

fishR Vignette - Stock-Recruitment Models

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The functions required to perform growth analyses in R are contained in the `FSA` and `FSAdata` packages maintained by the author and `nlstools` and `plotrix` maintained by others. These package are loaded into R with

```
> library(FSA)
> library(FSAdata)
> library(nlstools)
> library(plotrix) # for plotCI()
```

1 Background

Quinn II and Deriso (1999) provide a simple schematic that represents the cycle of regeneration for fish populations (Figure 1). Most readers are likely familiar with the terms “spawners” (often time called “spawning stock” or just “stock”), “eggs”, “larvae”, and “juveniles” and have likely heard of “recruits.” However, the definition of “recruits” is very important to stock-recruit analysis and fisheries science in general.

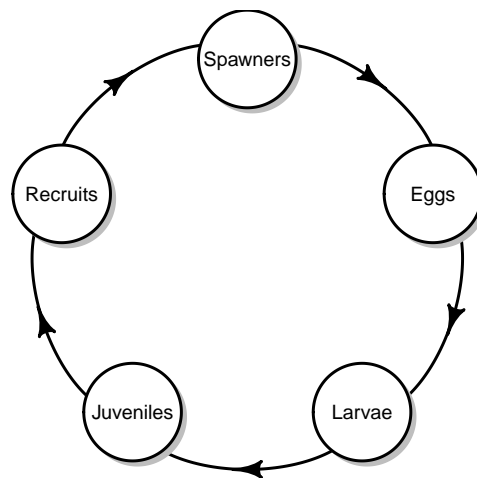


Figure 1. Representation of the stages in the life cycle of a fish population (adapted from Quinn II and Deriso (1999)).

In its most basic form, recruitment is the addition of young fish to the parent stock of fish. In practice, though, the definition is not as simple. Recruitment can be defined by the age of the fish. For example, fish that have matured to an **age** where they are able to reproduce are said to have “recruited to the breeding population” and fish that have survived to age-1 are said to have “recruited to age-1.” Some situations require recruitment to be defined by the size of the fish. For example, fish that have survived to a **length** where they are able to reproduce are said to have “recruited to the breeding population” and fish that have survived to a catchable size (defined by tackle, gear, or minimum size by regulation) are said to have “recruited to the fishery.” Most stock-recruit analyses will consider “recruitment to the fishery” based on size or “recruitment to the breeding population” based on size or age. However, as these examples illustrate, it is critically important to explicitly define what measure of recruitment one is using in a stock-recruit analysis.

1.1 Density Independent Model

In the simplest models, the abundance of individuals at each stage is assumed to be proportional to the abundance of individuals at the previous stage (Quinn II and Deriso 1999). For example, if each individual in the spawning stock (S) produces an average of f eggs¹ (Figure 2), then the number of eggs produced (N_0) can be estimated with

$$N_0 = fS \quad (1)$$

Similarly, if g represents the probability of survival from an egg to the time of recruitment (Figure 2), then the number of recruits (R) can be estimated with

$$R = gN_0 \quad (2)$$

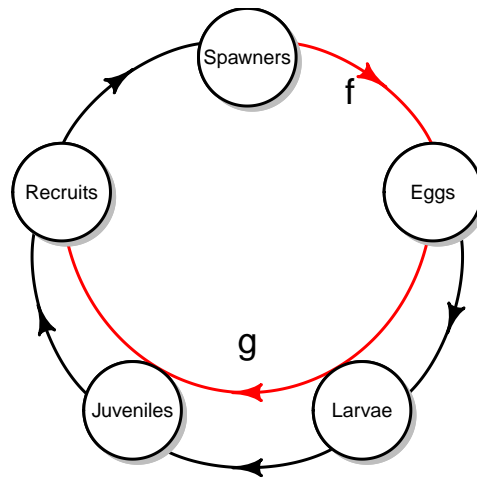


Figure 2. Representation of the stages in the life cycle of a fish population with variables representing transition constants between some stages (adapted from Quinn II and Deriso (1999)).

If one substitutes (1) into (2) for N_0 and replaces the fg product with a , then it can be seen that R is proportional to S . As all of the models presented here are representative of an average of the response variable rather than the individual observations themselves, the left-hand-side (i.e., the response side) of the model will be written as an expectation. Thus, in this case, R will be replaced with $E[R|S]$ on the left-hand-side and $E[R|S]$ will be read as the “expected value of R given S .” Thus, the simplest non-trivial stock-recruitment model is given as

$$E[R|S] = aS \quad (3)$$

While (3) is unrealistic, in the sense that the number of recruits can increase without bound as a function of the number of spawners (Figure 3), it does provide some valuable insight into more realistic stock-recruit models to be discussed later. A simple rearrangement of (3),

$$\frac{R}{S} = a$$

shows that the ratio of recruits to spawners is a constant (Figure 3). In other words, the ratio of recruits to spawners does not depend on, or is independent of, the number of spawners. For this reason, (3) is often referred to as the “density independent” stock-recruitment model and a is often referred to as the “density independent” parameter.

