MODELS FOR VARIABLE RECRUITMENT (continued)

Fitting Real Data to the Spawner-Recruit Models

One strategy for fitting these spawner-recruit models to real data is to linearize the models by means of some suitable transformation and then apply standard linear regression methods. This was routine practice in the past when computers were unavailable. Better techniques are available now, but the linearization approach is worth exploring because it illustrates some important general lessons.

The Linearized Ricker SR Model

$$R = a \cdot S \cdot \exp(-b \cdot S) \quad \Longrightarrow \quad \frac{R}{S} = a \cdot \exp(-b \cdot S)$$

Divide both sides by S.

$$\Longrightarrow \quad \ln\left(\frac{R}{S}\right) = \ln(a) - b \cdot S$$

Apply the logarithm function to both sides.

$$Y = A + B \cdot X$$

We get a linear equation.

To estimate the parameters a and b, one can regress ln(R/S) against S. The parameter estimates are

$$\hat{a} = \exp(\text{intercept}) \qquad \hat{b} = -\text{slope}$$

The estimate for parameter a will be subject to the logarithmic transformation bias that we examined in one of the early lectures.

Explore the Excel demonstration of fitting the Ricker SR model with data from Table 11.6 of Ricker (1975).

The Linearized Beverton and Holt SR Model

$$R = \frac{S}{c + d \cdot S} = \frac{1}{\frac{c}{S} + d} \quad \Longrightarrow \quad \frac{1}{R} = d + c \cdot \frac{1}{S} \quad \text{or} \quad \frac{S}{R} = c + d \cdot S$$

To estimate the parameters c and d, one can regress 1/R against 1/S, or S/R against S. In the first case the parameter estimates are

$$\hat{c} = \text{slope} \qquad \hat{d} = \text{intercept}$$

Explore the Excel demonstration of fitting the Beverton & Holt SR model with data from Table 11.8 of Ricker (1975).

These linearization methods are quick and easy, but it is likely that the parameter estimates will be biased because the linearized models violate one or more of the assumptions that underlie the method of linear regression.

A Brief Review of Linear Regression Theory

The basic model of linear regression is of the following form.

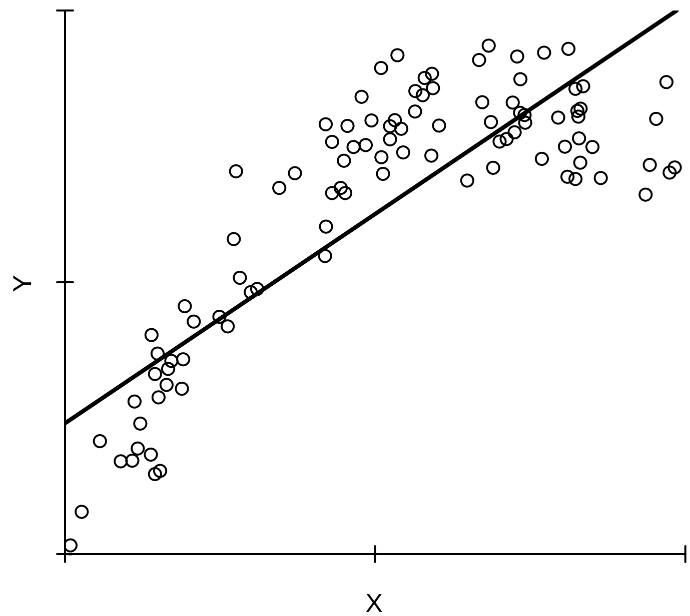
$$Y = a + b \cdot X + \varepsilon$$

where parameters a and b are constants, Y is the dependent variable, X is the independent variable, and ε is an error term to account for discrepancies between the observed values of Y and those values predicted by the model.

The following assumptions underlie linear regression:

- The variables Y and X are related as specified in the model.

We can fit a straight line to any XY data set, but the results may be meaningless if the underlying relationship is not linear.



