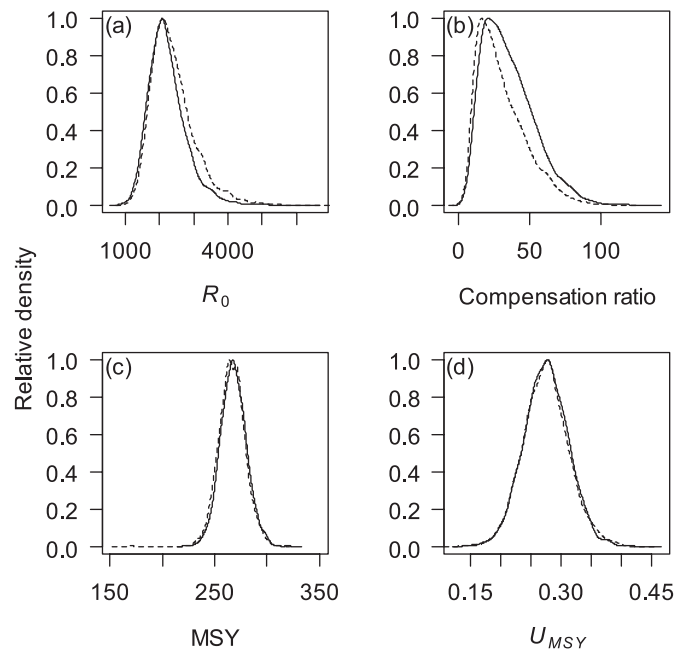
Estimation of key management parameters was robust to the choice of leading parameters (Fig. 3). Density plots of the posterior distributions of the leading parameters in each model are shown (Fig. 3). The two models give very similar results for the biological parameters and almost identical results for the management parameters. Note that  $R_0$  and CR were obtained analytically in model 1 and that MSY and  $U_{MSY}$  were estimated numerically in model 2. There was no evidence that the parameter estimates did not converge (Fig. 4).

**Discussion**

Schnute and Kronlund (1996) derived  $\alpha$  from  $U_{MSY}$  for semelparous species. They demonstrated the advantages of their reparameterised recruitment function in terms of its amenability to Bayesian fitting procedures and, because a parameter with policy relevance could be directly estimated from data, improved communicability of results. The idea was extended to a generalised age-structured model for iteroparous species by Schnute and Richards (1998), who assumed knife-edged maturity and recruitment. The approach presented here extends these previous works by allowing the inclusion of age-specific maturity and recruitment via the Botsford “incidence” functions, which incorporate age schedules of fecundity, mortality, and vulnerability. We demonstrated the approach using logistic, age-based selectivity and maturity schedules, but the approach is flexible to any formulation of these. For example, dome-shaped or lognormal selectivity curves may be more appropriate for species in which large or old individuals are able to escape fishing because of behavioural, spatial, or market-based effects. We made certain simplifying assumptions, notably that  $M = 1.5\kappa$ . This relationship, suggested by Beverton and Holt (1959) to be an invariant property of fish populations, is widely applied in fisheries models. However, our model is flexible to this assumption, as well as to the assumption that  $M$  is constant with age.

We used our model to illustrate some important relationships between density dependence, life history traits, and  $U_{MSY}$ . We stress that the relationship between CR and  $U_{MSY}$  shown in Fig. 1 is not dynamic, but rather represents the degree of improvement in juvenile survival that would be required for each hypothesised value of  $U_{MSY}$  to be true. For a species with a given growth, survival, maturity, and selectivity schedule, there will be a mean curve describing the relationship between  $U_{MSY}$  and CR representing the set of

