

Incorporating Allee effects in fish stock–recruitment models and applications for determining reference points

D.G. Chen, J.R. Irvine, and A.J. Cass

Abstract: A new type of stock–recruitment model is examined that incorporates Allee effects, which may occur when fish populations are small. The model is a natural extension of traditional models, which only incorporate the negative effects of increasing density on fecundity and (or) survival. Because the new model is intrinsically nonlinear and because of convergence problems at local optima, we use a maximum likelihood approach with a global genetic search algorithm to estimate model parameters. Parameter uncertainty is obtained from the inverse of the Fisher information matrix. Based on this new model, an extinction probability curve is developed using the parameter defining the Allee effects. This curve can readily be used to calculate the theoretical probability of extinction for a single brood line in one generation for any particular spawner number or biomass. Alternatively, because managers may wish to assign reference points corresponding to particular extinction probabilities, spawner numbers can be determined for these reference points. Two Pacific salmon populations, North Thompson coho (*Oncorhynchus kisutch*) and Chilko sockeye (*O. nerka*), are used to demonstrate the approach. It is found that the Allee effect parameter is statistically significant for the Thompson coho, but not for Chilko sockeye.

Résumé : Nous examinons un nouveau modèle de stock–recrutement qui incorpore les effets Allee qui peuvent se manifester lorsque les densités de populations de poissons sont faibles. Le modèle est une extension naturelle des modèles courants qui ne tiennent compte des effets négatifs sur la fécondité et (ou) la survie que dans le cas de densités croissantes. Cependant, puisque le nouveau modèle est essentiellement non linéaire et qu'il y a des problèmes de convergence aux optimums locaux, nous adoptons, pour estimer les paramètres du modèle, une approche basée sur la vraisemblance maximale et utilisons un algorithme de recherche génétique global. L'incertitude des paramètres a été obtenue à partir de l'inverse de la matrice d'information de Fisher. Le nouveau modèle permet d'établir une courbe de probabilité d'extinction à l'aide du paramètre qui décrit les effets Allee. La courbe peut servir à calculer facilement la probabilité théorique d'extinction pour une seule lignée dans une génération, pour toute densité ou biomasse de reproducteurs. D'autre part, parce que les gestionnaires peuvent vouloir déterminer des points de référence correspondant aux diverses probabilités d'extinction, il est possible de déterminer des densités de reproducteurs pour ces points de référence. Deux populations de saumons du Pacifique, les saumons coho (*Oncorhynchus kisutch*) de la North Thompson et les saumons rouges (*O. nerka*) de la Chilko, servent à illustrer le fonctionnement de la méthode. Le paramètre décrivant l'effet Allee est significatif chez les Saumons coho de la Thompson, mais pas pour les Saumons rouges de la Chilko.

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Introduction

The analysis of fish stock–recruitment (S – R) is often the first step to evaluate and implement fishery policies designed to optimize spawner numbers and exploitation rates. The

analysis typically begins with the assumption of a functional relationship, denoted by $F(\cdot)$, between spawners and recruits:

$$(1) \quad R_t = S_t F(S_t, \theta)$$

where S_t is the spawners at year t , $t = 1$ to n , and R_t is the corresponding recruits for the spawners at that brood year t calculated as total escapements and catches. θ is a vector of parameters associated with this relationship and may be associated with a fishery management policy.

The two most commonly used functional forms based on biologically and statistically sound grounds are the Beverton–Holt model (Beverton and Holt 1957) and the Ricker model (Ricker 1975):

$$(2) \quad R_t = \frac{\alpha S_t}{1 + \beta S_t} \quad (\text{Beverton–Holt model})$$

$$(3) \quad R_t = S_t e^{\alpha - \beta S_t} \quad (\text{Ricker model})$$

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where a and b are the parameters to describe productivity of the population at low density and capacity limited by density dependence, respectively. As a unified S - R model, Deriso (1980) introduced an additional shape parameter γ and proposed the following model:

$$(4) \quad R_t = \alpha S_t (1 - \gamma \beta S_t)^{1/\gamma} \quad (\text{Deriso model})$$

where γ is a shape parameter to modify the S - R relationship. It can be seen that the Beverton-Holt model (2) and Ricker model (3) are in fact special cases of the Deriso model (4) when $\gamma = -1$ and $\gamma \rightarrow 0$, respectively.

These models allow for compensatory mortality. At high population densities, resources will become limiting and recruits per spawner will decrease. However, the models ignore depensatory population dynamics, which may occur when the population is small. This is known as the Allee effect (Allee et al. 1949) when population growth declines as population density declines. A variety of processes can result in depensation at low abundance. Inbreeding may occur, spawning fish may not find mates, higher mortality may result from predator saturation or fishing, and poor conditioning of the spawning environment and low efficiency of food location may result (Asmussen 1979; Emlen 1984; Hilborn and Walters 1992). When abundances are low, depensation (if it exists) will accelerate population declines and increase their probability of extinction (McElhany et al. 2000). With the depensatory effects, the stock rebuilding could be delayed or prevented (Walters and Kitchell 2001).

Whether depensation is a significant factor for fish populations is not clear. Myers et al. (1995) found that three of 26 fish stocks had lower than expected recruits per spawner at low densities than would be expected using a Beverton-Holt model. Liermann and Hilborn (1997) examined the same data and found that the most likely values for the stock-recruit relationship were usually close to or within the range of no depensation. However, because there was a significant amount of uncertainty about whether depensation existed, Liermann and Hilborn (1997) concluded that analyses of stock-recruitment data should incorporate spawner-recruit curves that allow for the possibility of depensation.

