

Reference priors for Bayesian fisheries models

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Abstract: Bayesian models require the specification of prior distributions for all unknown parameters. This work addresses the situation where it is not possible to construct priors based on existing knowledge and instead one must obtain a suitable prior via some formal method. To maintain consistency of terminology with the statistical literature such priors are herein called reference priors in recognition that there is no general consensus about what constitutes a “non-informative” prior. Here, the Jeffreys’ reference prior is demonstrated for several well known fisheries models, including the Ricker and Beverton-Holt stock-recruit curves; Von-Bertalanffy growth curve; Schaefer surplus production model; and sequential population analysis. Reference priors for relevant derived parameters, including the steepness parameter of the Beverton-Holt stock-recruit curve, are derived. The practical application of these priors is discussed.

Introduction

In the context of fisheries science, Bayesian modeling has been promoted as a methodology for realistically capturing the uncertainties and resulting risks inherent to any fishery (Punt and Hilborn 1997). Fundamental to this is the requirement to specify the information (if any) that exists about unknown parameters prior to collection of the data, and the current popularity of Bayesian models in fisheries owes much to the recognition by fisheries scientists that substantial prior information often does exist. For example, Hilborn and Liermann (1998) show how to use meta-analysis to utilize existing information from studies on related stocks.

In many situations there will, however, be little reliable existing knowledge about some or all unknown model parameters. This could arise simply because of the absence of any related studies. Moreover, when studies on related stocks are available then care must be taken to apply meta-analysis only to those parameters satisfying the underlying assumptions of this approach. Meta-analysis typically requires that the parameters be exchangeable, which in this context requires that the parameter of interest can be reasonably modeled as having a common distribution over all stocks considered. This may be appropriate for parameters such as catchability, natural mortality and recruitment depensation (Hilborn and Liermann 1998), but would not be appropriate for stock-specific parameters such as virgin biomass.

In the absence of prior knowledge it has been common practice to seek an appropriate “non-informative” prior. It is well known that flat priors are not non-informative (in general) and considerable effort has been devoted to obtaining gen-

eral purposes methods for constructing priors that express the state of ignorance. This pursuit has met with mixed success with different axiomatic assumptions leading to different constructions for non-informative priors. For this reason, the viewpoint of Kass and Wasserman (1996) is adopted here — that is, we seek to establish a catalog of default/reference priors for a variety of fisheries models. These priors are not presented as formal expressions of ignorance, but rather, as reference priors that have good properties and that are sensible to use in situations where prior information can not be exploited.

The search for reference priors is also far from clear cut. Kass and Wasserman's (1996) review article gives details on more than a dozen proposed methods for obtaining reference priors, however, they do give special emphasis to the Jeffreys' method and show that several of the other methods produce reference priors similar to Jeffreys'. Jeffreys' method is by far the most widely used approach for obtaining reference priors and has previously been used in Bayesian fisheries modeling (e.g., Hoenig et al. 1994). Here, the Jeffreys' method is employed throughout.

The dominance of Jeffreys' method for specification of priors is largely due to its property of parameterization invariance. That inference should not depend on the particular, possibly arbitrary, choice of model parameterization is generally considered the most fundamental requirement of a reference prior. Jeffreys' method is introduced in the next section, and in the following section is applied to the Ricker and Beverton-Holt stock-recruit curves, the Von-Bertalanffy growth curve, the Schaefer surplus production model, and sequential population analysis.

Jeffreys' Method

Parameterization invariance

The particular form of parameterization used in a model can be somewhat arbitrary, or may be driven by numerical considerations (e.g., Ratkowsky 1986). For example, from Hilborn and Walters (1992) and Quinn and Deriso (1999), the Beverton-Holt stock-recruit curve appears in the following four forms (and a fifth form is considered in the Fisheries models section below)

$$R = \frac{aS}{b+S} \equiv \frac{a^*S}{1+\frac{a^*}{b^*}S} \equiv \frac{\alpha S}{1+\beta S} \equiv \frac{S}{\alpha^*+\beta^*S} .$$

The primary motivation for Jeffreys' method is the desire that inference should not depend on the particular parameterization of the model.