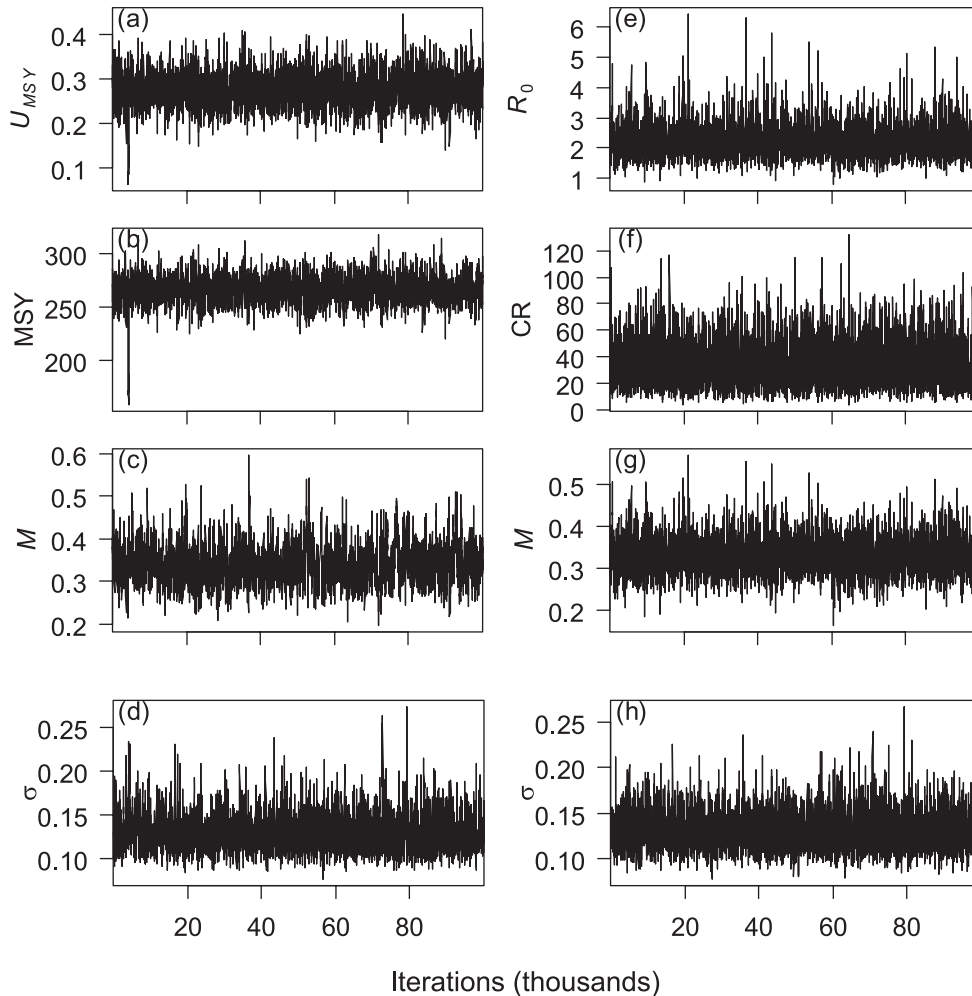
**Fig. 3.** Density plots showing relative posterior probability density distributions of  $R_0$ , compensation ratio (CR), maximum sustainable yield (MSY), and  $U_{MSY}$  for model 1 (broken line) and model 2 (solid line). Plots obtained from Markov chain Monte Carlo (MCMC) sample of length 100 000 (burn-in: 10 000 cycles).



values of CR and  $U_{MSY}$  that can be considered possible for the species. This curve can be calculated from life history and selectivity parameters alone, prior to any time series fitting. Figure 1 implies that for some species, there will be a finite range of possible values of  $U_{MSY}$ , with its upper bound at the asymptotic value of  $U_{MSY}$ . This is because  $U_{MSY}$  maximises yield in terms of weight and is therefore determined by growth, survival, and selectivity (Beverton and Holt 1957). The upper bound of  $U_{MSY}$  represents the harvest rate beyond which long-term yield can no longer be maximised for a given growth and selectivity schedule, no matter how strong recruitment compensation is. If there is no other prior information about the productivity of a species and Beverton–Holt type recruitment can be assumed, then there is an upper boundary of  $U_{MSY}$  that can be estimated from life history and selectivity data alone. For species with very steep  $U_{MSY}$ –CR curves (curves with an upper boundary very far to the left of the  $U_{MSY}$  axis), uncertainty in  $U_{MSY}$  can be reduced considerably, even if the actual value of  $U_{MSY}$  cannot be estimated because of a lack of historical data. If reasonable estimates of CR are available for similar species or from meta-analysis, it may also be possible to construct a reasonable prior for  $U_{MSY}$  for data-limited species.