Several approaches have been used to incorporate possible depensatory effects in the analysis of stock-recruit data. Hilborn and Walters (1992) and Routledge and Irvine (1999) show how to modify the S - R curve to incorporate a depensatory parameter. Hilborn and Walters (1992) recommended replacing αS with αS^m where the power parameter m is greater than 1.0. Routledge and Irvine (1999) introduced a cutoff value c to allow for the effects of possible depensation at low abundance and modified their formulas when $S \leq c$. Myers et al. (1995), in a meta-analysis of 129 fish stocks, found little statistical evidence for widespread depensation. Liermann and Hilborn (1997) used a Bayesian hierarchical model to calculate the prior distribution for the depensatory parameter. They concluded that the broad tails of distributions for various taxa extend into the depensatory range and suggested that the possibility of depensation should be considered in the population dynamics of fishes.

In the discussion of compensatory population dynamics within a stock complex, Frank and Brickman (2000) were the first to introduce a S - R model that incorporated Allee effects by permitting a non-zero intercept representing recruit-

ment failure. They concluded from simulation experiments that aggregated populations could obscure detection of Allee effects. Incorporating depensation, the S - R model in eq. 1 becomes

$$(5) \quad R_t = (S_t - S_{\text{offset}}) F(S_t - S_{\text{offset}}, \theta)$$

where S_{offset} is the parameter associated with the Allee effects and is the offset from the origin representing zero recruitment (Frank and Brickman 2000). Hereafter model 5 (eq. 5) will be called Allee S - R model. For the S - R models 2-4, the corresponding Allee S - R models would be

$$(6) \quad R_t = \frac{\alpha(S_t - S_{\text{offset}})}{1 + \beta(S_t - S_{\text{offset}})}$$

$$(7) \quad R_t = (S_t - S_{\text{offset}}) e^{\alpha - \beta(S_t - S_{\text{offset}})}$$

$$(8) \quad R_t = \alpha(S_t - S_{\text{offset}}) [1 - \gamma \beta(S_t - S_{\text{offset}})]^{1/\gamma}$$

In this paper, we apply a maximum likelihood estimation (MLE) approach to estimate S - R parameters using a global search algorithm. We discuss the properties of the parameter S_{offset} associated with Allee effects in the new model, apply it and develop an operational extinction probability curve for a single brood line in one generation, and use this approach to quantify reference points in the domain of risk analysis. The methodology is applied using S - R data from North Thompson coho salmon (*Oncorhynchus kisutch*) and Chilko River sockeye salmon (*O. nerka*).

Parameter estimation and global genetic search algorithm

For the purpose of illustration, we shall use model 7, hereafter referred to as the Allee-Ricker model, to illustrate the development of the new model, the estimation of parameters, and also the development of an extinction probability curve and reference points. The same procedures can be readily applied for models 6 and 8, or any extensions of these.

Parameter estimation

To be compatible with the traditional assumptions for the S - R analyses, we assume that recruitment is log-normally distributed. Therefore, model 7 is

$$(9) \quad \ln(R_t) = \ln(S_t - S_{\text{offset}}) + \alpha - \beta(S_t - S_{\text{offset}}) + \varepsilon_t$$

where $\varepsilon_t \sim N(0, \sigma^2)$. The commonly used linear regression estimation approach cannot be used because the new model (eq. 9) is nonlinear for the parameters (S_{offset} , α , β). We therefore utilize theories of nonlinear regression (e.g., Draper and Smith 1981) and MLE (e.g., Kalbfleisch 1985) to estimate model parameters and associated statistical inferences for the parameters and model.

The log-likelihood function for model 9 is defined as

$$(10) \quad \ln L(S_{\text{offset}}, \alpha, \beta | \text{data}) \propto -\frac{n}{2} \ln(\sigma^2) - \frac{\sum_{i=1}^n [\ln(R_i) - \ln(S_i - S_{\text{offset}}) - \alpha + \beta(S_i - S_{\text{offset}})]^2}{2\sigma^2}$$

Conventionally, twice the negative log likelihood is used as the “inference function” in the MLE, which is $l(S_{\text{offset}}, \alpha, \beta) = -2\ln[L(S_{\text{offset}}, \alpha, \beta|\text{data})]$. According to the theory of MLE, $l(S_{\text{offset}}, \alpha, \beta)$ is asymptotically chi-square distributed by the degrees of freedom $n - 3$, i.e., $l(S_{\text{offset}}, \alpha, \beta) \sim \chi_{n-3}^2$. Estimates of the parameters $\hat{\Theta} = (\hat{S}_{\text{offset}}, \hat{\alpha}, \hat{\beta})$ are obtained by minimizing $l(S_{\text{offset}}, \alpha, \beta)$. The uncertainty in $\hat{\Theta} = (\hat{S}_{\text{offset}}, \hat{\alpha}, \hat{\beta})$ is assessed from the estimated covariance matrix, which is obtained from the inverse of the Fisher information matrix defined as

$$(11) \quad \text{Cov}(\hat{S}_{\text{offset}}, \hat{\alpha}, \hat{\beta}) = -\frac{1}{2} E \begin{pmatrix} \frac{\partial^2 l}{\partial S_{\text{offset}}^2}, & \frac{\partial^2 l}{\partial S_{\text{offset}} \partial \alpha}, & \frac{\partial^2 l}{\partial S_{\text{offset}} \partial \beta} \\ \frac{\partial^2 l}{\partial \alpha \partial S_{\text{offset}}}, & \frac{\partial^2 l}{\partial \alpha^2}, & \frac{\partial^2 l}{\partial \alpha \partial \beta} \\ \frac{\partial^2 l}{\partial \beta \partial S_{\text{offset}}}, & \frac{\partial^2 l}{\partial \beta \partial \alpha}, & \frac{\partial^2 l}{\partial \beta^2} \end{pmatrix}$$