More generally, if a model is expressed in terms of parameters θ , then it can also be expressed in terms of parameters $\zeta = g(\theta)$ where g is any invertible transformation. If a formal rule for obtaining prior distributions is used then there are two legitimate ways to calculate the prior on ζ :

1. Calculate the prior on θ and then apply the transformation of random variables formula (Freund 1992)

$$\pi(\zeta) = \pi(\theta(\zeta)) \left| \det \left(\frac{\partial \theta}{\partial \zeta} \right) \right| \quad (1)$$

where $\frac{\partial \theta}{\partial \zeta}$ is the Jacobian matrix with i, j 'th element $\frac{\partial \theta_i}{\partial \zeta_j}$.

2. Express the likelihood in terms of ζ and apply the formal rule.

Jeffreys' rule is termed parameterization invariant because the two above approaches result in the same prior for ζ .

Jeffreys' prior

Jeffreys (1961) used measure-theoretic concepts to motivate his choice of a parameterization invariant prior. Jeffreys' prior is obtained as the squareroot of the determinant of the information matrix obtained from the likelihood function for the data. That is, denoting the parameters by $\theta = (\theta_1, \theta_2, \dots, \theta_p)$ and the loglikelihood by $l(\theta)$, $I(\theta)$ is the $p \times p$ information matrix with i, j^{th} element

$$I_{ij}(\theta) = E \left[\frac{\partial l(\theta)}{\partial \theta_i} \frac{\partial l(\theta)}{\partial \theta_j} \right] ,$$

and Jeffreys' prior is given by

$$\pi(\theta) \propto \det(I(\theta))^{1/2} . \quad (2)$$

Apriori independence

Jeffreys (1961) noted that (2) should not be applied verbatim in all situations, but rather, could be used to help establish conventions for representation of prior ignorance. One convention that has been justified on several grounds (Jeffreys 1961, Box and Tiao 1973, Kass and Wasserman 1996) is that scale parameters (e.g., variances) be excluded from the parameter vector θ and that (2) be applied separately to θ and the scale parameters. This convention is often justified on the grounds that the scale parameters can be presumed apriori independent from other parameters under the state of prior ignorance. Sun and Berger (1998) provide a

formalization of this notion.

Fisheries models

Jeffreys' prior depends on the likelihood posed for the data and so will depend on the assumed form of the error terms. For example, the Jeffrey's prior on the asymptotic length parameter of a Von-Bertalanffy growth curve will depend on whether the length data are assumed to be normally or lognormally distributed. This is justifiable if one considers that the specification of the error term implicitly provides information about the parameters. For example, a Von-Bertalanffy growth model that puts normal error on the length data is theoretically permitting lengths to be negative, and so it is not unreasonable that a "non-informative" prior would put positive prior probability on asymptotic length being negative. This would not occur with lognormal errors.

In the five models considered below, the data are necessarily non-negative and lognormal error has been assumed throughout. Consequently, separate application of (2) to the standard error of the data gives the familiar reference prior (e.g., Box and Tiao 1973)

$$\pi(\sigma) = 1/\sigma . \quad (3)$$

This is equivalent to $\log(\sigma)$ having a flat prior (from equation (1)).

Here, the "standard" forms of the models have been used. For example, in the stock-recruit models there are the considerations of autocorrelated recruitments and measurement error in estimation of spawners (Ludwig and Walters 1981). These

considerations are not covered here and the number of spawners is treated as a known explanatory variable. In the Schaefer surplus production model there is the consideration of process error (Meyer and Millar 1999), however, here the more traditional observation error only model (Polacheck, Hilborn and Punt 1993) is used. The parameterization invariance of Jeffreys' method ensures that the results do not depend on the particular model parameterizations used below.

1: Ricker stock-recruit curve (a, b)

Model

Let S_t be the spawners at time t and let R_t be the measured number of recruits resulting from spawning at time t . The Ricker stock-recruit model with multiplicative lognormal errors is

$$R_t = aS_t e^{-bS_t} e^{\nu_t} \quad , a > 0, b \geq 0 \quad , \quad (4)$$

where ν_t are independent and identically distributed $N(0, \sigma^2)$ random errors.