The effects of selectivity and life history parameters on the relationship between CR and  $U_{MSY}$  are not surprising. Increasing (long-term) age at 50% first harvest,  $a_h$ , causes the  $U_{MSY}$ –CR curve to become less steep and shift to the right. Assuming that the value of CR is a fixed property of a population independent of  $a_h$ , this implies that a greater maximum sustainable harvest rate could be achieved by more selective fishing gear allowing younger fish to escape. This idea is a well-known result of per-recruit type analyses (Beverton and Holt 1957). The relationship between  $\kappa$  and

**Fig. 4.** Trace plots of iterations versus sampled values for each estimated parameter indicating convergence of the estimates. Results are shown for model 1: (a)  $U_{MSY}$ , (b) maximum sustainable yield (MSY), (c)  $M$ , and (d)  $\sigma$ ; and model 2: (e)  $R_0$  (thousands), (f) compensation ratio (CR), (g)  $M$ , and (h)  $\sigma$ .



$U_{MSY}$  was also very strong. In our equilibrium formulation,  $\kappa$  was used in the model twice: (i) as growth rate affecting the rate at which fish reach maximum weight and (ii) as a proxy for natural mortality,  $M$ , affecting the survivorship schedule (eq. 3). Although these two effects are confounded, they have the same qualitative effect on the  $U_{MSY}$ –CR curve, i.e., increasing  $\kappa$  caused the curve to become less steep. For a given value of  $U_{MSY}$ , the amount of recruitment compensation required to support that  $U_{MSY}$  is less for faster-growing species because (i) asymptotic maximum weight is reached earlier and (ii) the population has faster turnover. Increasing  $a_{mat}$  had a weak influence on the relationship between  $\kappa$  and  $U_{MSY}$ , although it did cause a slight increase in steepness and a shift to the left. All other things equal, species with later maturity have a smaller lifetime reproductive capacity and a greater chance of being harvested before they have reproduced. Increasing  $a_{max}$  similarly caused the curve to shift to the left. Higher CR required to support a given  $U_{MSY}$  for longer-lived species could be a result of the relatively smaller contribution of older age classes to the total yield due to the decaying survivorship function.

It should be noted that life history parameters tend to covary and can rarely be considered in isolation, i.e., longer-

lived species tend to mature later, grow slower, and have lower natural mortality. We chose to separate out the effects of single parameters on the steepness of the  $U_{MSY}$ –CR curve, not because these curves have applicability in themselves, but because they allow the complexity of the interaction between life history traits, selectivity, density dependence, and sustainable harvest rate to be seen. Maximum sustainable harvest rate is not a simple function of selectivity, density dependence, or individual life history parameters but a complex result of them all. Simplistic assumptions about the effects of one of these factors on  $U_{MSY}$  should not be made without consideration of the other influential factors.

Life history information is easier and cheaper to obtain than recruitment and abundance data and is routinely collected. Growing conservation concerns and current trends towards more ecosystem-based approaches of managing fisheries (e.g., Food and Agriculture Organization of the United Nations 2003; Pikitch et al. 2004) require consideration of the impacts of fisheries on many more species than previously and there is now a very large body of literature studying the link between life history traits and productivity for data-limited fish. For example, McAllister et al. (2001) demonstrated three approaches that could be used to esti-