¹Thus, f is the average net fecundity.

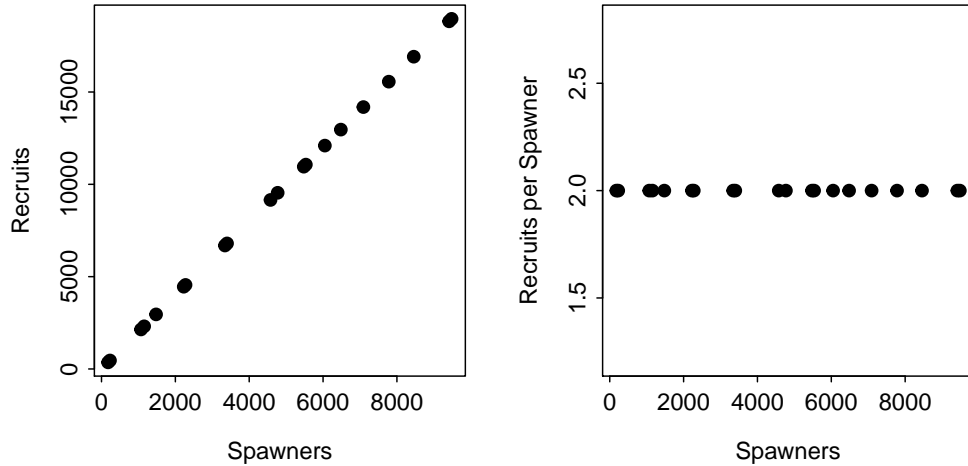


Figure 3. Plot of number of recruits (Left) and number of recruits per spawner (Right) against number of spawners for idealistic data constructed using equation 3, random number of spawners from a uniform distribution between 0 and 10000, and $a=2$.

The density-independent model in (3) is an unrealistic model if there is any density-dependent effect on mortality, fecundity, or growth of fishes (Wootton 1990). As such, a variety of models have been developed that extend the density-independent model by incorporating a density-dependent term. These models are discussed in the Section 1.2 and Section 1.3.

1.2 Beverton-Holt Model

Beverton and Holt (1957) proposed a model that assumed that recruitment approached an asymptote at high spawning stock abundance (Figure 4). Specifically, their model can be expressed as

$$E[R|S] = \frac{aS}{1 + bS} \quad (4)$$

This model expresses a density-dependent relationship because the number of recruits per spawner is a decreasing function of the number of spawners (Figure 4). In (4), a is still the density-independent parameter that is proportional to fecundity. The units of a are “recruitment per spawner” and the value of a is the slope of the model near $S = 0$. However, b is a density-dependent parameter that is proportional to both fecundity and density-dependent mortality (Quinn II and Deriso 1999). If density-dependence in the stock-recruitment relationship does **not** exist, then $b = 0$ and (4) reduces to the density-independent model (3). The asymptote, or peak recruitment (denoted by R_p), of (4) is defined by $R_p = \frac{a}{b}$ (Figure 4). The Beverton-Holt model is based on the assumptions that juvenile competition results in a mortality rate that is linearly dependent upon the number of fish alive in the cohort at any time and that predators are always present. The Beverton-Holt model is appropriate “if there is a maximum abundance imposed by food availability or space, or if the predator can adjust its predatory activity immediately to changes in prey abundance” (Wootton 1990, p. 264).

1.2.1 Alternative Parameterizations

A model can often be cast into a different form where the model is functionally the same – i.e., predictions are exactly the same – but it has different parameters. This alternative form is called a parameterization. All parameterizations of a model can ultimately be shown to be equivalent via algebra. Different parameterizations of models are created for a variety of reasons, but the two most important reasons are that the re-parameterized model has parameters (i) for which the interpretation meets some need and (ii) that are

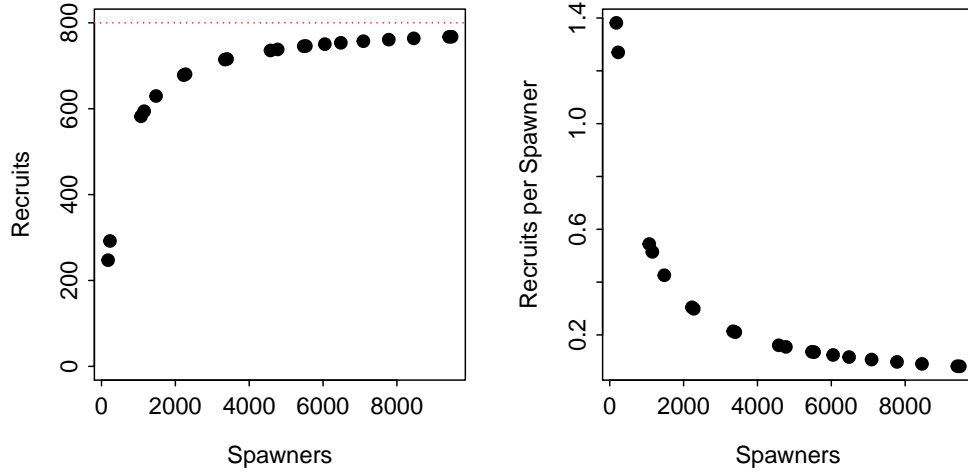


Figure 4. Plot of number of recruits (Left) and number of recruits per spawner (Right) against number of spawners for idealistic data constructed using equation 4, random number of spawners from a uniform distribution between 0 and 10000, $a=2$, and $b = 0.0025$. A horizontal line on the left plot is shown at $\frac{a}{b} = \frac{2}{0.0025} = 800$ for reference.

less correlated. The Beverton-Holt stock-recruitment model has been re-parameterized in a variety of ways, with the four most common re-parameterizations shown and discussed briefly below.