The estimated standard error for each parameter can be obtained from the corresponding elements from eq. 11. According to theory of MLE, the parameter estimates \hat{a} , \hat{b} , and \hat{S}_{offset} in eqs. 9 and 10 are asymptotically normally distributed (Mood et al. 1974, p. 359) as

$$(12) \quad \hat{a} \sim N(a, \sigma_a^2), \quad \hat{b} \sim N(b, \sigma_b^2), \\ \text{and } \hat{S}_{\text{offset}} \sim N(S_{\text{offset}}, \sigma_{S_{\text{offset}}}^2)$$

Special attention is paid to the parameter \hat{S}_{offset} because this parameter represents the number of spawners that will theoretically produce zero recruitment. As abundance decreases, there is an increasing probability of extinction. By definition, if the spawning biomass were below \hat{S}_{offset} , this brood line would have a high probability of going extinct. Therefore, for a specific population with maximum life span K years, if the spawning biomass were below \hat{S}_{offset} for K years, this population would have a high probability of extinction.

We wish to evaluate whether including the Allee parameter \hat{S}_{offset} improves the model fit from model 7 relative to the traditional Ricker model 3. Because models 3 and 7 are nested, the likelihood ratio test can be used to test whether the inclusion of \hat{S}_{offset} significantly improves the model fit:

$$(13) \quad l(\alpha, \beta) - l(S_{\text{offset}}, \alpha, \beta) \sim \chi_1^2$$

where $l(\alpha, \beta)$ and $l(S_{\text{offset}}, \alpha, \beta)$ are twice the negative log-likelihood function from models 3 and 7, respectively.

Global genetic search algorithm

The parameter estimates can be obtained from eq. 10 by any of various search algorithms, including gradient and hill-climbing search methods. These search algorithms are known as local search algorithms where the initial starting points are essential. We found that there is more than one local optima for the minimization of eq. 10, depending on the choice of starting points. The global genetic search algorithm (GA) was used to avoid convergence on local optima, often problematic when using classical hill-climbing techniques that require initial starting values. Genetic algorithms designed to find global optima originated from studies of the mechanics of natural selection and genetics with natural

populations evolving according to the principles of “survival of the fittest” (Holland 1975). The highly fit individuals are given high opportunities to “reproduce”, by “crossing-over” with others in the population. GA differs from conventional search techniques in that it considers many points in the search space simultaneously and therefore has a reduced chance of converging to some local optimum. Since Holland (1975) introduced and investigated this algorithm, the approach has been used in many areas, such as in curve fitting, mathematical optimization, and training neural network models. Recent descriptions of the approach with applications to fisheries are found in Saila (1996) and Chen et al. (2000).

To use the GA in this paper, we specify a large but reasonable range for each parameter in $\theta = (S_{\text{offset}}, \alpha, \beta)$ and randomly generate an initial population with 100 starting points. Based on the fundamental “genetic” operators as reproduction, crossover, and mutation, 10% of the best solutions among the 100 are reproduced. By analogy with a biological genetic system where mutations are rare, a higher probability is given to the crossover process than to the mutation process. Therefore, we chose an 80% probability for crossover processes and a 5% probability for mutation processes; convergence was achieved at these levels. This provides a “crossover” mechanism for the search to mix and match desirable qualities through a random process with the occasional “mutation” of a value at a particular search position.

Definition of an extinction probability curve for a single brood line

Spawner numbers or biomass is the most readily available and also the most commonly used quantity in fisheries research and management. Clearly we would like to manage stocks above the parameter S_{offset} with known probability. The extinction probability function of the stock for a single brood line in one generation can be defined as $\text{Pr}(\text{Stock Extinction}) = \text{Pr}(S \leq S_{\text{offset}})$. Because S_{offset} can be estimated from the MLE (eq. 10) with the distribution in eq. 11, the operational definition of the extinction probability (denoted by $\text{OPr}(\text{EP})$) is

$$(14) \quad \text{OPr}(\text{EP}) = \text{Pr}(S \leq \hat{S}_{\text{offset}}) = \text{Pr}(\hat{S}_{\text{offset}} > S) = 1 - \Phi\left(\frac{\hat{S}_{\text{offset}} - S}{\sigma_{S_{\text{offset}}}}\right)$$

for any level of spawner numbers or biomass S . In eq. 14, $\Phi(\cdot)$ is the cumulative density function for the standard normal distribution. Because $\sigma_{S_{\text{offset}}}$ in eq. 14 is generally unknown, then the MLE estimate from eq. 11 can be used to give an estimate of $\text{OPr}(\text{EP})$:

$$(15) \quad \widehat{\text{OPr}(\text{EP})} = \text{Pr}(\hat{S}_{\text{offset}} > S) = 1 - T\left(\frac{\hat{S}_{\text{offset}} - S}{\hat{\sigma}_{S_{\text{offset}}}}\right)$$

where $T(\cdot)$ is the cumulative density function for the t distribution with degrees of freedom $n - 3$.

