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STOCK-RECRUITMENT MODEL

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Abstract

Bayesian statistics were applied to analyze the Ricker stock-recruitment model. This model is used for salmon fishery management and predicts the resulting recruits for a specified level of spawners. The Ricker model is transformed into a linear regression form, and the uncertainty in the model parameters and the 'noise' of the model are calculated using Bayesian regression analysis. Application to the Skeena River Sockeye fishing with 67 years of data showed that parameter uncertainty was much less than model noise, thus putting in question the applicability of the Ricker model for management decisions. The analysis is extended to experimentation on the 'optimal' spawning level, non-stationarity of the fishery, and model uncertainty.

Introduction

A number of simple models have been proposed and used to establish fishery regulations and optimal catch quotas, for example, the 'Ricker model' (Ricker, 1954) and the 'Shaeffer model' (Schaeffer, 1954). A model will be assumed that describes the fishery; the model parameters are estimated from the available data and the 'optimal' harvest rates established. Walters (1975), Allen (1973) and others have tried to establish control laws for non-equilibrium situations, still using the simple dynamic fishery models described above. Walters and Hilborn (1975) extended the adaptive control laws to consider parameter uncertainty in the models, which could arise from a lack of data for the fishery or non-stationarity of the fishery (changes in environmental carrying capacities and in genetic structure, etc.; Walters and Hilborn, 1975). Walters and Hilborn (1975) must nevertheless assume that the simple model adequately describes

the fishery behaviour. If this is not true, then the control laws may bring the fishery into a non-equilibrium situation or an equilibrium that may have dire long-term consequences to the fishery.

This paper considers the statistical properties of the Ricker model used by Walters and Hilborn (1975) for the adaptive control analysis. Such a statistical analysis can also treat questions of experimentation, should the control be altered to gain more information about the model or parameters of the fishery. The approach followed in this paper is Bayesian statistics. Bayesian analysis has as its foundation the concept that unknown states of nature can be treated as random variables. Then the equilibrium stock parameter b can be described by a probability density function $f(b)$ estimated from the available information. As will be described later, the fishery model should be modified to reflect the uncertainty in the parameters. Such statistical procedures allow a formal analysis of questions concerning the value of experimentation and the effect of parameter and model uncertainty.

Bayesian Analysis of the Ricker Model

The simple model developed by Ricker (1954) has been widely used for analysis of stock-recruitment and in the management of fisheries. Its form is:

$$R_t = S_{t-1} \cdot \exp \left[a \left(1 - \frac{S_{t-1}}{b} \right) \right] \quad (1)$$

where

R_t = recruits at the end of generation t ,

S_{t-1} = spawners at the start of generation t ,

a = a stock production parameter,

b = the equilibrium stock level (in the absence of fishing).

Since the model is not a perfect predictor of fishery dynamics, the model of Equation (1) can be modified to include a

'noise term' or random environmental factor. This form can be written as

$$R_t = S_{t-1} \cdot \exp \left[a \left(1 - \frac{S_{t-1}}{b} \right) + \xi_t \right] \quad (2)$$

where

ξ_t = the random environmental factor, Normally distributed with mean 0, variance σ^2 .

There is both empirical evidence (Allen, 1973) and theoretical justification (Walters and Hilborn, 1975) that ξ_t is Normally distributed. From Equation (2), the recruits R_t , given a spawning level S_{t-1} , will be Log-Normal distributed.

By rewriting Equation (2) as

$$y_t = \beta_1 + \beta_2 S_{t-1} + \xi_t, \quad (3)$$

where

$$y_t = \ln \left(\frac{R_t}{S_{t-1}} \right)$$

$$\beta_1 = a$$

$$\beta_2 = -a/b,$$

the Ricker model can be analyzed as a Normal regression. y_t will be Normally distributed with mean $\beta_1 + \beta_2 S_{t-1}$ and variance σ^2 .

We assume that the set of observations $Y (Y = y_1, y_2, \dots, y_n)$ and $X (X = [1, S_0], [1, S_1], \dots, [1, S_{n-1}])$ come from the distribution for y , $f_y(y|\beta_1, \beta_2, \sigma)$, which is conditional upon the parameter set σ and $\underline{\beta} \equiv [\beta_1, \beta_2]^t$. The distribution of the uncertain parameters can be found by a simple application of the Bayes Theorem:

$$f''(\underline{\beta}, \sigma | Y, X) \propto f(Y, X | \underline{\beta}, \sigma) \cdot f'(\underline{\beta}, \sigma), \quad (4)$$

where

$f'(\underline{\beta}, \sigma)$ = the prior distribution of $\underline{\beta}, \sigma$. If no prior information is available, then $f'(\underline{\beta}, \sigma)$ can be represented by a uniform distribution over the interval of the parameter,

$f(Y, X | \underline{\beta}, \sigma) \equiv L(\underline{\beta}, \sigma | Y, X)$ = the sample likelihood function of the parameter set, conditional upon the observations (or the probability of the observations given the parameters),

$f''(\underline{\beta}, \sigma | Y, X)$ = the posterior density function of the parameter considering sample information and prior information.

The way the information about $\underline{\beta}$ and σ is analyzed depends upon the objectives of the analysis. Consider the case when decisions are to be made concerning y (or, in our case, R_t which is embedded in y). Here the inferences about y should reflect the uncertainty in $\underline{\beta}, \sigma$ by applying compound distribution theory in a Bayesian framework (Wood and Rodriguez-Iturbe, 1975). This procedure results in obtaining the predictive density for y , $\tilde{f}(y|x)$, found by

$$\tilde{f}(y|x) = \int_{\underline{\beta}, \sigma} f(y|x, \underline{\beta}, \sigma) \cdot f''(\underline{\beta}, \sigma) d\underline{\beta} d\sigma, \quad (5)$$

where

$f(y|x, \underline{\beta}, \sigma)$ = the probabilistic form of the Ricker model, Equation (3),

$f''(\underline{\beta}, \sigma)$ = the posterior distribution of the parameters,

$\tilde{f}(y|x)$ = the predictive density of y , now parameter-free.

$\tilde{f}(y|x)$ should be interpreted as being the model for y , $f(y|x, \underline{\beta}, \sigma)$, weighted by the distribution of the uncertain parameters $\underline{\beta}, \sigma$. The above will be applied to the Ricker stock recruitment model.