- The residuals (the ε values) are normally distributed with zero mean and constant variance.
- The residuals are mutually independent.
- The X values are known without error.

If we look at either of the linearized stock-recruit models, we can see that they violate at least one of these assumptions. For example, if R for a given level of S is a normally distributed random variable, then (1/R) is not normally distributed, and neither is ln(R/S) or (R/S). Also, there are problems with the assumption of independent residuals because usually the R value in one data pair becomes the S value in the next pair. Furthermore, the independent variable S is never known exactly.

One partial solution is to use **nonlinear least squares regression** and fit the original forms of the models.

The Ricker Model: $$R = a \cdot S \cdot \exp(-b \cdot S) + \varepsilon$$

The Beverton & Holt Model: $$R = \frac{S}{c + d \cdot S} + \varepsilon$$

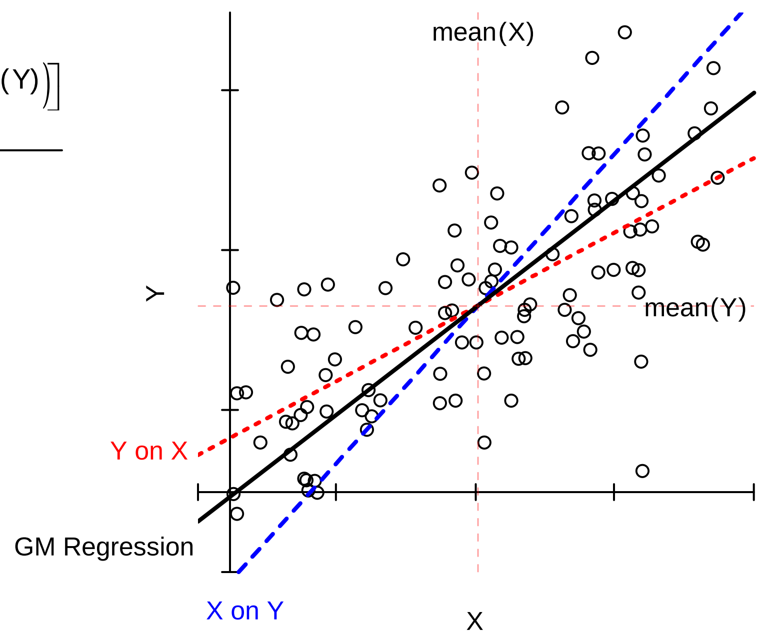
As in linear regression, this method chooses those parameter values that minimize the **residual sum of squares** ($\Sigma\varepsilon^2$) as the best parameter estimates. In nonlinear regression, however, the model is not a linear combination of the parameters. Nonlinear regression will produce unbiased parameter estimates even when the ε values are not normally distributed and do not have constant variance (assumption 2). However, this method will not properly account for lack of independence in the residuals (assumption 3). Also, it does not account for the influence of measurement error in the independent (X) variables (assumption 4).

Geometric Mean Functional Regression

With spawner-recruit data we almost always have the problem of errors in both the dependent variable (R) and the independent variable (S). In this situation Ricker (1975) suggests using the so-called **geometric mean** (**GM**) **functional** regression. The GM functional regression essentially splits the difference between the two extremes cases, all the measurement error in Y versus all the measurement error in X. In the first case (all the measurement error in Y, which is what we assume in the standard linear regression model), we regress Y on X and estimate the slope parameter using the formula

$$\hat{b} = \frac{\sum_n \left[\left(X_i - av(X)\right)\cdot\left(Y_i - av(Y)\right)\right]}{\sum_n \left(Y_i - av(Y)\right)^2}$$

We get different predicted regression lines depending on whether we regress Y on X or X on Y.