mate  $r$  for elasmobranchs using only life history information. Beddington and Kirkwood (2005) presented a method for estimating  $F_{MSY}$  based on Beverton and Holt (1959) invariants and parameters describing growth, length at first capture, and the steepness parameter,  $h$ . Goodwin et al. (2006) showed correlations between a composite life history parameter (unfished spawners per recruit,  $SPR_{F=0}$ ), Ricker  $\alpha$ , and CR for 54 Atlantic teleosts for which stock–recruitment data were available. They found a strong negative correlation between  $SPR_{F=0}$  and  $\alpha$  and a positive correlation between  $SPR_{F=0}$  and CR and discussed evolutionary reasons for these observations. Jennings et al. (1999) and Denney et al. (2002) also searched for correlations between life history and productivity. The general approach of these papers was to analyze stocks for which informative data exist about productivity (e.g., measured as population response to fishing pressure) and draw conclusions that could be used in development of management strategies for data-limited species. We suggest that our model could contribute to such approaches as it provides a link between life history, density dependence, and  $U_{MSY}$  simultaneously.

We used a simple Bayesian estimation routine to illustrate the parameter estimation process. We compared a model with leading management parameters ( $MSY$  and  $U_{MSY}$ ) with a model structurally identical except for its leading parameters ( $R_0$  and CR). We showed that the same posterior probability densities for management parameters could be obtained in either case. However, we argue that the first model is advantageous for two reasons: (i) it is more efficient (there is no need to numerically estimate  $MSY$  and  $U_{MSY}$ ) and (ii) it enables improved communication of scientific results. Determination of appropriate informative priors is one of the most difficult aspects of stock assessment (see Punt and Hilborn 1997), and the preliminary phases of stock assessment often involve intensive modelling and testing sessions to determine plausible ranges of leading biological parameters. These ranges are often based on the plausibility of the model's predicted  $MSY$  (or  $U_{MSY}$ ). Hoenig et al. (1994) have suggested methods for constructing informative priors on  $MSY$  based on historical catch and effort data. Simple analytical relationships have also been suggested for obtaining rough estimates of  $MSY$  and  $U_{MSY}$  (e.g., Gulland 1971; Patterson 1992), which could be used in construction of priors. Models such as ours and that of Schnute and Richards (1998) enable this information to be used in direct estimation of  $U_{MSY}$ , a parameter of primary management interest. We suggest that dialogue between scientists and managers will be improved if the parameters at the forefront of the analysis are familiar to all parties. We suggest this may work in both directions, as managers with a long history of involvement in a fishery will be better able to contribute to the stock assessment process if the focus is on parameters with which they have direct experience.

In summary, we have presented a model that has several advantages: (i) it enables direct estimation of parameters of principle management interest; (ii) it is flexible to a very wide range of assumptions about growth, survival, maturity, and selectivity, including the form of these relationships; and (iii) it provides a means of analysing the interaction among important selectivity and life history parameters, density dependence, and maximum sustainable harvest rate. It is ame-

nable to Monte Carlo type approaches to account for uncertainty in input parameters, as well as to Bayesian or likelihood approaches for estimating leading parameters.

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## Appendix A. Derivation of $\alpha$ from $U_{MSY}$

For a given selectivity schedule, equilibrium yield ( $Y$ ) for any long-term fixed exploitation rate ( $U$ ) is predicted to be

$$(A1) \quad Y = UR\phi_{VB}$$

where recruits ( $R$ ) are defined as fish of age 1 and  $\phi_{VB}$  is equilibrium vulnerable biomass per recruit (eq. 5). Substituting the Beverton–Holt recruitment function (eq. 4) into eq. A1 and rearranging gives

$$(A2) \quad Y = \frac{\alpha U \phi_{VB}}{\beta} - \frac{U \phi_{vb}}{\beta \phi_E}$$