Reference prior

$$\pi(a, b) \propto \frac{1}{a} \quad , a > 0, b \geq 0$$

That is, the reference prior for a is uniform on the log scale and for b is uniform on $[0, \infty)$.

2: Beverton-Holt stock-recruit curve (a, b)

Using the same notation as in the previous model, the Beverton-Holt stock-recruit model with multiplicative lognormal errors is

$$R_t = \frac{aS_t}{1 + bS_t} e^{\nu_t} \quad , a > 0, b \geq 0 . \quad (5)$$

Reference prior

$$\pi(a, b) \propto \frac{\text{sd}(y(b))}{a} \quad , a > 0, b \geq 0 ,$$

where $y_t(b) = S_t/(1 + bS_t)$ and $\text{sd}(y(b))$ is the standard deviation of $y_t(b)$, $t = 1, \dots, n$.

Remarks

1. The reference prior for b ,

$$\pi(b) \propto \text{sd}(y(b)) \quad (6)$$

is proper (Appendix). That is, with the appropriate normalizing constant it integrates to unity and corresponds to a proper density function.

2. For the purposes of meta-analysis of stock-recruit relationships, the Beverton-Holt stock-recruit model must be reparameterized in a form which permits a parameter that can reasonably be considered exchangeable over related stocks. This can be done by expressing the model in terms of a (in equation (5)) and a steepness parameter h_ρ (Hilborn and Liermann 1998). Specifically, if S_0 is chosen as some pre-specified virgin number of spawners, then for ρ between zero and unity,

$$h_\rho = \frac{R(\rho S_0)}{R(S_0)} \quad (7)$$

where $R(S) = aS/(1 + bS)$. It is common practice to take $\rho = 0.2$, which gives $h_{0.2}$ the interpretation as the ratio of recruitment at 20% of virgin numbers to recruitment in the virgin state.

It is necessarily the case that $\rho \leq h_\rho \leq 1$. If h_ρ is close to ρ then recruitment decreases in a near linear relationship with spawners (as spawners are reduced in number from S_0 to ρS_0), and if h_ρ is close to unity then recruitment is little reduced by the reduction in spawners.

The reference prior for steepness is obtained from applying the change of variables technique to $\pi(b)$ (Appendix). This gives

$$\pi(h_\rho) = \frac{1 - \rho}{\rho S_0 (1 - h_\rho)^2} \pi(b) \quad , \rho \leq h_\rho < 1 .$$

Example

Equation (6) was applied to the Alaska pink salmon escapement (spawners) values (Fig. 1) from Quinn and Deriso (1999). The reference prior for b (Fig. 2) has a maximum of $\text{sd}(S) = 1.436$ at $b = 0$ (Appendix).

The reference prior for the steepness parameter was calculated for four different specified values of the virgin number of spawners (S_0), 5, 10, 20 and 50 million fish, respectively (Fig. 3). The reference prior puts increasingly high prior probability on low values of steepness (corresponding to a greater decrease in recruitment due to a reduction in spawners) as S_0 decreases.

3: Von-Bertalanffy growth curve (L_∞, k, t_0)

Model

Let L_a be the observed length of an age a fish, modeled using the Von-Bertalanffy growth model with multiplicative lognormal errors:

$$L_a = L_\infty \left(1 - e^{-k(a-t_0)}\right) e^{\nu_a} \quad , L_\infty > 0, k > 0, t_0 > \min(a) \quad , \quad (8)$$

where L_∞ is asymptotic length, k is the growth rate, t_0 is the time at which expected length is zero, and ν_a are independent and identically distributed $N(0, \sigma^2)$ random errors.

Reference prior

The reference prior $\pi(L_\infty, k, t_0)$ can not be written in a compact form because of the summations in the terms of the information matrix (Appendix). However, it can be written in the form

$$\pi(L_\infty, k, t_0) \propto \frac{1}{L_\infty} \pi(k, t_0) \quad , L_\infty > 0, k > 0, t_0 > \min(a) \quad . \quad (9)$$

That is, the reference prior for L_∞ is uniform on the log scale and is independent of the joint reference prior for k and t_0 .