If all the measurement error is in X, then we would probably invert the model (i.e., regress X on Y) and estimate the inverted slope parameter using

$$\hat{b}' = \frac{1}{b} = \frac{\sum_n \left[\left(X_i - av(X)\right)\cdot\left(Y_i - av(Y)\right)\right]}{\sum_n \left(X_i - av(X)\right)^2}$$

In geometric mean functional regression we estimate the slope using

$$\hat{b}_{gm} = \sqrt{\frac{\sum_n \left(Y_i - av(Y)\right)^2}{\sum_n \left(X_i - av(X)\right)^2}} = \sqrt{\frac{b}{b'}}$$

This procedure has been criticized by statisticians, but it is used nevertheless by some fisheries scientists.

Walters and Ludwig's Analysis of Fitting Spawner-Recruit Data

The problem of fitting spawner-recruit data has been studied in detail by Walters and Ludwig (1981) on the *Supplemental Reading* list. Here is a brief summary.

Suppose the true spawner-recruit relationship is given by

$$S_{t+1} = S_t \cdot A \cdot \exp\left(u_t\right)$$

where u_t is environmentally induced random error that is normally distributed with mean zero and variance $\sigma_u{}^2$.

We do not observe the S values exactly, however. Instead we see

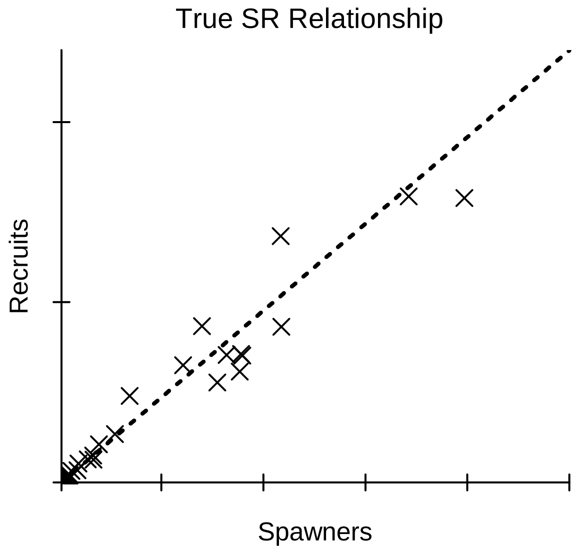
$$S'_t = S_t \cdot \exp\left(v_t\right)$$

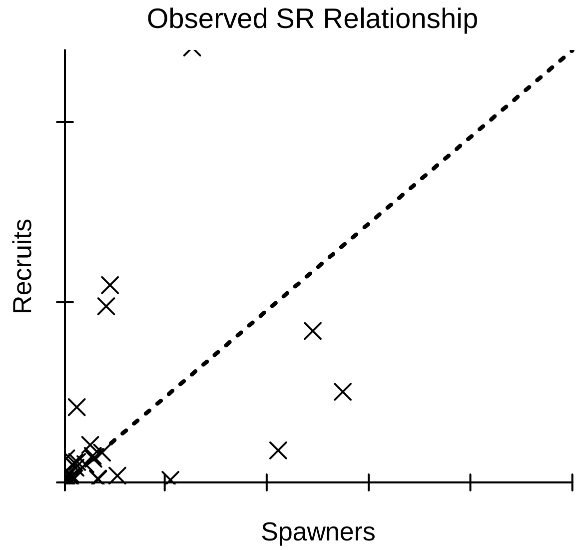
where v_t is normally distributed random measurement error with mean zero and variance $\sigma_v{}^2$. In this case we have both **process error**, (the u_t values) and **measurement error** (the v_t values). Statisticians sometimes describe this as an **errors in variables** problem.

Notice that in this simplified spawner-recruit model there is no density dependence. The model is strictly linear.

Walters and Ludwig describe this stock as being severely overexploited because all the observed values for stock size are close to the origin, well past the maximum equilibrium catch. In a less heavily exploited stock the true values for (S_{t+1},S_t) would show some curvature.