The operational definition of extinction probability (eq. 15) can be used to calculate the probability of extinction for one brood line for any given spawner number or biomass S_j . It can also be used to obtain reference points for a given

extinction probability that is based on an acceptable level of extinction risk.

Data applications

North Thompson coho

Identification of reference points and extinction probabilities at low spawner numbers are needed for coho salmon from the Thompson River watershed in central British Columbia. Numbers of coho salmon returning to the Thompson River have declined significantly in recent years and these fish have been the focus of much attention (Bradford and Irvine 2000). Precise estimates of spawner numbers are available for North Thompson coho commencing in 1975, and annual recruitment (catch plus spawners) was estimated using a time series of fishery exploitation rates (Irvine et al. 2001):

$$(16) \quad R_t = S_t / (1 - \exp(-l_t)) R_t = S_t / (1 - \exp(-l_t))$$

where all spawners were assumed to be 3 years old, and $\exp(-l_t)$ is the fishery exploitation rate (catch/(catch + spawners)) in year t .

We first fit the Ricker model (eq. 3) to S - R data for North Thompson coho by a simple regression approach and then fit the same S - R data with the Allee-Ricker S - R model (eq. 9) by the MLE with the GA approach (Fig. 1). The GA search algorithm with 100 sets of initial points in the search space is illustrated in Fig. 2. It can be seen from Fig. 2 that convergence is achieved after ~60 generations (generation is a term used in GA, which is equivalent to "iterations" in most other search algorithms). Parameter estimates and resulting values for the twice-negative likelihood function are summarized in Table 1. The Allee-Ricker model (eq. 9) gave the lower value (-6.518 for Allee-Ricker model and -4.818 for Ricker model) for the negative log-likelihood function, indicating that the Allee-Ricker model fit the data better than the Ricker S - R model. This indicates that the inclusion of the parameter S_{offset} improved the model fit. We conclude that the Allee-Ricker model (eq. 9) should be used to analyze the S - R relationship.

For the new model, the estimate of S_{offset} is 5211 coho salmon (Fig. 1) with a standard error of 1680. Therefore, the distribution for $\chi^2_{0.80,1} = 1.642$ can be constructed using eq. 12 (Fig. 3) with the 95% confidence interval, which is (1736, 8686). Because this 95% confidence interval does not cover 0, S_{offset} is statistically significant and therefore the inclusion of S_{offset} significantly improves the model fit.

With the new Allee-Ricker model (eq. 9), the operational extinction probability function from eq. 15 can be constructed. For this stock, the extinction probability as a function of spawner numbers is produced using $S_{offset} = 5211$ and $\hat{S}_{offset} = 1680$ (Fig. 4). From this figure, we provide several extinction probabilities calculated from different levels of spawner number, such as, at S_{offset} , the observed historical minimum spawning biomass, 2000, 5000, and 10 000 coho (Table 2). Also, with any extinction probability suggested by managers, the corresponding spawner numbers can be calculated from this function as a management reference point (Fig. 4). In Table 2, we list several reference points for the probabilities of extinction at 0.1, 0.3, 0.5, 0.7, and 0.9.

Fig. 1. Stock–recruitment relationships for North Thompson coho salmon. The solid curve is the Ricker model (eq. 3) fit, the broken line is the Allee–Ricker model (eq. 9) fit, and the straight line is the replacement line. Value “5.211” is the estimated S_{offset} (= 5.211 × 1000).

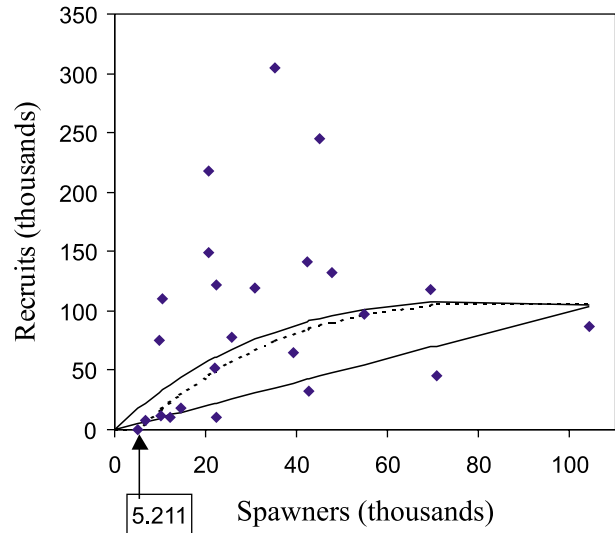
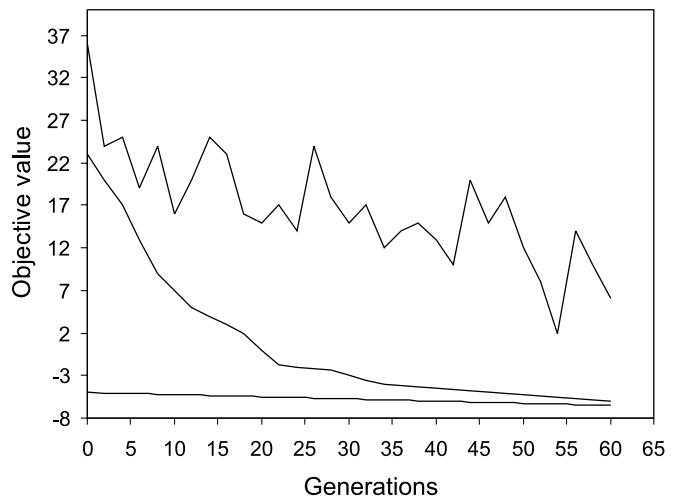


Fig. 2. The performance of the genetic search algorithm using the North Thompson coho data. From top to bottom, the lines represent the worst, median, and best values from the 100 points in every generation.