If $R_p = \frac{a}{b}$ is solved for b and substituted into (4), then the Beverton-Holt model can be re-written as

$$E[R|S] = \frac{aS}{1 + a\frac{S}{R_p}} \quad (5)$$

In this parameterization, the two parameters, a and R_p , are as defined above. Thus, this parameterization provides a direct estimate of the peak recruitment value.

If $\tilde{a} = \frac{1}{a}$ and $\tilde{b} = \frac{b}{a}$ are substituted into (4) and algebraically simplified, then the Beverton-Holt model can be re-written as

$$E[R|S] = \frac{S}{\tilde{a} + \tilde{b}S} \quad (6)$$

In this parameterization, \tilde{a} is still related to density-independence but the relationship is in the opposite direction of a in (4) and (5). In other words, if a is “large” then \tilde{a} will be small. The asymptote of (6) is then at $R_p = \frac{1}{\tilde{b}}$.

Additionally, if $R_p = \frac{1}{\tilde{b}}$ is solved for \tilde{b} and substituted into (6), then the Beverton-Holt model can be re-written as

$$E[R|S] = \frac{S}{\tilde{a} + \frac{S}{R_p}} \quad (7)$$

As with (5), this parameterization provides a direct estimate of R_p .

All parameterizations of the Beverton-Holt model fit the data in exactly the same way (Figure 5). In addition, the correlations among model parameters do not differ substantively (Table 1). Thus, the only real reason for choosing any particular parameterization lies in choices you make regarding which parameters should be estimated. Throughout the remainder of this vignette the first, i.e., (4), or second, i.e., (5), parameterizations will be used as they allow for a direct comparison to the general density independence model (i.e., (3)).

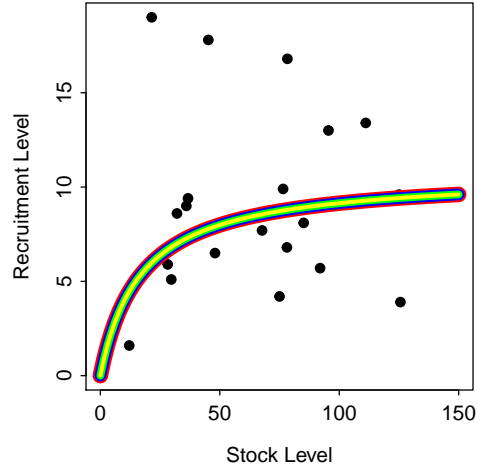


Figure 5. Fits of the four parameterizations of the Beverton-Holt stock-recruitment model to the Lake Trout data from area MI7 in Lake Superior. Note that the results of all fits are identical and, thus, the fitted lines are directly on top of each other. Different colors and different line widths were used to try to illustrate this point but may not be readily apparent on the screen or printed page.

Table 1. Parameter estimates and model results from fitting, with multiplicative errors, different parameterizations of the Beverton-Holt stock-recruitment model (in the order presented in the text) to Lake Trout from area MI-7 in Lake Superior. The parameters are as defined in the text. Note that “calc R_p ” is R_p computed from other parameters (rather than estimated directly, “SE” is the residual variability, and “ r ” is the correlation coefficient between the two parameters.

Models	a	b	\tilde{a}	\tilde{b}	R_p	calc R_p	SE	r
1	0.632	0.059	-	-	-	10.69	0.56	0.99
2	0.632	-	-	-	10.69	-	0.56	-0.82
3	-	-	1.581	0.094	-	10.69	0.56	-0.82
4	-	-	1.581	-	10.69	-	0.56	0.82

1.3 Ricker Model

Ricker (1954) proposed a stock-recruitment model that was “dome-shaped” – i.e., the peak level of recruitment occurred at an intermediate spawning stock abundance (Figure 6). Specifically, the Ricker model can be expressed as

$$E[R|S] = aSe^{-bS} \quad (8)$$

This model expresses a density-dependent relationship because the number of recruits per spawner is a decreasing function of the number of spawners (Figure 6). In (8), a is still the density-independent parameter that is proportional to fecundity and b is the density-dependent parameter (Quinn II and Deriso 1999). If density-dependence in the stock-recruitment relationship does **not** exist, then $b = 0$ and (8) reduces to the density-independent model (3). The peak level of recruitment is given by $R_p = \frac{a}{be}$ and occurs at a spawning stock biomass of $\frac{1}{b}$ (Figure 6)