The following graphs illustrate the difference between the true spawner-recruit relationship and what we observe.





Explore the Excel demonstration of the effects of changing
σ_u^2 and σ_v^2 in the Walters and Ludwig model.

Walters and Ludwig go on to develop estimators for the Ricker model that account for the problems caused by simultaneous process and measurement errors. They use the following form of the Ricker model,

$$R = S \cdot \exp(a + b \cdot S + u) \qquad \text{where u is } N\left(0, \sigma_v^{\,2}\right)$$

Normally distributed environmental noise.

The linearized model is $Q = \ln\left(\frac{R}{S}\right) = a + b \cdot S + u$.

With ordinary least squares regression the estimator for the slope parameter is

$$\hat{b} = \frac{Cov(S \cdot Q)}{Var(S)}$$

This estimator is a **consistent estimator** only if the values for S (and therefore R , because S_{t+1}=R_t) are measured without error. In mathematical statistics the notion of consistency has to do with whether an estimator will on average produce increasingly precise estimates as the sample size increases.

For example, suppose Θ' is an estimate of some parameter Θ. In general the estimate Θ' will depend on the number of observations from which it was calculated. The formula for Θ', the estimator for Θ, is said to be consistent if the mean square error of the estimates approaches zero as the sample size (n) approaches infinity.

$$\lim_{n \to \infty} E\left[\left(\Theta'_n - \Theta\right)^2\right] = 0$$

Walters and Ludwig prove that the following estimator is consistent.

$$\hat{b} = \frac{Cov(S \cdot Q) + av(S) \cdot \sigma_v^2 \cdot B^3}{Var(S) - av(S)^2 \cdot (B^2 - 1)} \qquad \text{where} \qquad B = \exp(0.5 \cdot \sigma_v^2)$$

They compare their new consistent estimator with the least-squares estimator and draw the following conclusions. When there is weak density dependence (i.e., parameter b is near zero), then observation errors cause an overestimate of the amount of density dependence, which could lead to overexploitation. When there is strong density dependence (i.e., -b is large), then observation errors cause an underestimate of the amount of density dependence, which could also lead to overexploitation.

In general, many of the estimators that we use in fisheries science do not take proper account of measurement error in the independent variable. For example, errors in age determination will affect estimates of mortality rates from catch curve analyses and estimates of growth rates from length-at-age relationships.

Beverton and Holt's Derivation of the Ricker SR Model

In our derivation of Ricker's spawner-recruit model, the curvature in the graph of R(S) arose because a portion of the mortality on the cohort was proportional to the size of the parental population. Beverton and Holt (1957) give an alternative mechanism that also results in a Ricker type of spawner-recruit model. Here is a brief outline of the logic.

If predation is very high while young fish are in some critical size range, then the losses to the population will depend on the rate at which the young fish are able to grow out of the critical size range. Assume that predation occurs at instantaneous rate M_1 when the fish in a cohort are younger than t_c and hence weigh less than $W(t_c)$; for fish between the ages of t_c and t_R the instantaneous rate of natural mortality is M_2.

The number of recruits is

$$R = E_0 \cdot \exp(-M_1 \cdot t_c) \cdot \exp[-M_2 \cdot (t_R - t_c)]$$

R = fish that survive to age t_R	=	Eggs	X	*Fraction surviving to critical age t_c*	X	*Fraction surviving from age t_c to t_R*

Assume that the von Bertalanffy growth parameter W_{inf} is proportional to the amount of food eaten, which is inversely proportional to the density of larval fish. The more fish there are, then the less food there is per fish. These relationshionships are summarized by the equations

$$W_{inf} = k_1 \cdot Food\_Eaten = \frac{k_2}{Larval\_Fish\_Density}$$

where k_1 and k_2 are constants of proportionality. Now assume that growth is proportional to the von Bertalanffy growth parameter W_{inf}, which is approximately valid for short time spans and at low weights. The amount of time required to grow to $W(t_c)$ is inversely proportional to W_{inf} and directly proportional to the larval fish density and directly proportional to the amount of eggs spawned.