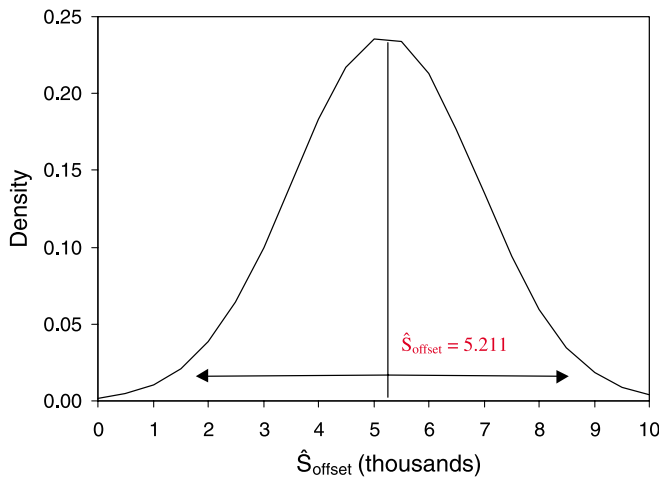
Patterns in the residuals were examined after the Ricker model (eq. 3) was fit to the data. No apparent relationship was seen between the size of the population and the residuals, but there was evidence of nonstationarity. A sequence of strong positive residuals in the early 1980s preceded a declining trend, with negative residuals occurring in most recent years. In this instance, trends in the residuals do not negate the value of calculating S_{offset} because recent low productivities (α) result in a positive bias in estimates of S_{offset} . We consider that a small positive bias when computing a reference point is acceptable because it is risk averse. The patterns in the residuals may provide an explanation as to why the Allee-Ricker model fit the data better than the traditional

Table 1. Summary of parameter estimates for North Thompson coho and Chilko sockeye salmon and under Ricker S - R (stock–recruitment) models and the new Allee–Ricker models.

Stock	Model	α	β	S_{offset}	l
North Thompson coho	Ricker	1.281 (0.346)	1.22×10^{-5} (8.39×10^{-6})	NA	–4.818
	Allee–Ricker	1.808 (0.458)	2.13×10^{-5} (9.75×10^{-6})	5 211 (1 680)	–6.518
Chilko sockeye	Ricker	2.155 (0.253)	1.61×10^{-6} (4.95×10^{-7})	NA	–36.715
	Allee–Ricker	2.179 (0.232)	1.65×10^{-6} (5.03×10^{-7})	1 585 (11 065)	–36.740

Note: The column “ l ” is the value for the twice the negative log-likelihood function. Values in parentheses represent the estimated standard error. NA, not applicable.

Fig. 3. The distribution of \hat{S}_{offset} for North Thompson coho. The vertical line is the estimated $\hat{S}_{\text{offset}} = 5.211$ and the horizontal line with arrows at both ends is the 95% confidence interval.



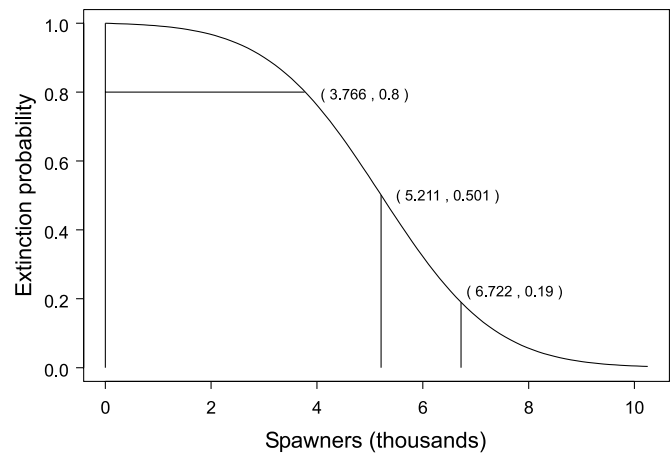
Ricker S - R model (Table 1). The first-order autocorrelation was significant when the Ricker S - R model was applied (Lag 1, autocorrelation coefficient $\rho = 0.42$) but was not when the Allee-Ricker model was fit to the data (Fig. 5).

Chilko sockeye

Spawner and recruit data for Chilko Lake sockeye are available for brood years 1948 to 1995 (Fig. 6). Chilko Lake is one of the largest producers of sockeye within the Fraser River watershed with an average of 340 000 spawners and 1.4 million recruits per year. This stock has rebuilt since the 1980s and the numbers of spawners has increased to nearly 700 000 per year since 1989. The S - R relationship suggests the stock is now near the maximum capacity of Chilko Lake. Chilko Lake was fertilized intermittently in 4 years beginning in 1987 and ending in 1992. Bradford et al. (2000) present evidence for increased sockeye freshwater productivity as a result of fertilization. The S - R data used in our analysis exclude the 4 years of fertilization to avoid potential problems of parameter bias.