Likelihood of the Observed Sample

Previously, it was discussed that the Ricker model has an error term ξ_t , whose distribution could be assumed Normal with mean 0 and variance σ^2 . Then the Ricker model has a Normal density function with mean $X_t\beta$ and variance σ^2 . That is,

$$f(y_t | \beta, \sigma, x_t) = (2\pi)^{-1/2} \cdot \sigma^{-1} \cdot \exp \left[-\frac{1}{2\sigma^2} (y_t - x_t\beta)^t (y_t - x_t\beta) \right] , \quad (6)$$

where

$$\begin{aligned} y_t &= \ln \left(\frac{R_t}{S_{t-1}} \right) \\ x_t &= [1, S_{t-1}] , \text{ a row vector,} \\ \beta &= \begin{bmatrix} a \\ -a/b \end{bmatrix} , \text{ a column vector.} \end{aligned}$$

The likelihood function for the sample $Y (Y = y_1, y_2, \dots, y_n)$ is the product of the density function for the individual y_t 's and is given by

$$L(\beta, \sigma | Y, X) \propto \frac{1}{\sigma^n} \exp \left\{ -\frac{1}{2\sigma^2} \left[v s^2 + (\beta - \hat{\beta})^t X^t X (\beta - \hat{\beta}) \right] \right\} ,$$

where

$$\begin{aligned} v &= n - 2, \\ \hat{\beta} &= (X^t X)^{-1} X^t Y, \\ v s^2 &= (Y - X) ^t (Y - X) . \end{aligned}$$

The likelihood function has the form of the product of Bivariate-Normal and Inverted-Gamma-2 density functions (Zellner, 1971).

Assume that no prior information exists concerning the parameters β, σ ; then the prior probability density function can be expressed (Jefferys, 1961) as

$$f'(\underline{\beta}, \sigma) \propto \frac{1}{\sigma} \quad . \quad (7)$$

On combining the likelihood function and the prior density function, the joint posterior probability density function for $\underline{\beta}, \sigma$ is

$$f(\underline{\beta}, \sigma | Y, X) \propto \frac{1}{\sigma^{n+1}} \exp \left\{ -\frac{1}{2\sigma^2} \left[v s^2 + (\underline{\beta} - \hat{\underline{\beta}})^t X^t X (\underline{\beta} - \hat{\underline{\beta}}) \right] \right\} \quad . \quad (8)$$

From Equation (8), it is observed that the marginal density function for $\underline{\beta}$ is a Bivariate-Normal with mean $\hat{\underline{\beta}}$ and covariance $(X^t X)^{-1} \sigma^2$. Because σ is not known, the distribution of $\underline{\beta}$ can be obtained from (8) by integrating over σ . That is,

$$f(\underline{\beta} | Y, X) = \int_{\sigma} f(\underline{\beta}, \sigma | Y, X) d\sigma \quad , \quad (9)$$

which is in the form of a Bivariate-Student-t density function. This distribution serves as a basis for making inferences about $\underline{\beta}$. The marginal density function for σ can be obtained from Equation (8) by integrating with respect to $\underline{\beta}$. This results in

$$f(\sigma | Y, X) \propto \frac{1}{\sigma^{v+1}} \exp \left(-\frac{v s^2}{2\sigma^2} \right) \quad , \quad (10)$$

which is in the form of an Inverted-Gamma-2 density function.

Predictive Density for y

It may be of interest to make inferences from the density function for $\underline{\beta}$ and σ , but usually fishery managers are more concerned with the distribution of $\tilde{y}$, the future observation given future control $\tilde{x}$. In this case, it is important to calculate the predictive density for $\tilde{y}$, given $\tilde{x}$, that will reflect the uncertainty in $\underline{\beta}$ and σ :

$$\tilde{f}(y | Y, X, \tilde{x}) = \int_{\underline{\beta}, \sigma} f(\tilde{y} | \underline{\beta}, \sigma, \tilde{x}) \cdot f''(\underline{\beta}, \sigma | Y, X) \quad , \quad (11)$$

where

$f(\tilde{y}|\underline{\beta}, \sigma, \tilde{x})$ = the density function of the Ricker model
without considering parameter uncertainty,

$f''(\underline{\beta}, \sigma|Y, X)$ = the posterior density function of the parameter $\underline{\beta}, \sigma$.

Integrating Equation (11) and rearranging the terms (Zellner, 1971) gives

$$f(\tilde{y}|Y, X, \tilde{x}) \propto \left[v + (\tilde{y} - \tilde{x}\underline{\beta})^t H(\tilde{y} - \tilde{x}\underline{\beta}) \right]^{-(v+1)/2} , \quad (12)$$

where

$$H = \frac{1}{s^2} \left(I - \tilde{x}M^{-1}\tilde{x}^t \right) ,$$

$$M = X^t X + \tilde{x}^t \tilde{x} .$$

Equation (12) is in the form of a Student-t distribution with moments

$$E[\tilde{y}] = \tilde{x}\underline{\beta} \quad \text{for } v > 1 ,$$

$$V[\tilde{y}] = \frac{v}{v-2} H^{-1} \quad \text{for } v > 2 .$$

Distribution of R

Equation (12) gives the distribution of $\tilde{y}$, $\ln \frac{\tilde{R}_t}{\tilde{S}_{t-1}}$, when the distribution for R_t may be of greater interest. Let

$$\tilde{y} = \ln(\tilde{R}_t) - \ln(\tilde{S}_{t-1}) ,$$

where

$$\tilde{S}_{t-1} = \text{a known (future) control} ;$$

then the Jacobian transform from

$$\tilde{y} \rightarrow \ln(\tilde{R}_t) - \ln(\tilde{S}_{t-1})$$

is

$$\tilde{R}^{-1}$$

and the distribution of $\tilde{f}(\tilde{R}_t)$ is derived from:

$$\begin{aligned} f(\tilde{R}_t) &= f(\tilde{y}) \cdot \left| \frac{dy}{dR} \right| \\ &= \tilde{R}^{-1} f(\tilde{y}) \Big|_{y = \ln\left(\frac{\tilde{R}_t}{\tilde{S}_{t-1}}\right)} \end{aligned} \quad (13)$$

The distribution of $\tilde{R}_t$ is in the form of a Log-Student-t probability density function.