Example

The reference prior $\pi(k, t_0)$ from equation (9) was calculated for the rougheye rockfish age values from Quinn and Deriso (1999). The prior density increases as k decreases or t_0 increases (Fig. 4).

Quinn and Deriso (1999) assumed additive normal errors in their fit of the Von Bertalanffy growth curve to these data. By analagous calculations to those shown in the Appendix, this model also results in prior independence of L_∞ and (k, t_0) ,

but with $\pi(L_\infty) \propto L_\infty^2$. Also, $\pi(k, t_0)$ increases with increasing t_0 , but is unimodal in k (Fig. 4).

4: Schaefer surplus production model (Q, K, r)

Hoenig et al. (1994) used the equilibrium Schaefer surplus production model and calculated the Jeffrey's prior for the parameter corresponding to optimal effort. Hilborn and Walters (1992) and Polacheck et al. (1993) demonstrate serious inadequacies with the equilibrium model and recommend use of the observation error version of the dynamic surplus production model, and this model is presented below.

Model

Letting B_y denote the biomass at the start of year y , and C_y the catch in year y . The dynamic Schaefer surplus production model gives the biomass in year y according to the equation

$$B_y = B_{y-1} + rB_{y-1} \left(1 - \frac{B_{y-1}}{K}\right) - C_{y-1} \quad , r > 0, K > 0 \quad , \quad (10)$$

where K is carrying capacity and r is the productivity parameter. B_0 is the biomass at the start of the fishery and it is usual to set $B_0 = K$, and this will be assumed here.

It is assumed that a relative biomass index, I_y , measured with multiplicative lognormal error, is observed each year. That is,

$$I_y = QB_y e^{\nu_y} \quad Q > 0 \quad , \quad (11)$$

where ν_y are independent and identically distributed $N(0, \sigma^2)$ random errors.

Reference prior

The elements of $I(r, K, Q)$ can not be written in closed form because of the recursive definition of the sequence of biomasses. However, it can be shown (Appendix) that the resulting reference prior can be written in the form

$$\pi(r, K, Q) \propto \frac{1}{Q} \pi(r, K) \quad , Q > 0, r > 0, K > 0 .$$

That is, the reference prior for Q is uniform on the log scale and is independent of the joint reference prior for r and K .

Example

The reference prior $\pi(r, K)$ was calculated for the catch values of the South Atlantic albacore tuna used in Polacheck et al. (1993) and Meyer and Millar (1999). The prior density increases with decreasing values of K and r (Fig. 5).

5: Sequential population analysis ($Q_{a_0}, \dots, Q_A, m$)

There are many variants of sequential population analysis depending on the nature of the fishery and the data that are available. Here, it will be assumed that instantaneous natural mortality and fishing mortality can reasonably be taken as constant throughout each year and that a relative index of numbers-at-age, I , is available.

Model

Let $N_{a,t}$ be the number of age a fish at time t , and let $F_{a,t}$ denote the instantaneous fishing mortality applied to these fish. Numbers-at-age are modeled as

$$N_{a,t} = N_{a-1,t-1} e^{-(m+F_{a-1,t-1})} \quad , m > 0 ,$$

and the statistical model for the data is

$$I_{a,t} = Q_a N_{a,t} e^{\nu_{a,t}} \quad , Q_a > 0 \quad (12)$$

where Q_a is the catchability of age a fish and $\nu_{a,t}$ are independent and identically distributed $N(0, \sigma^2)$ random errors.

Reference prior

If a_0 is age of recruitment and A is maximum age, then the reference prior for $Q_{a_0}, \dots, Q_A$ and m is (Appendix)

$$\pi(Q_{a_0}, \dots, Q_A, m) \propto \prod_{a=a_0}^A \frac{1}{Q_a} \quad , Q_a > 0, m > 0 \quad .$$

That is, the reference priors for the catchabilities are independent and uniform on the log scale and are independent of the reference prior for instantaneous mortality which is uniform on $(0, \infty)$. Consequently, the reference prior on natural annual survival $s = e^{-m}$ is $\pi(s) = 1/s$, $0 < s < 1$.