We first fit the Ricker model (eq. 3) by a simple regression approach and then fit the Allee Ricker S - R model (eq. 9) by the MLE with the GA for the same data. The parameter estimates and the resulting value for the twice-negative likelihood function are summarized in Table 1. The estimate of S_{offset} is 1585 fish with standard error of 11 065. Because S_{offset} is close to the origin of the S - R relationship, an inset is provided (Fig. 6) to illustrate S_{offset} relative to the Ricker S - R curve. Observed spawning escapements ranged

Fig. 4. Probability of extinction of one brood line as a function of North Thompson coho spawner numbers. From left to right, the two vertical lines are the extinction probabilities corresponding to the estimated S_{offset} and the historical minimum spawner number, respectively. The horizontal line depicts the calculated spawner numbers corresponding to the 80% extinction probability.



from 17 300 to 1 038 000 fish. The 95% confidence interval of the probability distribution of S_{offset} (12) includes 0 (Fig. 7). Therefore the inclusion of S_{offset} does not significantly improve the model fit.

Even though S_{offset} is not statistically significant different from zero, the estimated distribution can still be used for the calculation of extinction probabilities because eq. 15 is only dependent on the estimated parameter and its associated variance. The extinction probability for Chilko sockeye can be calculated for a given spawner abundance (Fig. 8), and depending on the level of risk tolerance, a management reference in terms of spawner abundance can be calculated from this function. In Table 2, we list several reference points for given probabilities.

Discussion

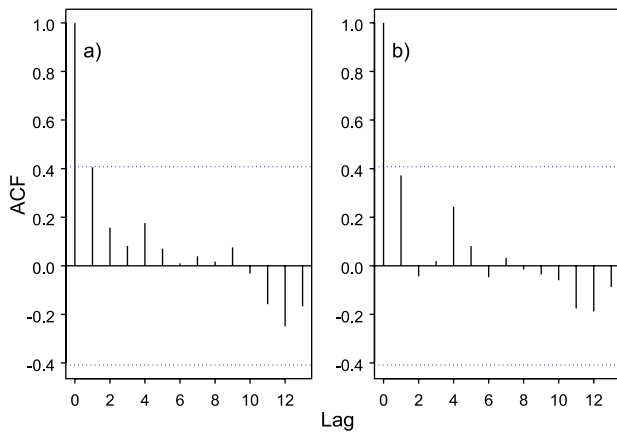
In this paper we make several contributions to the field of conservation biology and in particular the evaluation of extinction risk. First, we demonstrate a new way that traditional S - R models can be extended to incorporate potential Allee effects. Methods to estimate parameters and associated statistical inferences are developed including the use of GA. Second, with the extended Allee–Ricker model, we develop an operational formula for the extinction probability function. This formula can be used to calculate the extinction probability for any given spawner abundance and also allows

Table 2. Relationship between calculated extinction probabilities for given spawner numbers (the second and third columns) and the calculated spawner abundance for given extinction probabilities based on eq. 15 (the fourth and fifth columns).

	Spawner abundance	Extinction probability	Extinction probability	Spawner abundance
North Thompson coho	S_{offset}	0.501	0.1	7 438
	Hist. min.	0.191	0.3	6 106
	2 000	0.968	0.5	5 222
	5 000	0.551	0.7	4 316
	10 000	0.005	0.9	2 984
Chilko sockeye	S_{offset}	0.898	0.1	19 200
	Hist. min.	0.139	0.3	12 270
	10 000	0.401	0.5	8 084
	20 000	0.086	0.7	4 680
	30 000	0.009	0.9	1 550

Note: S_{offset} is estimated from the new Allee–Ricker model; Hist. min., the historical minimum of the observed spawner numbers.

Fig. 5. Autocorrelation function (ACF) for the residuals applying (a) the standard Ricker model and (b) the Allee–Ricker model to North Thompson coho data. The first-order (i.e., Lag 1) autocorrelation with the standard Ricker model was just significant as it was barely outside the 95% confidence band (dotted lines).

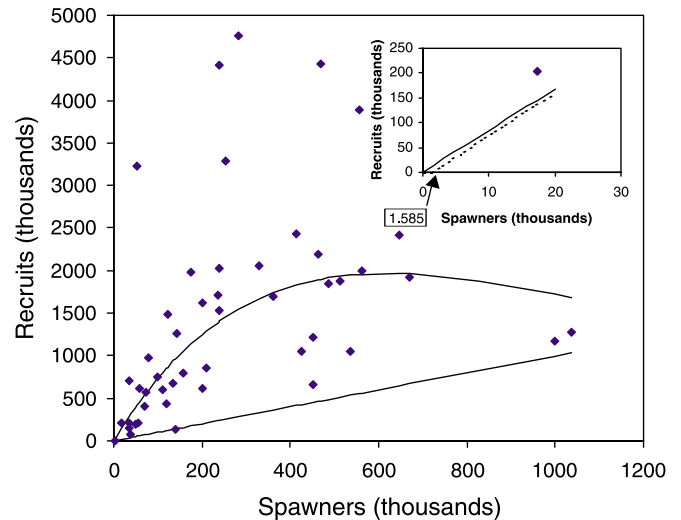


managers the opportunity to define reference points according to particular extinction probabilities.

The precautionary approach is increasingly being applied in fisheries management to comply with international agreements for sustainable resource use (e.g., Richards and Maguire 1999). This approach is intended to ensure that conservation takes precedence over other objectives (NMFS 1999). Reference points provide the primary mechanism by which the precautionary approach can be applied (Richards and Maguire 1999). In our paper, we define the probability distribution associated with S_{offset} and propose this as a suitable reference point that can be used by managers to minimize the possibility of population extinction.