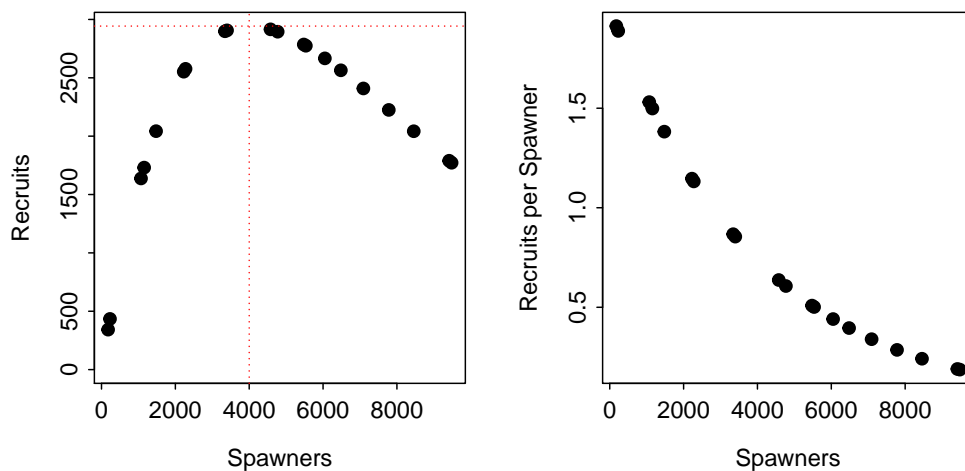


Figure 6. Plot of number of recruits (Left) and number of recruits per spawner (Right) against number of spawners for idealistic data constructed using equation `efeqn:SRRicker1`, random number of spawners from a uniform distribution between 0 and 10000, $a=2$, and $b = 0.00025$. A horizontal line on the left plot is shown at $\frac{a}{be} = \frac{2}{0.00025e} = 2943$ and a vertical line is shown at $\frac{1}{b} = \frac{1}{0.00025} = 4000$ for reference.

The Ricker stock-recruitment model assumes that the mortality rate of the eggs and juveniles is proportional to the initial cohort size. In other words, if, for example, the initial number of eggs is high then the mortality rate of the eggs and juveniles will also be high. Biological realities that might lead to this assumption being met are (1) cannibalism of the juveniles by the adults (Ricker 1975), (2) disease transmission, (3) damage by adults of one another's spawning sites (e.g., redd superimposition), (4) density-dependent reductions in growth coupled with size-dependent predation (e.g., increase in the time it takes for the young fish to grow through a size range vulnerable to predation; Ricker (1975)), and (5) a time-lag in the response of a predator or parasite to the abundance of the fish (Wootton 1990).

1.3.1 Alternative Parameterizations

As shown with the Beverton-Holt model above, the Ricker model can also be written in different forms. Two common parameterizations are shown below.

Ricker (1954) commonly defined $\tilde{a} = e^a$ such that (8) is modified to

$$E[R|S] = Se^{\tilde{a}-bS} \quad (9)$$

With (9) the peak level of recruitment is $R_p = \frac{e^{\tilde{a}}}{be}$ at a stock level of $\frac{1}{b}$.

The first parameterization, i.e., (8), can be modified to include a parameter for the peak level of recruitment by solving $R_p = \frac{a}{be}$ for b and substituting into (8) to produce

$$E[R|S] = aSe^{-a\frac{S}{R_p e}} \quad (10)$$

Thus, fitting (10) will result in a direct estimate of the peak level of recruitment (R_p) at a stock level of $\frac{R_p e}{a}$.

All parameterizations of the Ricker model fit the data in exactly the same way (Figure 7). The correlation between model parameters was substantially lower for the third parameterization (Table 1). The first or third parameterizations will be used throughout the remainder of this vignette as they allow direct comparison to the general density independence model (i.e., (3)).

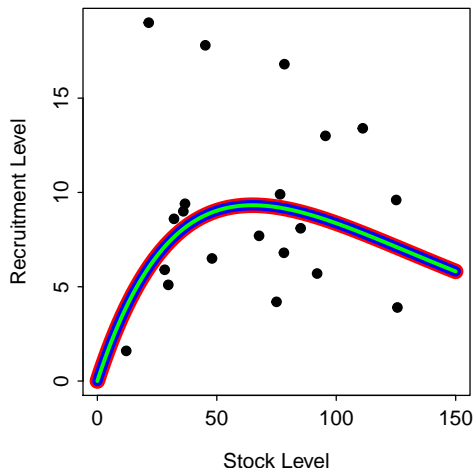


Figure 7. Fits of the three parameterizations of the Ricker stock-recruitment model to the Lake Trout data from area MI7 in Lake Superior. Note that the results of all fits are identical and, thus, the fitted lines are directly on top of each other. Different colors and different line widths were used to try to illustrate this point but may not be readily apparent on the screen or printed page.