A more convenient approach to find the moments of $\tilde{R}_t$ is by using first-order analysis (Cornell, 1972). First-order analysis is characterized by single-moment treatment of random components and first-order analysis of functional relationships among variables. The implication of this characterization is that information about random variables is represented only by their means and covariance, and that in dealing with functional relationships among random variables only the first-order terms in a Taylor expansion will be retained. For example,

$$Z = g(\underline{w}) \doteq g(\underline{\mu}_w) + \underline{h}^t(\underline{w} - \underline{\mu}_w) \quad , \quad (14)$$

where

$\underline{w}$ = a column vector of random variables,

$\underline{\mu}_w$ = the vector of their means,

$\underline{h}^t$ = the transpose of a column vector of partial derivatives:

$h_i = \partial g(\underline{w}) / \partial w_i$, evaluated at the mean.

The symbol $\doteq$ is used to mean 'equal' in a first-order sense. The moments of Z are

$$E[Z] \doteq g(\underline{\mu}_w) \quad (15)$$

$$V[Z] \doteq b^t \cdot \text{cov}[\underline{w}] \cdot \underline{b} \quad (16)$$

Returning to the problem of finding the moments of $\tilde{R}_t$, given the control, the relationship between variables is

$$\tilde{R}_t = \tilde{S}_{t-1} \cdot e^{\tilde{Y}} \quad (17)$$

so that the moments from Equations (15) and (16) for $\tilde{R}_t$ given the control $\tilde{S}_{t-1}$ are

$$E[\tilde{R}_t | \tilde{S}_{t-1}] \doteq \tilde{S}_{t-1} \cdot e^{\tilde{Y}} \quad (18)$$

$$V[\tilde{R}_t | \tilde{S}_{t-1}] \doteq \tilde{S}_{t-1}^2 \cdot e^{2\tilde{Y}} \quad (19)$$

It should be remembered that $e^{\tilde{Y}}$ is evaluated at its mean.

The same approach can be used to find the moments of b , the equilibrium stock parameters:

$$b = g(\underline{\beta}) = -\frac{\beta_1}{\beta_2} \quad (20)$$

Then the first-order approximations are

$$E[b] \doteq -\frac{\beta_1}{\beta_2} \quad (21)$$

$$\begin{aligned} V[b] &\doteq \left(\frac{\partial g(\underline{\beta})}{\partial \beta_1} \right)^2 \text{var}(\beta_1) + \left(\frac{\partial g(\underline{\beta})}{\partial \beta_2} \right)^2 \text{var}(\beta_2) \\ &\quad + 2 \frac{\partial g(\underline{\beta})}{\partial \beta_1} \cdot \frac{\partial g(\underline{\beta})}{\partial \beta_2} \text{cov}(\beta_1 \beta_2) \\ &\doteq \frac{1}{\beta_2^2} \text{var}(\beta_1) + \frac{\beta_1^2}{\beta_2^4} \text{var}(\beta_2) - 2 \frac{\beta_1}{\beta_2^3} \text{cov}(\beta_1 \beta_2) \quad (22) \end{aligned}$$

A second-order approximation for $E[b]$ can be expressed using first moments (Benjamin and Cornell, 1970):

$$\begin{aligned} E[b] &\doteq g(\underline{\beta}) + \frac{1}{2} \frac{\partial^2 g(\underline{\beta})}{\partial \beta_1 \partial \beta_2} \text{cov}(\beta_1 \beta_2) \\ &\doteq - \frac{\beta_1}{\beta_2} + \frac{1}{2} \frac{1}{\beta_2^2} \text{cov}(\beta_1 \beta_2) \quad . \end{aligned} \quad (23)$$

Again, all functions and partial derivatives of $\underline{\beta}$ are evaluated at its vector of means.

Application to Skeena River Sockeye Fishery

The Ricker model has previously been applied to the Skeena River Sockeye salmon fishery by Walters (1975). Walters' data, 67 years of record from 1908 through 1974, is presented in Figure 1 and will be used in this study. First, the full record is used to obtain inferences on the parameters β_1 , β_2 , and σ . The resulting predictive density is calculated and a first-order analysis performed to find the moments of the recruits R_t , given the control S_{t-1} . After this analysis, the sample was divided into four 15-year records (the first 7 years being discarded). An analysis of the divided record may indicate whether the parameters of the Ricker model are changing with time. Furthermore, since the most recently collected data is probably of a higher quality, the analysis of the last 15 years should give better inferences about the parameters.

Finally, given the results of the analysis, the questions of experimentation with the control parameter S can be considered.

Table 1 presents the statistics for the parameters β_1 and β_2 for both the 67 years of record and for the four 15-year sub-records. Table 2 presents the statistics for a , b , and σ , the parameters of the Ricker model as formulated in Equation (1).

Figure 2 presents $f(\beta_1, \beta_2)$, using the full 67 years of record. Figure 3 gives the predictive density of $\tilde{y}$, $\ln \frac{\tilde{R}_t}{\tilde{S}_{t-1}}$, given $\tilde{S}_{t-1}$, also using the 67 years of record. Using a

second-order analysis for the mean of R and first-order analysis for the variance of R, the Ricker curve was constructed using the 67 years of data and the four 15-year samples. Included in the figures are not only the mean of R given S, but also the mean $\pm$ one standard deviation. These curves are presented in Figures 4 through 8. Similar results were found dividing the sample into 20-year blocks. Figure 9 presents the function R versus control S.

The results show that with samples in the order of 15 years, the parameters of the Ricker model can be estimated fairly well. The largest coefficient of variation is .25, with most being below .20. The results seem to support the hypothesis (Walters, personal communication) that the equilibrium stock size is decreasing. This decrease could reflect the shrinkage of the active spawning areas in the river fishery.

The most important insight of the statistical analysis is the inadequacy of the Ricker model to explain the behaviour of the fishery. The coefficient of variation $\sigma_{R|S}/\mu_{R|S}$ at the maximum yield ranges from .46 to .68 and rises, approaching 1 when S is around $2 \cdot 10^6$. This result leads one to question seriously the adequacy of the Ricker model for fishery management. Clearly, the model as formulated cannot capture the complexity of the problem and fishery managers should consider other management tools.

Extensions to the Analysis

Experimentation

Experimentation can be performed either to gain knowledge about the parameters of a particular model or to try to discriminate among alternative models. For the results presented here, experimentation for parameters would be of limited value. The parameters have rather low variance and the 'noise' in the data comes from the inadequacy of the model.