Managers applying the precautionary approach would like a low probability of populations going extinct. One way to do this is to “buffer” reference points by incorporating uncertainty. Sources of uncertainty and statistical pitfalls that can bias stock–recruitment model parameters are discussed in Hilborn and Walters (1992). These include lack of contrast in the spawning escapement variable, measurement errors in escapement and recruitment, temporal autocorrelation in the S – R series, and nonstationarity of S – R relationships. Apart from the lack of contrast in the escapement time

Fig. 6. Stock–recruitment relationships for Chilko River sockeye salmon. Solid curve is the Ricker model (eq. 3) fit, and the broken line is the Allee–Ricker model (eq. 9) fit. Because of the large data range and scale for the spawner abundance, both lines are so close that it is difficult to distinguish them. The straight line is the replacement line. Because the estimated value for S_{offset} ($1585 = 1.585 \times 1000$) is so close to the origin, a plot showing details close to the origin is embedded in the plot. For this embedded plot, the solid line is the Ricker model (eq. 3) fit and the broken line is the fit from the Allee–Ricker model (eq. 9). Value “1.585” is the estimated S_{offset} rescaled by 1000. The only dot in the figure is the last observed S – R (stock–recruitment) data point with 17.308 ($\times 1000$) spawners and 204.386 ($\times 1000$) recruits.



series, various statistical remedies can deal with S – R biases. To minimize the likelihood of a population falling below the S_{offset} , the limit should be set higher than the point estimate. For instance, one might wish to select a reference point corresponding to the 10% extinction probability rather than the 50% value. Uncertainty in S_{offset} as a result of S – R bias should be carefully examined on a case-specific basis as with any of the classical S – R models. If there is a temporal pattern in productivity, one could model productivity as a function of time. Reference points may need to be raised during periods of low productivity. In addition, S_{offset} could

Fig. 7. The distribution of \hat{S}_{offset} for Chilko sockeye salmon. The vertical line is the estimated \hat{S}_{offset} ($= 1.585 \times 1000$), and the horizontal line with arrows at both ends is the 95% confidence interval.

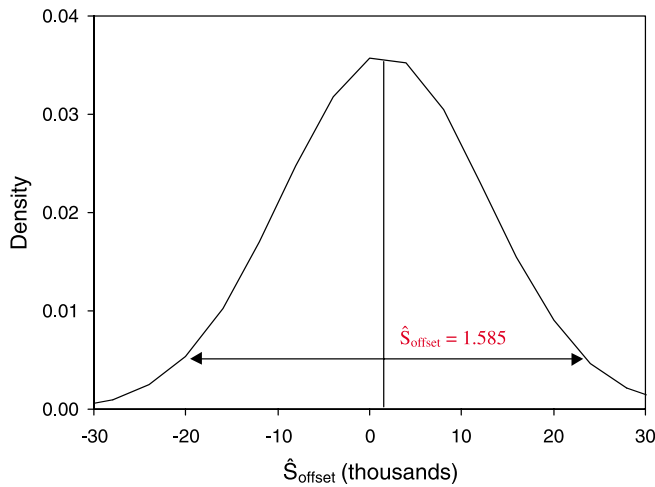
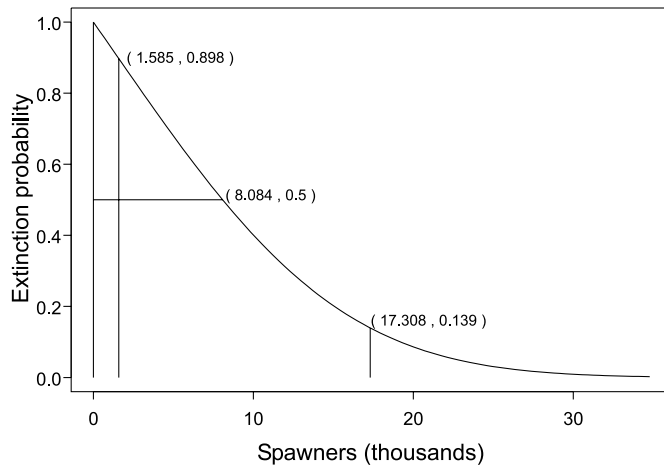


Fig. 8. Extinction probability as function of the Chilko sockeye spawner numbers rescaled so that the extinction probability is zero for the spawner abundance to be zero. From left to right, the two vertical lines are the extinction probabilities corresponding to the estimated S_{offset} and the historical minimum observed spawner numbers, respectively. The horizontal line depicts the calculated spawner numbers corresponding to the 50% extinction probability.



be used in a Bayesian decision analysis to evaluate the consequence of alternative management objectives on extinction risk.

The two salmon examples considered here demonstrate the potential effect of data variability at low spawner densities on estimates of S_{offset} . It would be instructive to apply this approach to other species. For North Thompson coho, S_{offset} is statistically significant from zero despite the variability in the data at low spawner densities. Because S_{offset} for Chilko sockeye is not significant, it is unclear if compensatory mortality at low spawner density is negligible or if compensatory mortality is masked by high survival variability and (or) data measurement error. As previously con-

cluded by Liermann and Hilborn (1997), one should not ignore the possibility of an Allee effect because uncertainty in parameter distributions may mask the presence of depensation at low abundance.

The extended model (eq. 5) can also be used to incorporate environmental information and fishery interventions, such as $R_t = (S_t - S_{\text{offset}})F(S_t - S_{\text{offset}}, \mathbf{X}_t, \theta)$, where \mathbf{X}_t is a vector of environmental and fishery intervention variables. This model can be combined with the semiparametric approach discussed in Chen and Irvine (2001) to analyze the compensatory and depensatory effects embedded in the S - R relationship with environmental and fishery interventions.