Table 2. Parameter estimates and model results from fitting, with multiplicative errors, different parameterizations of the Ricker stock-recruitment model to Lake Trout from area MI7 in Lake Superior. The parameters are as defined in the text. Note that “calc R_p ” is R_p computed from other parameters (rather than estimated directly, “calc S_p ” is the calculated stock level where the peak level of recruitment occurs, “SE” is the residual variability, and “r” is the correlation coefficient between the two parameters.

Models	a	b	\tilde{a}	R_p	calc R_p	calc S_p	SE	r
1	0.390	0.015	-	-	9.32	64.96	0.53	0.89
2	-	0.015	-0.941	-	9.32	64.96	0.53	0.89
3	0.390	-	-	9.32	-	64.96	0.53	0.46

2 Thoughts on Model Fitting

2.1 Statistical Error Types

Most linear and non-linear model fitting algorithms assume that the random errors in the model are additive and normal. If these errors are depicted by ϵ , then, for example, the Ricker² model (8) with additive errors would be written as (Quinn II and Deriso 1999)

$$R = aSe^{-bS} + \epsilon$$

Fitting the model with additive errors assumes that the variability around the model is the same in all areas of the data. It is often the case, where the variability will be greater near the peak of the model. In these cases, a multiplicative error structure may be more appropriate. A model with a multiplicative error structure is written as

$$R = aSe^{-bS}e^\epsilon$$

Most computer algorithms will not fit these models directly as the algorithm expects an additive error structure. However, taking natural logarithms of both sides transforms the model with a multiplicative error structure to one with an additive error structure (Quinn II and Deriso 1999). For example,

$$\log(R) = \log(aSe^{-bS}) + \epsilon$$

Thus, a model with a multiplicative error structure can be fit with most computer algorithms by using the model where both sides have been logged. Because of this relationship, a multiplicative error structure is often referred to as fitting the model with “lognormal errors.”

Fitting the model with different error structures can lead to substantially different parameter estimates (Figure 8). While one should carefully examine the residuals of each fitted model, Quinn II and Deriso (1999) suggest that the theory used to develop the Beverton-Holt and Ricker models suggests that the multiplicative error model should be the default choice. They also suggest that the multiplicative error model “fits the error structure of actual data sets fairly well” (Quinn II and Deriso 1999, p. 104).

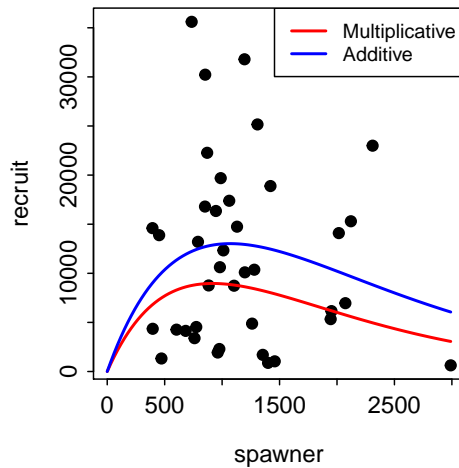


Figure 8. Number of recruits versus number of spawners for Escanaba Lake Walleye with the Ricker stock-recruitment model fit with additive and multiplicative errors superimposed.

2.2 Variability

Stock-recruitment data is notoriously “messy” with large year-to-year variability in recruitment (Figure 9) and a weak relationship between spawning stock and number of recruits (Figure 10). This variability or the

²From hereon the term “Ricker” model and “Beverton-Holt” model will refer to the first parameterizations of each model.

resultant difficulties in fitting or interpreting stock-recruitment models has been commented on by several authors:

Much ingenuity has been spent in fitting these curves to data sets and to developing the basic models. All this effort has largely foundered in the face of the variability in the relationships between stock and recruitment shown by most natural populations. The curves can be fitted, but it takes an act of faith to take the resulting curves seriously. – (Wootton 1990, p. 264)

Empirical relationships between spawning stock and recruitment shown extreme annual variability. – (Quinn II and Deriso 1999, p. 86)

... a number of tools are available for the analysis of stock and recruitment, but there are many pitfalls awaiting the unwary biologist who want to fit a curve and get an answer. ...

Analysis of stock-recruitment data provides an enormous number of traps for the unwary – good luck. (Hilborn and Walters 2001, p. 295)