There are actually three functions of  $U$  contained in eq. A2 because  $l_a$  (a component of the functions  $\phi_{VB}$  and  $\phi_E$ ) is also a function of  $U$ .  $Y$  is a convex function of  $U$ , with  $Y = 0$  at either  $U = 0$  or  $U_{\text{extinction}}$  and maximum  $Y$  occurring between these at  $U_{MSY}$ . Solving

$$\frac{\partial Y}{\partial U} = 0$$

for  $U$  therefore gives the value of  $U$  that maximises the function (i.e.,  $U_{MSY}$ ). Differentiating  $Y$  with respect to  $U$  in eq. A2 gives

$$(A3) \quad \frac{\partial Y}{\partial U} = \frac{\alpha \phi_{VB}}{\beta} + \frac{\alpha U}{\beta} \left( \frac{\partial \phi_{VB}}{\partial U} \right) - \frac{\phi_{VB} \phi_E + U \phi_E \left( \frac{\partial \phi_{VB}}{\partial U} \right) - U \phi_{VB} \left( \frac{\partial \phi_E}{\partial U} \right)}{\beta \phi_E^2}$$

Setting  $\frac{\partial Y}{\partial U} = 0$  and solving for  $U_{MSY}$  gives

$$(A4) \quad U_{MSY} = \frac{1 - \alpha\phi_E}{\frac{\alpha\phi_E - 1}{\phi_{VB}} \left( \frac{\partial\phi_{VB}}{\partial U_{MSY}} \right) + \frac{1}{\phi_E} \left( \frac{\partial\phi_E}{\partial U_{MSY}} \right)}$$

with  $\phi_E$  and  $\phi_{VB}$  evaluated at  $U_{MSY}$ . Note that the stock-recruitment scalar  $\beta$  is absent from eq. A4, as  $U_{MSY}$  is independent of the units used to count the population.

By setting

$$k_1 = \left( \frac{\partial\phi_E}{\partial U_{MSY}} \right) \phi_E^{-1} \text{ and } k_2 = \left( \frac{\partial\phi_{VB}}{\partial U_{MSY}} \right) \phi_{VB}^{-1}$$

eq. A4 can be expressed as

$$(A5) \quad U_{MSY} = \frac{1 - \alpha\phi_E}{k_1 + k_2(\alpha\phi_E - 1)}$$

and

$$(A6) \quad \alpha = \frac{1 - k_1 U_{MSY} + k_2 U_{MSY}}{\phi_E(1 + k_2 U_{MSY})}$$

$\frac{\partial\phi_E}{\partial U_{MSY}}$  and  $\frac{\partial\phi_{VB}}{\partial U_{MSY}}$  can be solved analytically as recursive

functions of  $\phi_E$  and  $\phi_{VB}$  in the following manner. Equation 5 expressed  $\phi_{VB}$  as the sum of the product of survivorship-at-age ( $l_a$ ), vulnerability-at-age ( $v_a$ ), and weight-at-age ( $w_a$ ). Expanding eq. 5 gives

$$(A7) \quad \frac{\partial\phi_{VB}}{\partial U_{MSY}} = \frac{\partial l_1 v_1 w_1}{\partial U_{MSY}} + \frac{\partial l_2 v_2 w_2}{\partial U_{MSY}} + \frac{\partial l_3 v_3 w_3}{\partial U_{MSY}} + \dots + \frac{\partial l_\infty v_\infty w_\infty}{\partial U_{MSY}}$$

Assuming that mean weight-at-age is independent of harvest rate, then the  $v$  and  $w$  terms factor out of the derivatives.

$$(A10) \quad \frac{\partial l_a}{\partial U_{MSY}} = \frac{(1 - s_{a\_fished}) \left( s_{a-1}(1 - v_{a-1} U_{MSY}) \left( \frac{\partial l_{a-1}}{\partial U_{MSY}} \right) - l_{a-1} s_{a-1} v_{a-1} \right) - s_a v_a s_{a-1\_fished} l_{a-1}}{(1 - s_{a\_fished})^2}$$

Because  $l_1$  (survivorship at age 1) is, by definition, 1, its derivative with respect to  $U_{MSY}$  is zero, so the first term disappears. Therefore,

$$(A8) \quad \frac{\partial\phi_{VB}}{\partial U_{MSY}} = \sum_a v_a w_a \frac{\partial l_a}{\partial U_{MSY}}$$