Comments

The derivation (Appendix) of the above reference prior made the assumption that recruitments were not functionally related to instantaneous mortality. This would be true in models which allow recruitments to be freely estimated, however, it would not be the case in models which use a spawner-recruit relationship because recruitment then depends on number of spawners which in turn depends on m .

Discussion

Reference priors have been used in the existing Bayesian fisheries literature, but only in the simplest of cases. These include the use of (3) for standard deviations and for the catchability coefficient Q (i.e., $\pi(Q) = 1/Q$) when the catch data are modeled as lognormal (McAllister, Pikitch, Punt and Hilborn 1994, Walters and Ludwig 1994, Punt, Butterworth and Penney 1995, Millar and Meyer 2000). This present work demonstrates the applicability of such priors to several standard multiparameter models.

Such reference priors should be utilized even in situations where there is prior information about the parameter(s). The elicitation and quantification of existing prior information is far from being an unequivocal practice and in particular it could be highly contentious regarding the selection of related stocks that can be considered exchangeable with respect to the chosen parameters. Also, if few related stocks are available then the prior obtained could be sensitive to the hyperpriors. Thus, sensitivity to the prior obtained from the meta-analysis should be examined, and in this endeavour the reference prior would be a natural alternative prior to use.

Reference priors calculated using Jeffreys' method can be both algebraically complex and improper. This could be problematic for some Bayesian software packages. For example, the symbolic BUGS software (Spiegelhalter, Thomas, Best and Gilks 1996) requires customized programming to use improper priors and may fail to compile if the prior is too complicated. Complex priors would be more reliably implemented in software which requires explicit algebraic expression of the prior and

data likelihood terms.

Algebraic complexity of Jeffreys' method will become a restrictive factor in many practical applications of fisheries models. A single fisheries model may require simultaneous inference about a multitude of parameters such as those arising in the stock-recruit curve, growth curve, and in specification of age-specific fishing mortalities for several gears. It would be a formidable task to determine the joint reference prior for so many unknowns. In such cases it may be reasonable to assume prior independence of particular subsets of parameters, and apply Jeffreys' method separately to each.

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Appendix

The derivation of the reference prior for the Ricker stock recruit curve model is presented in considerable detail. Only brief detail is provided for the other models.

1: Ricker stock-recruit curve (a, b)

Taking the log of (4) gives

$$r_t = \log(R_t) = \log(a) + \log(S_t) - bS_t + \nu_t$$

and the contribution to the loglikelihood from the data value R_t is therefore

$$l_t(a, b, \sigma) = \frac{1}{2} \log(2\pi\sigma^2) - \frac{(r_t - \log(a) - \log(S_t) + bS_t)^2}{2\sigma^2} .$$

Using the aprior independence form of Jeffreys' method we can remove σ from the likelihood, giving (to within a constant of proportionality)

$$l_t(a, b) = -(r_t - \log(a) - \log(S_t) + bS_t)^2 .$$

Thus,

$$\begin{aligned} \frac{\partial l_t}{\partial a} &= \frac{2}{a} (r_t - \log(a) - \log(S_t) + bS_t) = \frac{2}{a} \nu_t \\ \frac{\partial l_t}{\partial b} &= -S_t (r_t - \log(a) - \log(S_t) + bS_t) = -S_t \nu_t . \end{aligned}$$

Hence,

$$\frac{\partial l_t}{\partial a} \frac{\partial l_t}{\partial a} = \frac{4}{a^2} \nu_t^2 , \quad \frac{\partial l_t}{\partial b} \frac{\partial l_t}{\partial b} = S_t^2 \nu_t^2 , \quad \text{and} \quad \frac{\partial l_t}{\partial a} \frac{\partial l_t}{\partial b} = \frac{\partial l_t}{\partial b} \frac{\partial l_t}{\partial a} = \frac{-2S_t}{a} \nu_t^2 . \quad (13)$$