Experimentation to discriminate among models can be performed quite easily (see Wood, 1974). If the alternative model is a simple relationship between R and S, then it is suspected

(looking at the data of Figure 1) that neither model would perform very well. One would be choosing the better of two poor models.

The design of the experimentation can be guided by the expected costs and benefits in the following manner. If the experiment is to have S' spawners (the control) for T' years, then an expected cost $E[C(S', T')]$, is associated with the experiment; this can be found by Monte Carlo simulation using the distribution $f(R|S')$ and $f(R|S^*)$, where S^* is the a priori optimal spawning level. The experiment can yield information $I(S', T')$ which can lead to a new posteriori optimal spawning level S'^* , which each year would have expected incremented benefits above S^* of $E[\Delta B|S^*, S'^*]$; here

$$E[\Delta B|S^*, S'^*] = \int B(R) \cdot f(R|S^*) - \int B(R) \cdot f(R|S'^*) \quad . \quad (24)$$

Non-Stationarity

The analysis presented here assumed stationarity of the fishery. This may not be valid and some of the results support this feeling. It appears that the equilibrium stock parameter is decreasing, which could support the hypothesis that the salmon are abandoning part of the spawning ground. This result could imply that fewer spawners should be released; that is, S^* is decreasing. As a positive feedback system, more spawning ground would be abandoned. Therefore, thought should be given to increasing the spawners with the idea of rejuvenating the abandoned areas.

Non-stationarity can also be handled in the analysis presented here by putting a distribution on b to reflect the changes over time. Winkler and Barry (1973) have done some work in analyzing non-stationary means in a Multi-Normal process. Similarly, the uncertainty in the number of spawners can be analyzed.

Multi-Stock Models

Within the fishery analyzed, it is recognized that genetically isolated stocks of the same species exist. The management of salmon fisheries has not considered this aspect when the optimal spawning level S^* is established. Thus, one stock may be severely overfished by arriving 'early' at the estuary and waiting before moving upstream, while another stock may pass quickly upstream. Furthermore, each stock would have its own set of parameters a and b leading to its own S^* .

It is possible, with the Bayesian methodology presented here, to consider a hyper-model consisting of a set of models, one for each stock. The result would be a set of optimal control levels $\underline{S^*}$. Management policy would then consist of sampling throughout the fishing season to determine fishing policy--which would result in real-time fishing management.

Summary

This paper has attempted to analyze the Ricker model using Bayesian statistics, in the hope of gaining insight into the value of the model for management purposes. The results indicate that parameter certainty was small in comparison to the error term of the model. This result implies that the Ricker model is not a good predictive model of the Skeena River Sockeye.

Experimentation with the control S would produce limited information about the model but may help in the identification of alternative models. Future work on model selection among multi-stock models may lead to more positive results.

Table 1. Statistics for β_1, β_2 .

Years	$\beta_1 = a$	$\beta_2 = -a/b$	$\text{Cov}(\beta_1, \beta_2)$	
1908-1974	1.763	-1.175	.0244 -.0315	-.0315 -.0414
1915-1929	1.955	-1.133	.1164 -.1263	-.1263 .1583
1930-1944	2.115	-1.990	.1466 -.290	-.290 .651
1945-1959	1.802	-1.545	.1686 -.2207	-.2207 .3392
1960-1974	2.205	-2.172	.0903 -.1331	-.1331 .2245

Table 2. Statistics of a, b and σ .

Years	a		b*		σ	
	mean	variance	mean	variance	mean	variance
1908-1974	1.763	.0244	1.490	.028	.514	.0021
1915-1929	1.955	.1164	1.677	.118	.494	.0113
1930-1944	2.115	.1466	1.026	.067	.521	.0126
1945-1959	1.802	.1686	1.121	.048	.625	.0182
1960-1974	2.205	.0903	1.001	.011	.423	.0083

* Second-order analysis for the mean of b, first-order analysis for the variance.