As an extension and further research for the definition of the extinction probability function given by eqs. 14 and 15, we are exploring the possibility of defining the probability of stock extinction as $\Pr(\text{Stock Extinction}) = \Pr(S_t \leq S_{\text{offset}}, \forall t = 1, \dots, K)$, where K is the maximum life span (years) for the specific stock (K would be 4 and 6 for our coho and sockeye examples respectively) and \forall is a logic notation denoting “for all” t . Because S_{offset} is the critical value for the stock below which recruitment would be zero, if the spawner abundance for this stock is below this critical value for K years, the stock would be extinct.

We feel that the new Allee-Ricker model is a useful extension for the traditional S - R model to be used for fishery S - R analysis, and we believe that the operational definition of the extinction probability function developed in this paper is a useful tool for fishery management.

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References

- Allee, W.C., Emerson, A.E., Park, O., Park, T., and Schmidt, K.P. 1949. Principles of animal ecology. Saunders, Philadelphia.
- Asmussen, M.A. 1979. Density-dependent selection. II. The Allee effect. *Am. Nat.* **114**: 796–809.
- Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish population. *Fish. Invest. Ser. II, Mar. Fish. G.B. Minist. Agric. Fish. Food*, **19**.
- Bradford, M.J., and Irvine, J.R. 2000. Land use, fishing, climate change and the decline of Thompson River, British Columbia, coho salmon. *Can. J. Fish. Aquat. Sci.* **57**: 13–16.
- Bradford, M.J., Pyper, B.J., and Shortreed, K.S. 2000. Biological responses of sockeye salmon to the fertilization of Chilko Lake, a large lake in the interior of British Columbia. *N. Am. J. Fish. Manag.* **20**: 661–671.
- Chen, D.G., and Irvine, J.R. 2001. A semiparametric model to examine stock–recruitment relationships incorporating environmental data. *Can. J. Fish. Aquat. Sci.* **58**: 1178–1186.
- Chen, D.G., Hargreaves, N.B., Ware, D.M., and Liu, Y. 2000. A fuzzy logic model with genetic algorithm for analyzing fish stock–recruitment relationships. *Can. J. Fish. Aquat. Sci.* **57**: 1878–1887.
- Deriso, R.B. 1980. Harvesting strategies and parameter estimation for an age-structured model. *Can. J. Fish. Aquat. Sci.* **37**: 268–282.

- Draper, N.R., and Smith, H. 1981. Applied regression analysis. 2nd ed. John Wiley & Sons, Inc., New York.
- Emlen, J.M. 1984. Population biology, the coevolution of population dynamics and behavior. Macmillan, New York.
- Frank, K.T., and Brickman, D. 2000. Allee effects and compensatory population dynamics within a stock complex. *Can. J. Fish. Aquat. Sci.* **57**: 513–517.
- Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment and management: choice, dynamics, and uncertainty. Chapman and Hall Inc., New York.
- Holland, J. 1975. Adaptation in natural and artificial systems. University of Michigan Press, Ann Arbor, Mich.
- Irvine, J.R., Parken, C.K., Chen, D.G., Candy, J., Ming, T., Supernault, J., Shaw, W., and Bailey, R.E. 2001. 2001 assessment of stock status for coho salmon from the interior Fraser River. Canadian Stock Assessment Secretariat Research Document 2001/083. Available from CSAS, 200 Kent St., ON K1A 0E6, Canada, or at <http://www.dfo-mpo.gc.ca/csas/>.
- Kalbfleisch, J.G. 1985. Probability and statistical inference. Vol. 2. Statistical inference. 2nd ed. Springer-Verlag, New York.
- Liermann, M., and Hilborn, R. 1997. Depensation in fish stocks: a hierarchical Bayesian meta-analysis. *Can. J. Fish. Aquat. Sci.* **44**: 1976–1984.
- McElhany, P., Ruckelshaus, M.H., Ford, M.J., Wainwright, T.C., and Bjorkstedt, E.P. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. U.S. Department of Commerce, NOAA (National Oceanic and Atmospheric Administration), Washington, D.C., Tech. Memo. NMFS-NWFSC-42.
- Mood, A.M., Graybill, F.A., and Boes, D.C. 1974. Introduction to the theory of statistics. McGraw-Hill, Inc., New York.
- Myers, R.A., Barrowman, N.J., Hutchings, J.A., and Rosenberg, A.A. 1995. Population dynamics of exploited fish stocks at low population levels. *Science (Washington, D.C.)*, **269**: 1106–1108.
- National Marine Fisheries Service (NMFS). 1999. Our living oceans. Report on the status of U.S. living marine resources, 1999. U.S. Department of Commerce, NOAA (National Oceanic and Atmospheric Administration), Washington, D.C., Tech. Memo. NMFS-F/SPO-41.
- Richards, L.J., and Maguire, J.J. 1999. Recent international agreements and the precautionary approach: new directions for fisheries management science. *Can. J. Fish. Aquat. Sci.* **55**: 1545–1552.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can. Bull.* 191.
- Routledge, R.D., and Irvine, J.R. 1999. Chance fluctuations and the survival of small salmon stocks. *Can. J. Fish. Aquat. Sci.* **56**: 1512–1519.
- Saila, S.B. 1996. Guide to some computerised artificial intelligence methods. In *Computers in fisheries research*. Edited by B.A. Megrey and E. Moksness. Chapman and Hall, London. pp. 8–40.
- Walters, C., and Kitchell, J.F. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Can. J. Fish. Aquat. Sci.* **58**: 39–50.