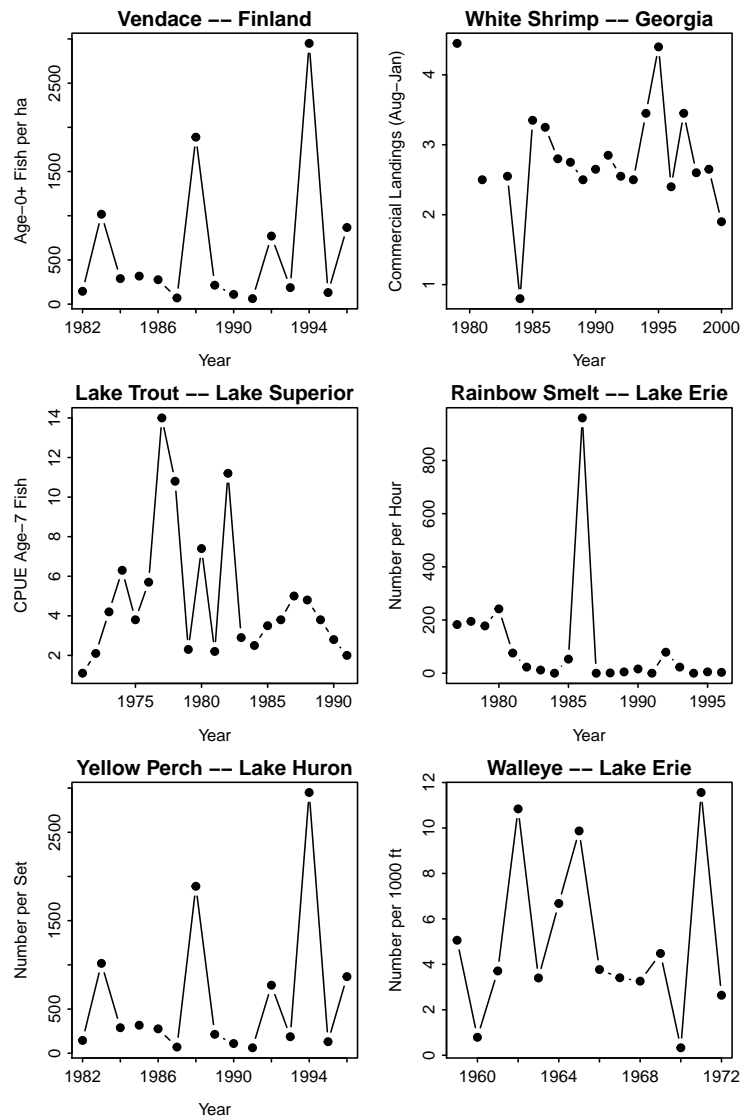


Figure 9. Plot of number of recruits versus year for a variety of species.

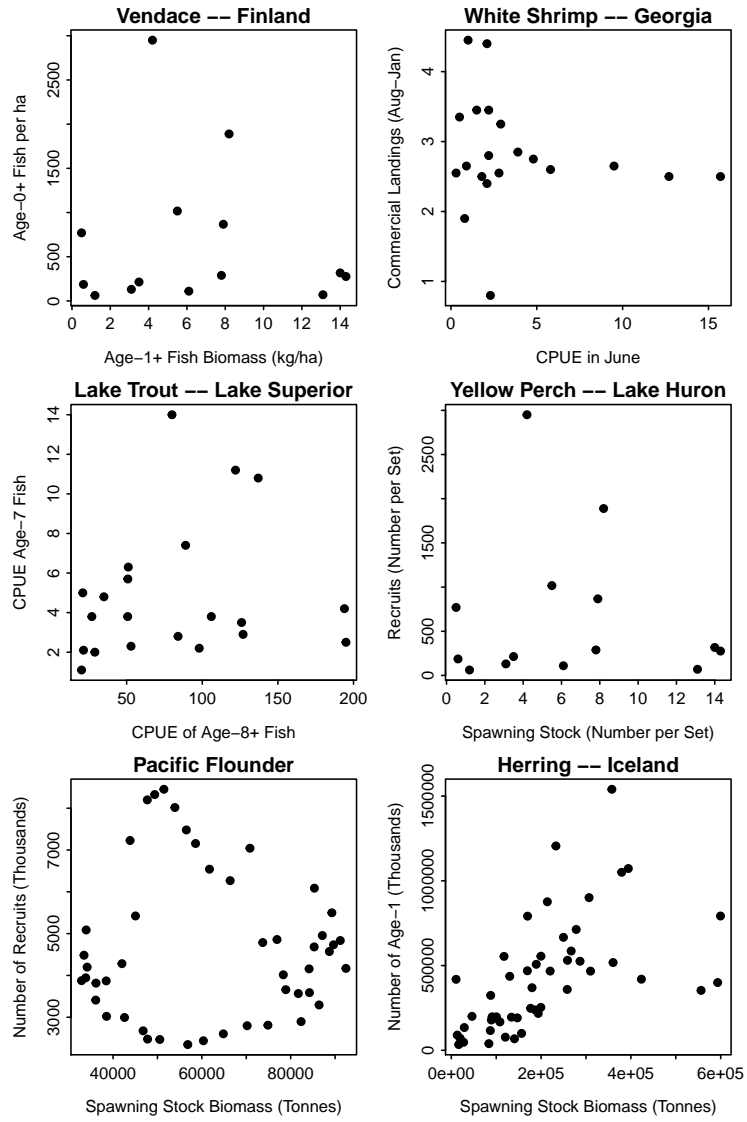


Figure 10. Plot of number of recruits versus spawning stock for a variety of species.