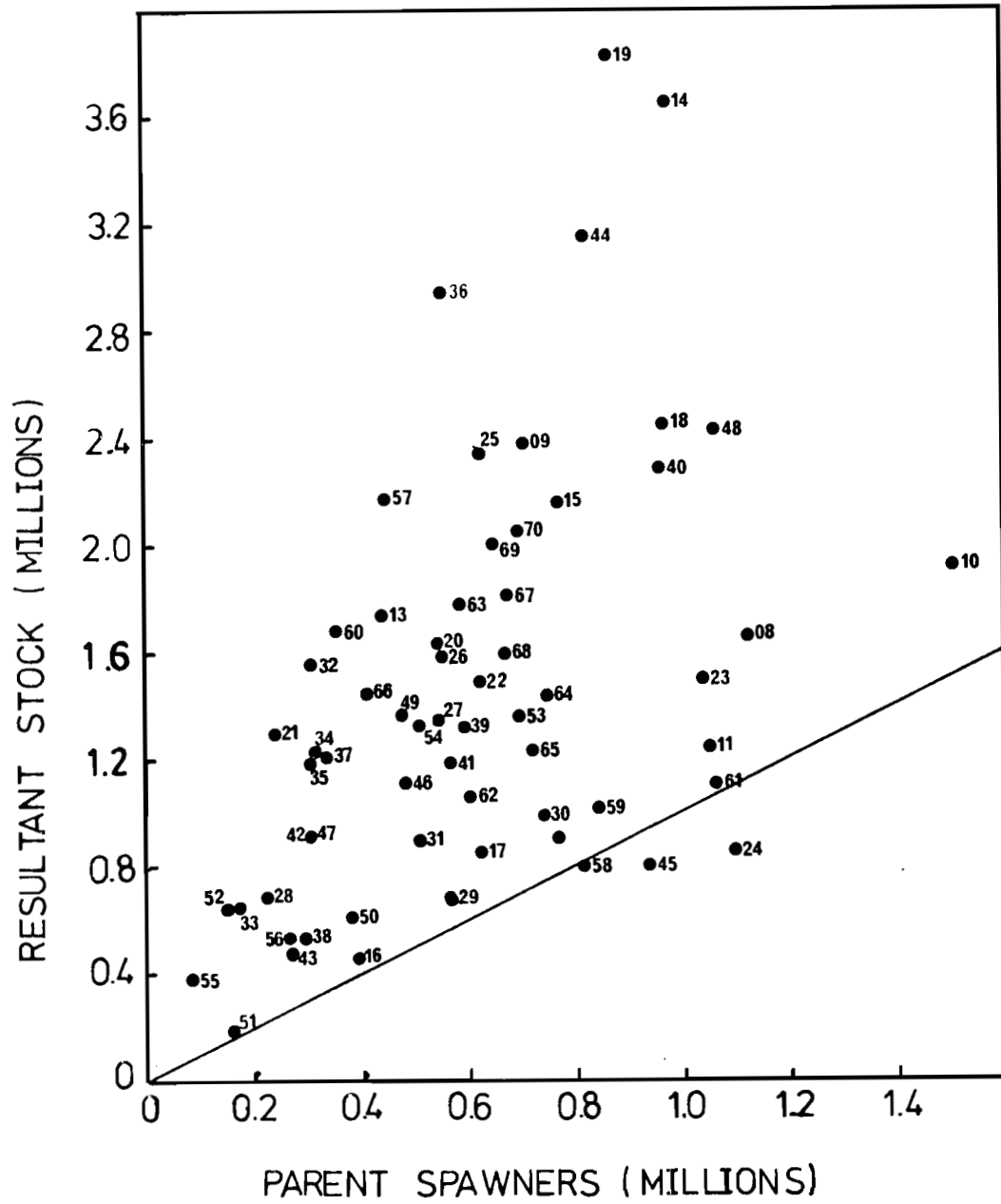


Figure 1. Stock-recruitment relationship for the Skeena sockeye, from Walters (1975).

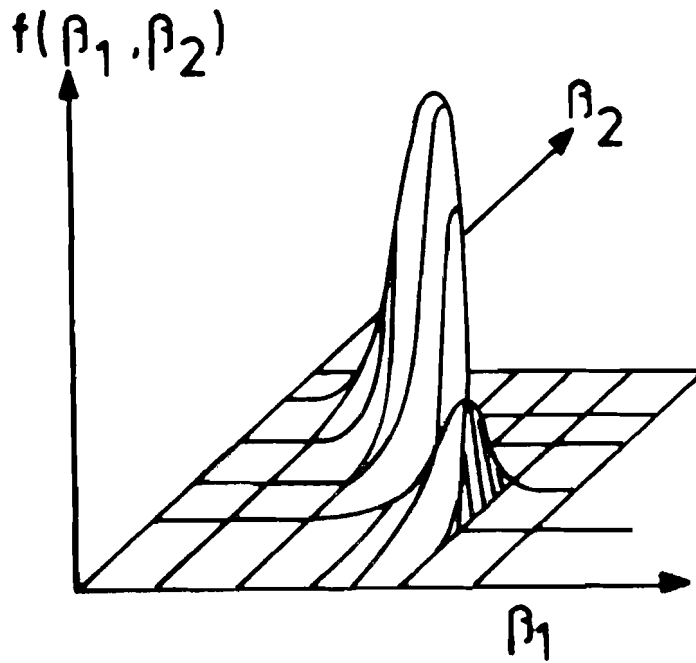


Figure 2. Probability density function for β_1, β_2 .

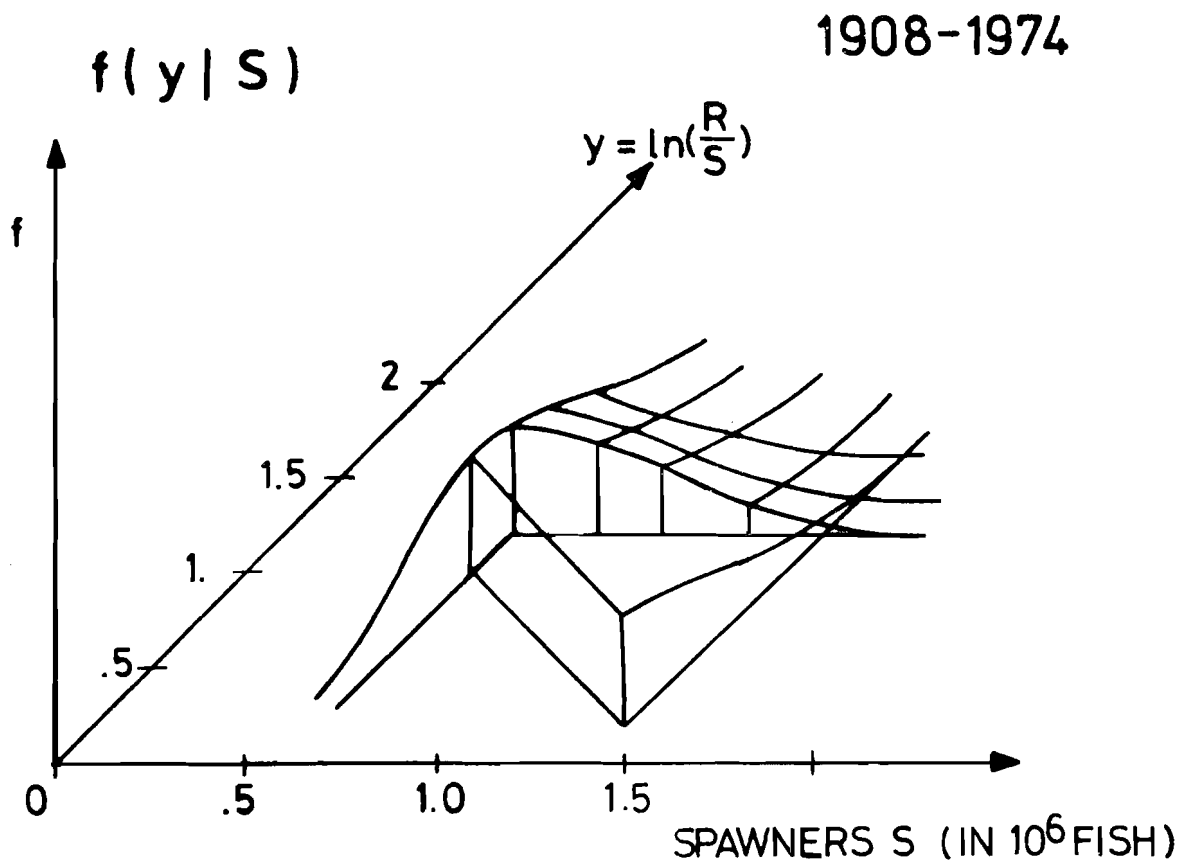


Figure 3. Predictive density $f(y|s)$: 1908-1974.