$\frac{\partial l_a}{\partial U_{MSY}}$  is then easily obtained, i.e.,  $l_a = l_{a-1} s_{a-1\_fished}$ , where

$s_{a-1\_fished}$  is given by  $s_{a-1}(1 - v_{a-1}U)$  with  $U$  set to  $U_{MSY}$ . The derivative of  $s_{a-1\_fished}$  with respect to  $U_{MSY}$  is simply  $(-s_{a-1}v_{a-1})$  and, therefore,

$$(A9) \quad \frac{\partial l_a}{\partial U_{MSY}} = s_{a-1}(1 - v_{a-1}U_{MSY}) \left( \frac{\partial l_{a-1}}{\partial U_{MSY}} \right) - l_{a-1} s_{a-1} v_{a-1}$$

Because  $\frac{\partial l_a}{\partial U_{MSY}}$  is by definition zero, eq. A9 can be solved

recursively and substituted into eq. A8.  $\frac{\partial\phi_E}{\partial U_{MSY}}$  is solved in

exactly the same way, except that  $f_a$  is used instead of  $v_a w_a$ . The parameters  $k_1$  and  $k_2$  can now be solved and substituted into eq. A6 to give a function expressing  $\alpha$  in terms of a leading productivity parameter,  $U_{MSY}$ . The resulting formula can be easily implemented in a spreadsheet or any appropriate programming language. The derivation can be checked numerically by running the model under a range of constant harvest rates and checking that the harvest rate that produces maximum long-term yield is the same as the leading  $U_{MSY}$ .

Note that, if desired, eqs. 3 and A9 can easily be modified to include a plus group (i.e., individuals of age  $a_{max}$  and older). For  $a = a_{max}$ , survivorship would be given by

$$l_a = \frac{l_{a-1} s_{a-1\_fished}}{1 - s_{a-1\_fished}}$$

For  $a = a_{max}$ ,  $\frac{\partial l_a}{\partial U_{MSY}}$  would then be given by

## Appendix B. Growth, maturity, and gear selectivity functions

### Growth schedule

We assumed von Bertalanffy (1938) growth:

$$(B1) \quad L_a = L_\infty(1 - e^{-\kappa(a-a_0)})$$

where  $L_a$  is the length at age  $a$ ,  $L_\infty$  is the theoretical maximum length of the fish,  $\kappa$  is the instantaneous growth rate, and  $a_0$  is the theoretical age at which the fish has zero length. Length is converted to weight using the conversion factors  $lwa$  and  $lwb$ , i.e.,  $w_a = lwa \cdot L_a^{lwb}$

### Maturity and selectivity schedules

We assumed logistic gear selectivity and maturity schedules, as we believe these to be common in fisheries, although other appropriate formulations could be substituted for these.

Relative fecundity-at-age,  $f_a$ , was assumed proportional to body weight and was modelled as

$$(B2) \quad f_a = w_a \text{Mat}_a$$

where maturity-at-age ( $\text{Mat}_a$ ) is given by the following logistic function:

$$(B3) \quad \text{Mat}_a = \frac{1}{1 + e^{\left(\frac{-(a-a_{\text{mat}})}{\sigma}\right)}}$$

where  $\sigma$  determines the steepness of the curve, with smaller values of  $\sigma$  resulting in a steeper curve. We assumed  $\sigma = 0.2a_{\text{mat}}$ , implying a relatively steep curve (i.e., most individuals mature around the same age).

Similarly, vulnerability to fishing gear at age ( $v_a$ ) is given by

$$(B4) \quad v_a = \frac{1}{1 + e^{\left(\frac{-(a-a_h)}{\sigma}\right)}}$$

with  $\sigma = 0.1a_h$ . This implies a relatively steep selectivity schedule. In the absence of other information, it is fairly common to assume steep or knife-edged maturity and selectivity schedules.