$$t_c = \frac{k_3}{W_{inf}} = \frac{k_4}{Food\_Eaten} = k_5 \cdot Larval\_Fish\_Density = k_6 \cdot E_0$$

Let $a' = \exp(-M_2 \cdot t_R)$ and $b' \cdot E_0 = (M_1 - M_2) \cdot t_c$

We can rearrange the earlier equation for R and substitute in a' and b'.

==> $R = a' \cdot E_0 \cdot \exp(-b' \cdot E_0)$

If E_0 is proportional to the parental stock size, then this equation has the same form as a Ricker spawner-recruit model.

Chapman's Salmon Spawner-Recruit Model

Chapman (1973), on the *Supplemental Reading* list, developed a spawner-recruit model for salmon that has a shape very similar to the Beverton and Holt model. Here is a brief overview of how it works.

Salmon redds may overlap and late-arriving spawners may destroy all or part of the earlier redds as they prepare their own. Suppose each redd covers an area a^2. On average the proportion of a stream bed that is covered by redds is equal to

$$1 - \exp\left[-(\pi \cdot a)^2 \cdot \frac{S}{A}\right]$$

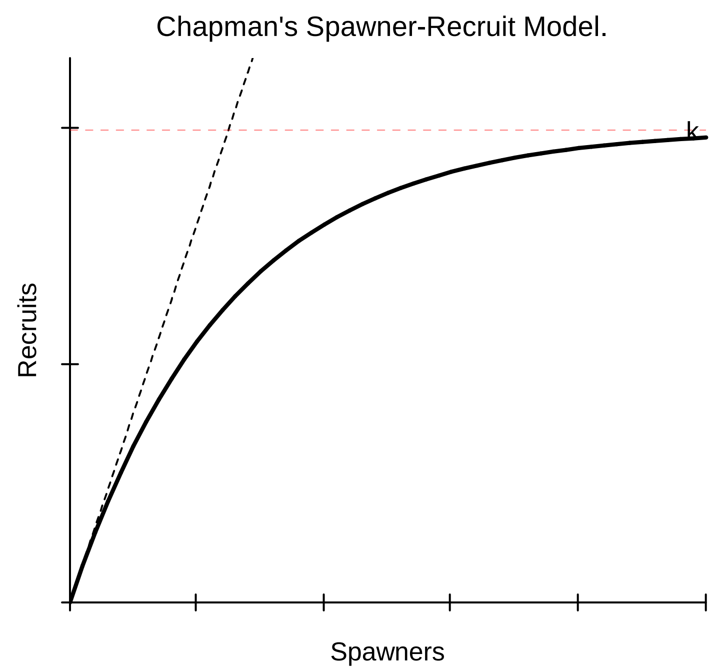
where A is the total area of the stream bed. The model is analogous to the "coverage of an area by randomly placed bombs." The above relationship leads to the following spawner-recruit model

$$R = k \cdot (1 - \exp(-h \cdot S))$$

where $h = (\pi \cdot a^2) / A$, and parameter k accounts for density independent mortality and the average number of eggs per redd.

The Chapman spawner-recruit model has the same basic form as the von Bertalanffy growth model and is very similar in appearance to the Beverton and Holt stock-recruit relationship.

The slope of the curve at the origin is k·h.