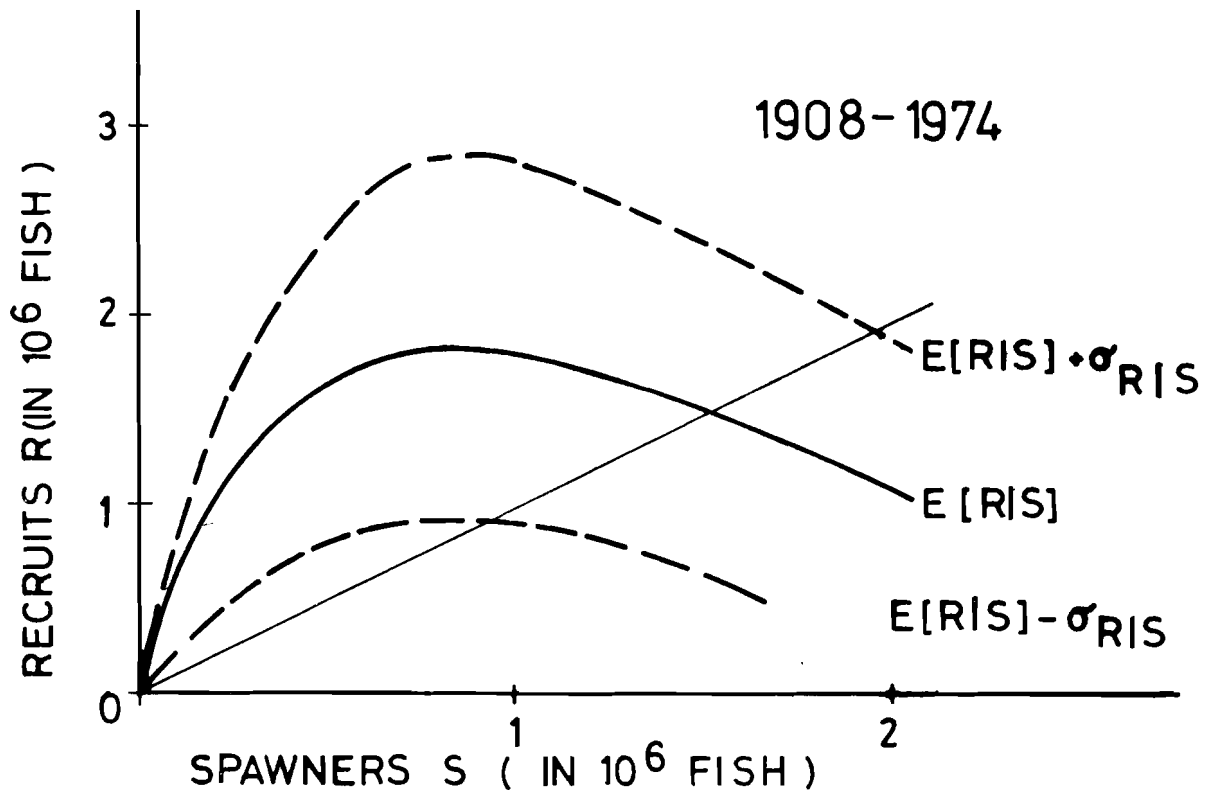


Figure 4. Expected recruits for spawning control levels: 1908-1974.