The expected value of ν_t^2 is σ^2 , giving

$$E \left[\frac{\partial l_t}{\partial a} \frac{\partial l_t}{\partial a} \right] = \frac{4}{a^2} \sigma^2 , \quad E \left[\frac{\partial l_t}{\partial b} \frac{\partial l_t}{\partial b} \right] = S_t^2 \sigma^2 , \quad (14)$$

$$\text{and } E \left[\frac{\partial l_t}{\partial a} \frac{\partial l_t}{\partial b} \right] = E \left[\frac{\partial l_t}{\partial b} \frac{\partial l_t}{\partial a} \right] = \frac{-2S_t}{a} \sigma^2 . \quad (15)$$

Using the fact that the information matrix for a data set with n independent observations is the sum of the information matrices calculated for each individual observation (Azzalini 1996), we have

$$I(a, b) = \sigma^2 \begin{pmatrix} \frac{4n}{a^2} & -\frac{2}{a} \sum_t S_t \\ -\frac{2}{a} \sum_t S_t & \sum_t S_t^2 \end{pmatrix} \quad (16)$$

and the determinant of this matrix is

$$\begin{aligned} \det(I(a, b)) &= \frac{4\sigma^4}{a^2} \left(n \sum_t S_t^2 - \left[\sum_t S_t \right]^2 \right) \\ &= \frac{4\sigma^4}{a^2} \sum_t (S_t - \bar{S})^2 \end{aligned}$$

where $\bar{S}$ is the average of the $S_t, t = 1, \dots, n$. Thus, the reference prior for a and b is

$$\pi(a, b) \propto \det(I(a, b))^{1/2} \propto \left(\frac{1}{a^2} \right)^{1/2} = \frac{1}{a} . \quad (17)$$

2: Beverton-Holt stock-recruit curve (a, b)

Taking the log of (5) gives

$$r_t = \log(R_t) = \log(a) + \log(S_t) - \log(1 + bS_t) + \nu_t$$

and the contribution to the loglikelihood from the data value R_t is therefore

$$l_t(a, b) \propto -(r_t - \log(a) - \log(S_t) + \log(1 + bS_t))^2 .$$

Thus,

$$\begin{aligned} \frac{\partial l_t}{\partial a} &\propto \frac{1}{a}(r_t - \log(a) - \log(S_t) + \log(1 + bS_t)) = \frac{1}{a}\nu_t \\ \frac{\partial l_t}{\partial b} &= -\frac{S_t}{1 + bS_t}(r_t - \log(a) - \log(S_t) + \log(1 + bS_t)) = -\frac{S_t}{1 + bS_t}\nu_t . \end{aligned}$$

Hence,

$$I(a, b) \propto \begin{pmatrix} \frac{n}{a^2} & -\frac{1}{a} \sum_t \frac{S_t}{1+bS_t} \\ -\frac{1}{a} \sum_t \frac{S_t}{1+bS_t} & \sum_t \left(\frac{S_t}{1+bS_t} \right)^2 \end{pmatrix} . \quad (18)$$

Denoting $y_t(b) = S_t/(1 + bS_t)$, the determinant of $I(a, b)$ is

$$\begin{aligned} \det(I(a, b)) &= \frac{1}{a^2} \left(n \sum_t y_t^2(b) - \left[\sum_t y_t(b) \right]^2 \right) \\ &= \frac{n}{a^2} \sum_t (y_t(b) - \bar{y}(b))^2 \propto \frac{\text{Var}(y(b))}{a^2} \end{aligned}$$

where $y_t(b) = S_t/(1 + bS_t)$ and $\bar{y}(b)$ is the average of the $y_t(b), t = 1, \dots, n$. Thus,

the reference prior for a and b is

$$\pi(a, b) \propto \det(I(a, b))^{1/2} \propto \frac{\text{sd}(y(b))}{a} . \quad (19)$$

Remarks:

1. The reference prior $\pi(b) = \text{sd}(y(b))$ is proper, that is, is integrable with respect to b . This is established by using the following two inequalities:

(i) $\text{sd}(y(b)) \leq \text{sd}(S)$, and

(ii) $\text{sd}(y(b)) \leq \frac{c}{b^2}$ for some constant c .