Shepherd's Generalized Stock-Recruit Model

The following stock-recruit model is developed in Shepherd (1982), which is on the *Supplemental Reading* list for our next major topic.

$$R = \frac{a \cdot S}{1 + \left(\frac{S}{K}\right)^{\beta}} \qquad \text{with parameters a, } \beta\text{, and K .}$$

The slope of R(S) is

$$\frac{dR}{dS} = \frac{a}{1 + \left(\frac{S}{K}\right)^{\beta}} - \frac{a \cdot S}{\left[1 + \left(\frac{S}{K}\right)^{\beta}\right]^2} \cdot \left(\frac{1}{K}\right)^{\beta} \cdot \left(\beta \cdot S^{\beta - 1}\right) = \frac{a \cdot \left[1 - (\beta - 1) \cdot \left(\frac{S}{K}\right)^{\beta}\right]}{\left[1 + \left(\frac{S}{K}\right)^{\beta}\right]^2}$$

When $S = 0$ the slope $\frac{dR}{dS} = a$, which means that parameter a is the slope of the R(S) curve at the origin.

The maximum value for R occurs when (and if)

$$\frac{dR}{dS} = 0 \qquad \text{==>} \qquad 1 = (\beta - 1) \cdot \left(\frac{S}{K}\right)^{\beta} \qquad \text{==>} \qquad \left(\frac{S}{K}\right)^{\beta} = \frac{1}{\beta - 1}$$

If $\beta < 1$, then R(S) is unbounded and has no finite maximum. To see this, consider that if β is less than1, then $\frac{1}{\beta - 1} < 0$. However, $\frac{1}{\beta - 1} = \left(\frac{S}{K}\right)^{\beta}$, which implies that S must be less than zero. R(S) cannot have a slope of zero for positve values of S if β is less than one.

This model with $\beta < 1$ is similar to a power law model

$$R = a \cdot S^{b} \qquad \text{with} \qquad b < 1$$

If $\beta > 1$, then R(S) has a finite maximum and the model is similar to Ricker's spawner-recruit model.

If $\beta = 1$, then the model is equivalent to a Beverton and Holt stock-recruit model.

$$R(S) = \frac{a \cdot S}{1 + \frac{S}{K}} = \frac{S}{\frac{1}{a} + \frac{1}{a \cdot K} \cdot S} = \frac{S}{c + d \cdot S} \qquad \text{with} \qquad c = \frac{1}{a} \qquad \text{and} \qquad d = \frac{1}{a \cdot K}$$

Shepherd describes parameter K as the threshold stock size. When S is greater than K, the density dependence effects dominate the stock-recruit relationship.

Semelparous versus Iteroparous Fish Stocks

Fish species such as Pacific salmon, which only spawn once and then die, are sometimes described as **semelparous** stocks. Fish species such as Atlantic salmon, and most fishes other than Pacific salmon, can and do spawn more than once in their lives. They are sometimes described as **iteroparous** stocks.

With a semelparous stock it is relatively easy to describe in theory the mechanics whereby the population adjusts to changed conditions, such as an increase in the harvest rate. With an iteroparous stock the mechanics are much more complicated because we need to account for those parents that survived previous spawnings.

Semelparous Stock: $S_1 = R(S_0) - C$

Iteroparous Stock: $S_1 = R(S_0) - C + S_0 \cdot e^{-Z_0} + S_{-1} \cdot e^{-Z_0 + -Z_{-1}} + ..$

Furthermore, the different age classes will probably differ in the number of eggs that they lay, because fecundity usually varies with size and age.

Supplemental Readings on Stock and Recruitment

Cushing (1973) discusses the role of various mechanisms such as density dependent fecundity, growth and increased natural mortality on older fish.

Walters and Ludwig (1981) and Ludwig and Walters (1981) discuss in detail the problem of measurement error.

Shepherd and Cushing (1980) develop a Beverton and Holt type of SR relationship from a model of larval growth and survival in which the instantaneous rate of growth in weight is inversely proportional to larval density.

Finally, the ICES Symposium "Fish Stock and Recruitment", Rapp. P.-v. Reun. 164, contains many interesting and relevant papers on the subject of stock-recruit models, including the following on the *Supplemental Reading* llist: Paulik (1973), Larkin (1973), Ricker (1973), and Gulland (1973).