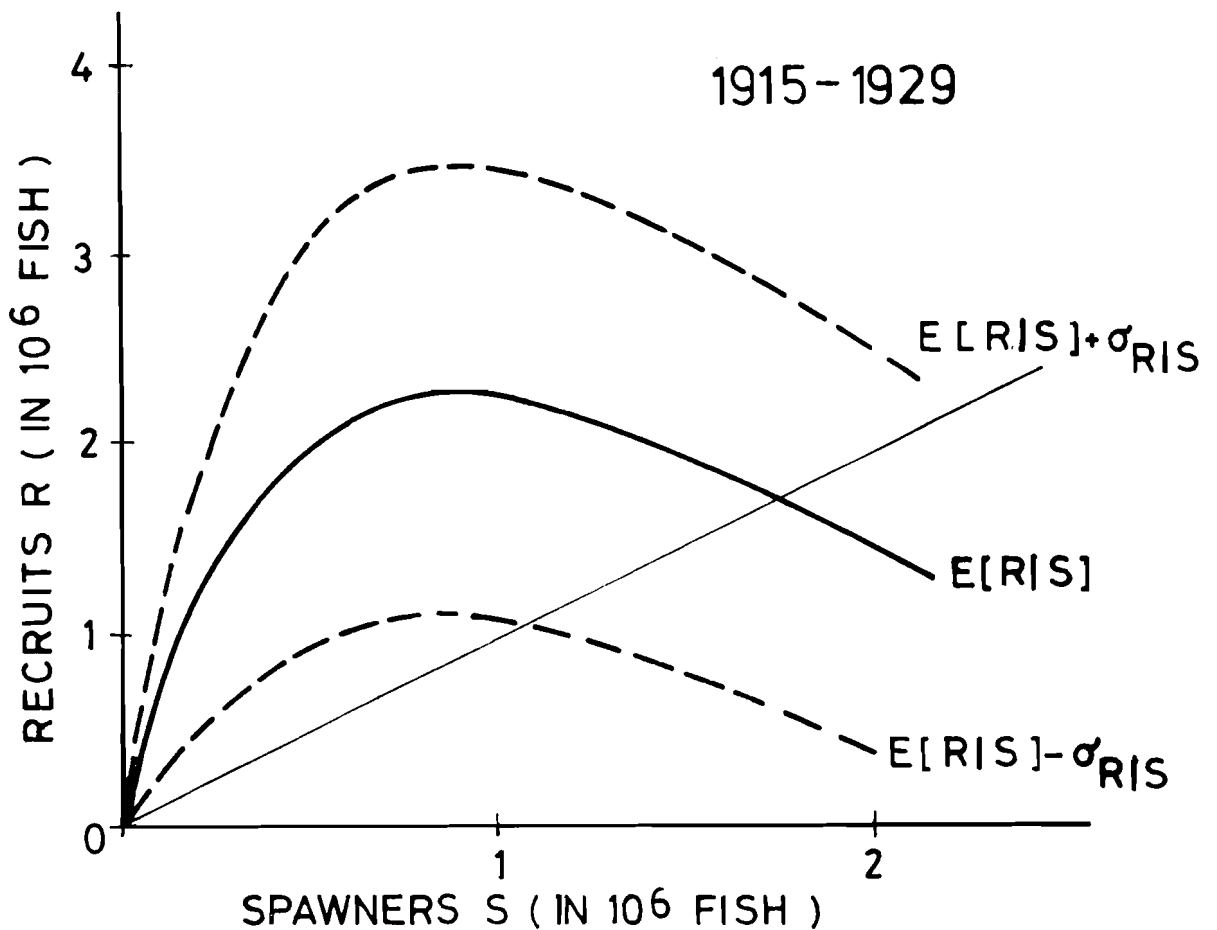


Figure 5. Expected recruits for spawning control levels: 1915-1929.

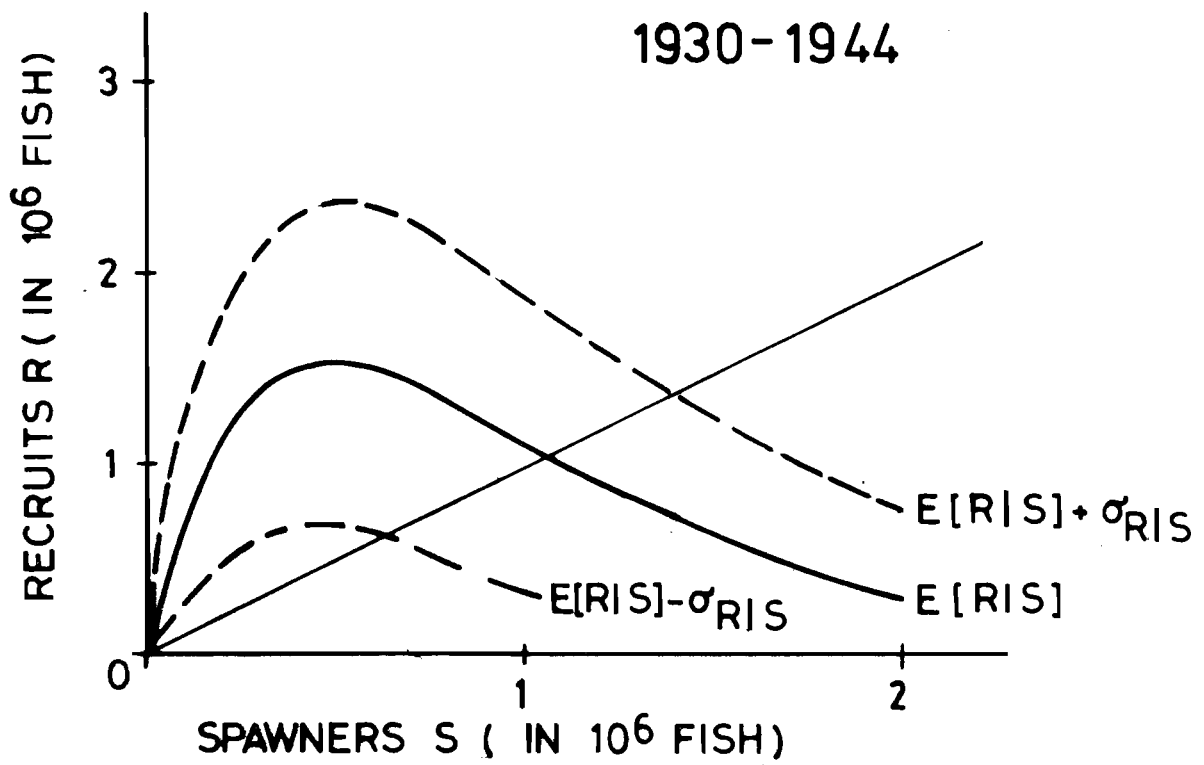


Figure 6. Expected recruits for spawning control levels: 1930-1944.