The first inequality is established by virtue of the fact that, for any i and j and all $b > 0$, $|y_i(b) - y_j(b)| < |S_i - S_j|$. The second inequality is established by noting that

$$\text{sd}(y(b)) = \frac{1}{b} \text{sd} \left(\frac{1}{1 + bS} \right) .$$

2. To obtain the prior on the steepness parameter, write equation (7) as

$$h_\rho = 1 - \frac{1 - \rho}{1 + \rho b S_0} .$$

The inverse of this is

$$b = \frac{h_\rho - \rho}{\rho S_0 (1 - h_\rho)} ,$$

which has derivative

$$\frac{\partial b}{\partial h_\rho} = \frac{1 - \rho}{\rho S_0 (1 - h_\rho)^2} .$$

3: Von-Bertalanffy growth curve (L_∞, k, t_0)

Letting a_i denote the age of the i^{th} fish in the sample, taking the log of (8) gives

$$\log(L_{a_i}) = \log(L_\infty) + \log\left(1 - e^{-k(a_i - t_0)}\right) + \nu_i$$

and the contribution to the loglikelihood from the data value L_{a_i} is therefore

$$l_i(L_\infty, k, t_0) \propto -(\log(L_{a_i}) - \log(L_\infty) - \log(1 - e^{-k(a_i - t_0)}))^2$$

Thus,

$$\begin{aligned} \frac{\partial l_{a_i}}{\partial L_\infty} &\propto \frac{1}{L_\infty} \nu_i \\ \frac{\partial l_{a_i}}{\partial k} &= \frac{(a_i - t_0)e^{-k(a_i - t_0)}}{1 - e^{-k(a_i - t_0)}} \nu_i \\ \frac{\partial l_{a_i}}{\partial t_0} &= -\frac{ke^{-k(a_i - t_0)}}{1 - e^{-k(a_i - t_0)}} \nu_i . \end{aligned}$$

Hence,

$$I(L_\infty, k, t_0) \propto \begin{pmatrix} \frac{n}{L_\infty^2} & \frac{1}{L_\infty} \sum_i \frac{\delta_i e^{-k\delta_i}}{1 - e^{-k\delta_i}} & -\frac{k}{L_\infty} \sum_i \frac{e^{-k\delta_i}}{1 - e^{-k\delta_i}} \\ \frac{1}{L_\infty} \sum_i \frac{\delta_i e^{-k\delta_i}}{1 - e^{-k\delta_i}} & \sum_i \left[\frac{\delta_i e^{-k\delta_i}}{1 - e^{-k\delta_i}} \right]^2 & -k \sum_i \delta_i \left[\frac{e^{-k\delta_i}}{1 - e^{-k\delta_i}} \right]^2 \\ -\frac{k}{L_\infty} \sum_i \frac{e^{-k\delta_i}}{1 - e^{-k\delta_i}} & -k \sum_i \delta_i \left[\frac{e^{-k\delta_i}}{1 - e^{-k\delta_i}} \right]^2 & k^2 \sum_i \left[\frac{e^{-k\delta_i}}{1 - e^{-k\delta_i}} \right]^2 \end{pmatrix} , \quad (20)$$

where $\delta_i = a_i - t_0$.

The determinant of $I(L_\infty, k, t_0)$ can be calculated by many familiar software packages, or directly using the formula for the determinant of 3 by 3 matrices (e.g., p. 150 of Jacob 1990). From this formula it can be noted that L_∞ appears in the determinant only as a multiplicative constant.