2.3 Starting Values

The Beverton-Holt and Ricker stock-recruit models are best fit using non-linear regression methods. Non-linear regression methods use an iterative algorithm that requires starting values for the model parameters. There are at least two ways to arrive at reasonable starting values for the parameters of the Beverton-Holt and Ricker stock-recruit models – (i) estimation from linearized models and (ii) visual estimation with dynamics graphics. Both methods are discussed below.

The first parameterization of the Beverton-Holt model can be viewed as a linear function as shown in (11)³. Thus, a linear regression of the inverse of R (i.e., $\frac{1}{R}$) on the inverse of S (i.e., $\frac{1}{S}$) will yield an equation where the slope is equal to $\frac{1}{a}$ and the intercept is equal to $\frac{b}{a}$. The slope and intercept equivalents can be solved for a and b to derive reasonable starting values for the non-linear regression algorithm. Starting values for other parameters in the other parameterizations can be derived by using the starting values of a and b in the parameter equivalency equations.

$$\frac{1}{E[R|S]} = \frac{1}{a} \frac{1}{S} + \frac{b}{a} \quad (11)$$

The first parameterization of the Ricker model can be viewed as a linear function as shown in (12)⁴. Thus, a linear regression of the log of $\frac{R}{S}$ on S will yield an equation where the slope is equal to $-b$ and the intercept is equal to $\log(a)$. Again, the slope and intercept equivalents can be solved for a and b to derive reasonable starting values. Starting values for the other parameters in the other parameterizations can be derived by using the starting values for a and b in the parameter equivalency equations.

$$\log\left(\frac{E[R|S]}{S}\right) = \log(a) - bS \quad (12)$$

The methodology described above has been implemented in `srStarts()` and is described in more detail in Section 3.

The selection of starting values for the stock-recruit models can also be easily estimated with `srSim()` from the `FSATeach` package⁵. This function produces a plot of R versus S with a stock-recruit model superimposed. The parameters of the superimposed stock-recruit model can be controlled with slider bars. Thus, the slider bars can be adjusted until a model is produced that “roughly” fits the observed recruit versus stock graphic. The parameters of the model when this rough fit is found can then be used as the starting values for the non-linear methods. For this purpose, `srSim()` has the same four arguments as `srStart()`. As an example, the starting values for the first parameterization of the Beverton-Holt model is shown by the slider bars on the graphic (Figure 11) produced with

```
> srSim(recruits~stock,data=LakeTroutGIS,type="BevertonHolt",param=1)
```

2.4 Assumption Checking

The non-linear regression, as it has been described here, requires that the variability about the model is constant (i.e., homoscedasticity), the errors are normally distributed, the model adequately fits the data, and there are no influential or outlying points. There are tests to determine if these assumptions have been violated, but these tests can be hyper-sensitive (i.e., tend to identify assumption violations) especially with large sample sizes. Thus, the adequacy of meeting these assumptions can be better determined by objectively analyzing two important graphics. The first graphic is a residual plot which plots the model residuals versus the fitted values (Figure 12-Left). In general, the assumptions of the model are met if NO pattern is observed

³Note that the critical step in deriving this model is to first invert both sides of (4).

⁴Again, the critical first step in deriving this function is inverting the original function (8).

⁵Note that the `FSATeach` package must be installed as described [here](#) and the loaded with `library(FSATeach)`.

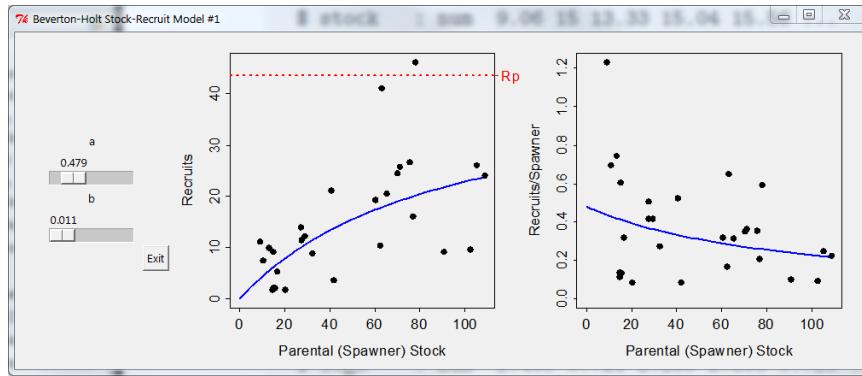


Figure 11. Example of using `srSim()` to find an approximate fit of the first parameterization of the Beverton-Holt stock-recruitment model to the Gull Island Shoal Lake Trout data.

in the residual plot. Curvature in this plot would suggest that the model does not represent the data very well and a “funneling” from left-to-right would suggest that the variability around the model is not constant (i.e., heteroscedasticity). The second graphic is a histogram of the residuals (Figure 12-Right). In general, the assumption of normality is adequately met if this histogram is symmetric without overly long “tails.”