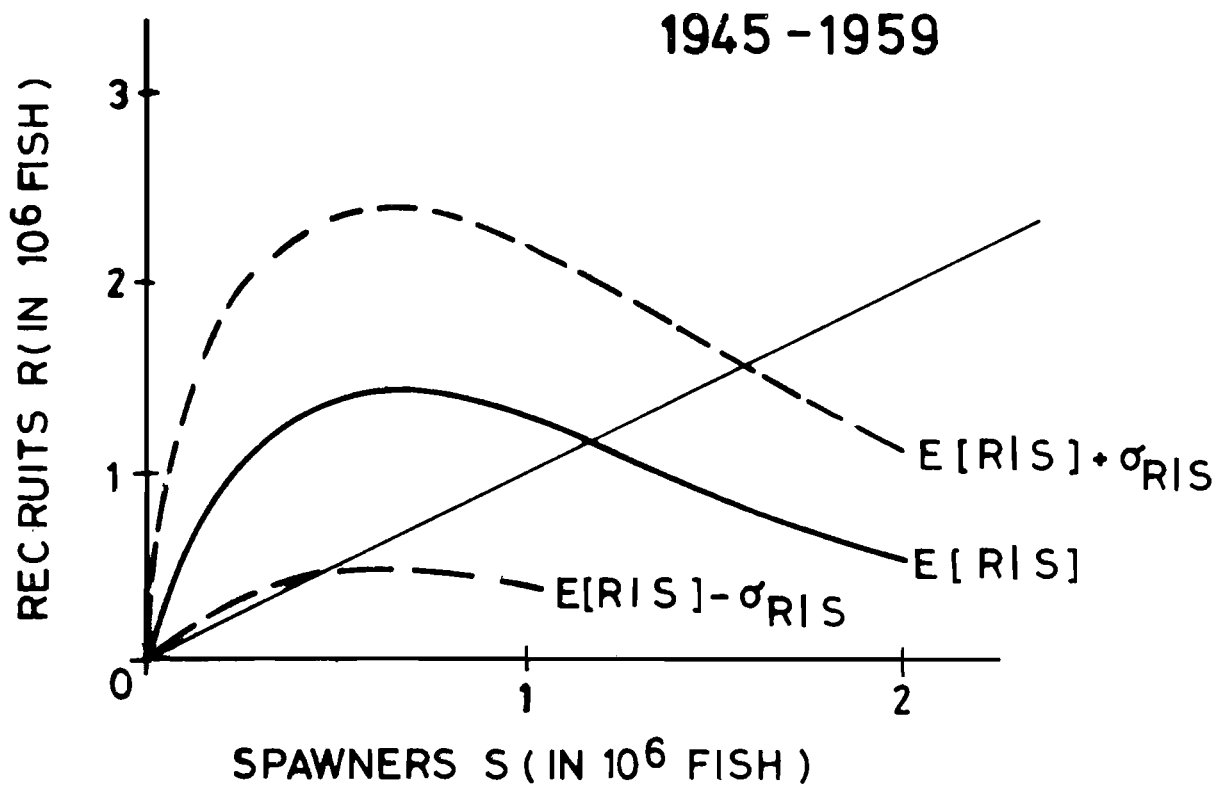


Figure 7. Expected recruits for spawning control levels: 1945-1959.

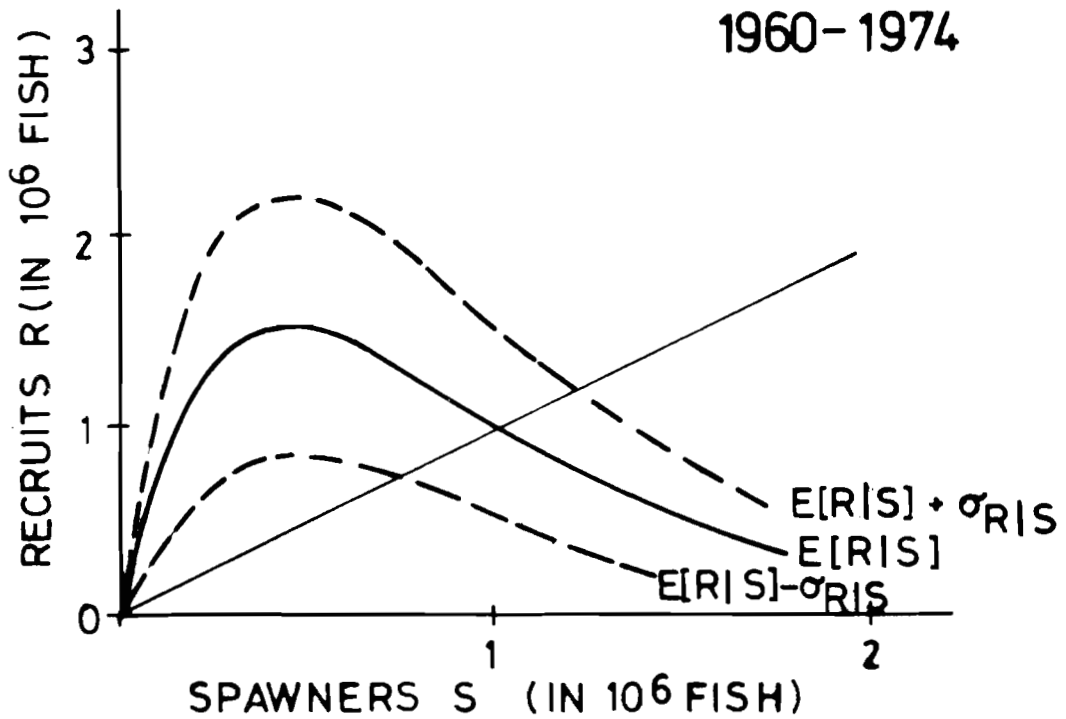


Figure 8. Expected recruits for spawning control levels: 1960-1974.

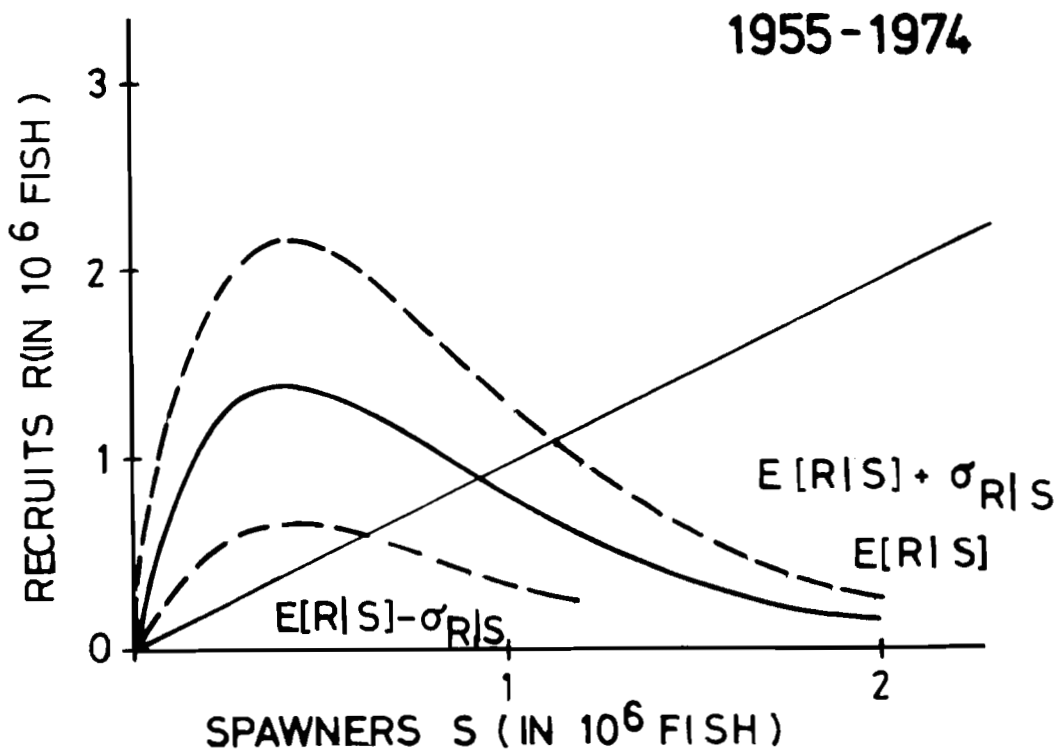


Figure 9. Expected recruits for spawning control levels: 1955-1974.

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