4: Schaefer surplus production model (Q, K, r)

Taking the log of equation (11) gives

$$i_y = \log(I_y) = \log(Q) + \log(B_y) + \nu_y \quad .$$

The contribution to the loglikelihood from the data value I_y is therefore

$$l_y \propto -(i_y - \log(Q) - \log(B_y))^2 / .$$

Thus, letting $k = 1/K$,

$$\begin{aligned} \frac{\partial l_y}{\partial Q} &\propto \frac{1}{Q} \nu_y \\ \frac{\partial l_y}{\partial r} &= \frac{\partial l_y}{\partial B_y} \frac{\partial B_y}{\partial r} = \frac{1}{B_y} \frac{\partial B_y}{\partial r} \nu_y \\ \frac{\partial l_y}{\partial K} &= \frac{\partial l_y}{\partial k} \frac{\partial k}{\partial K} = \frac{\partial l_y}{\partial B_y} \frac{\partial B_y}{\partial k} \frac{-1}{K^2} = \frac{-1}{K^2 B_y} \frac{\partial B_y}{\partial k} \nu_y \quad . \end{aligned}$$

The above derivatives of B_y are obtained from the recursive surplus production equation (10), which can be denoted $B_y = g(B_{y-1}, r, K)$. Then,

$$\frac{\partial B_y}{\partial r} = \frac{\partial g(B_{y-1}, r, K)}{\partial r} = \frac{\partial g(B, r, K)}{\partial B} \frac{\partial B}{\partial r} \Big|_{B_{y-1}, r, K} + \frac{\partial g(B, r, K)}{\partial r} \Big|_{B_{y-1}, r, K} \quad ,$$

and similarly for $\frac{\partial B_y}{\partial k}$. The partial derivatives of g are

$$\begin{aligned} \frac{\partial g(B, r, K)}{\partial B} &= 1 + r - 2rkB \\ \frac{\partial g(B, r, K)}{\partial r} &= B(1 - kB) \\ \frac{\partial g(B, r, K)}{\partial k} &= -rB^2 \quad . \end{aligned}$$

5: Sequential population analysis (natural mortality, m)

Taking the log of equation (12) gives

$$\log(I_{a,t}) = \log(Q_a) + n_{a,t} + \nu_{a,t}$$

where $n_{a,t} = \log(N_{a,t})$. The contribution to the loglikelihood from the data value $I_{a,t}$ is therefore

$$l_{a,t} \propto -(\log(I_{a,t}) - \log(Q_a) - n_{a,t})^2 \ .$$

With a_0 denoting the age of recruitment,

$$\begin{aligned} n_{a,t} &= n_{a-1,t-1} - m - F_{a-1,t-1} \\ &= n_{a_0,t-(a-a_0)} - (a - a_0)m - \sum_{i=1}^{a-a_0} F_{a-i,t-i} \\ &= r_{t-(a-a_0)} - (a - a_0)m - \sum_{i=1}^{a-a_0} F_{a-i,t-i} \end{aligned}$$

where r_t is the log-recruitment of age a_0 fish at time t . Assuming that recruitment is independent of m , differentiation of the loglikelihood gives

$$\frac{\partial l_{a,t}}{\partial Q_\alpha} \propto \begin{cases} \frac{1}{Q_a} \nu_{a,t} & , a = \alpha \\ 0 & , a \neq \alpha \end{cases}$$

and

$$\frac{\partial l_{a,t}}{\partial m} \propto -(a - a_0) \nu_{a,t} \ .$$

The derivative of the loglikelihood with respect to m is a constant that does not involve any parameters, and it follows that

$$\det(I(Q, m))^{1/2} \propto \left(\prod_{a=a_0}^A \frac{1}{Q_a^2} \right)^{1/2} = \prod_{a=a_0}^A \frac{1}{Q_a} \ .$$

Figures

Fig 1: Alaska pink salmon escapement (spawners) and recruitment data from p. 105 of Quinn and Deriso (1999).

Fig 2: Reference prior for parameter b of the Beverton-Holt stock-recruit model, calculated for the spawner data of Figure 1.

Fig 3: Reference prior for the steepness parameter of the Beverton-Holt stock-recruit model, calculated for the spawner data of Figure 1 for various S_0 values.

Fig 4: Joint reference prior for parameters k and t_0 of the Von-Bertalanffy growth curve, calculated for the age data from p. 136 of Quinn and Deriso (1999). Top plot is for multiplicative lognormal errors. Lower plot is for additive normal errors.

Fig 5: Joint reference prior for parameters K and r of the Schaeffer surplus production model, calculated for the tuna catch data of Meyer and Millar (1999).