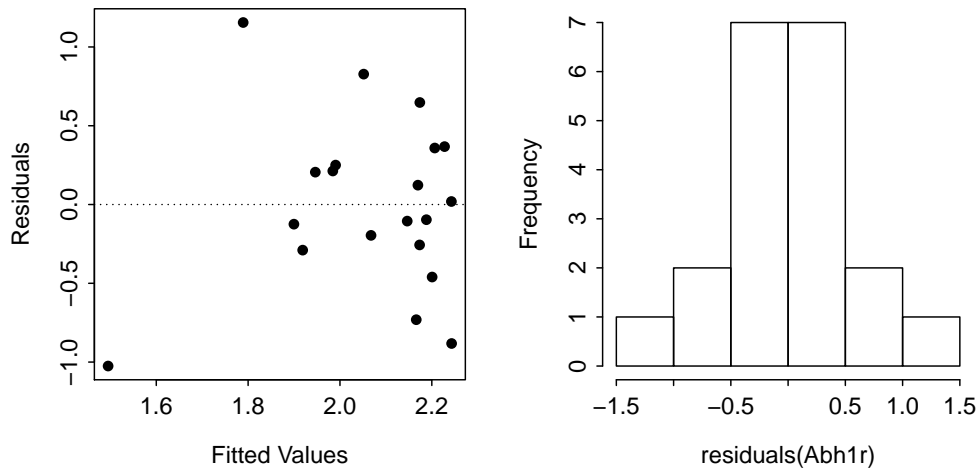


Figure 12. Residual plot (left) and residual histogram (right) from fitting the first parameterization of the stock-recruit model to the Lake Superior Lake Trout from area MI7 data.

The residual plot can be constructed by submitting the saved `nls` object to `residPlot()`. The histogram can be constructed by submitting the saved `nls` object to `residuals()` and then submitting this result to `hist()`. Interpretation of these graphics will be discussed further in the context of the examples in the following section.

3 Fitting Basic Models in R

Both the Beverton-Holt and Ricker stock-recruit models can be linearized and fit with least-square simple linear regression. However, the models can also be fit with non-linear least-squares methods that provide similar parameter estimates but provides a method that is more general and extensible. Fitting non-linear models in R is described in detail in the Von Bertalanffy Growth Model vignette. Briefly, the non-linear model fitting procedure in R is implemented with `nls()`, which requires the model formula, the list of starting values, and the data frame as arguments. In addition, `trace=TRUE` can be included in `nls()` to see the residual sum-of-squares and current values of the parameters for each iteration of the fitting process. For

simplicity and clarity, the starting values can be entered into a list and the formula can be created prior to calling `nls()`. The use of `nls()` is illustrated with the following examples.

The mean catch-per-unit-effort of adult female Lake Trout per 1000 m of gillnet from fall spawning surveys (i.e., the “stock”) and the density of age-0 fish per ha captured the following fall in bottom trawls (i.e., the “recruits”) were recorded from an area near Gull Island Shoal in the Apostle Islands region of Lake Superior (Schram *et al.* 1995). These data are loaded and the structure is observed with

```
> data(LakeTroutGIS)
> str(LakeTroutGIS)

'data.frame': 28 obs. of 3 variables:
 $ year      : int  1964 1965 1966 1967 1968 1969 1970 1971 1972 1973 ...
 $ stock     : num  9.06 15 13.33 15.04 15.56 ...
 $ recruits  : num  11.12 2.06 9.87 9.05 2.06 ...
```

In order to fit a stock-recruitment model with multiplicative errors, a new variable consisting of the natural log of the “recruit” variable must be constructed and appended to the data frame with

```
> LakeTroutGIS$logR <- log(LakeTroutGIS$recruit)
> str(LakeTroutGIS)

'data.frame': 28 obs. of 4 variables:
 $ year      : int  1964 1965 1966 1967 1968 1969 1970 1971 1972 1973 ...
 $ stock     : num  9.06 15 13.33 15.04 15.56 ...
 $ recruits  : num  11.12 2.06 9.87 9.05 2.06 ...
 $ logR      : num  2.409 0.721 2.289 2.203 0.723 ...
```

3.1 Fitting Beverton-Holt Model in R – Case I

The linear models used to generate starting values discussed previously are implemented in R with `srStarts()`. This function which requires a model of the generic form $R \sim S$ as the first argument, the data frame from which to find R and S in the `data=` argument, the type of model (either “BevertonHolt” or “Ricker”) in the `type=` argument, and the “number” of the parameterization in the `param=` argument. The “numbers” used in `param=` correspond to the order the parameterizations were presented in this vignette⁶. Starting values for the Lake Trout example were generated, and saved to an object, with

```
> bh1s <- srStarts(recruits~stock,data=LakeTroutGIS,type="BevertonHolt",param=1)
> unlist(bh1s) # unlist used just to save space when displaying
      a      b
0.36437 0.01857
```

For simplicity, the Beverton-Holt model should be declared and saved to an object before proceeding to use `nls()`. For example, the first parameterization is declared with⁷

```
> bh1 <- logR~log((a*stock)/(1+b*stock))
```

The Beverton-Holt model is then fit and saved to an object with⁸

⁶The models can also be seen with `srModels()`

⁷The `srFuns()` function can be used to declare this and other stock-recruit model functions. In this case, one would use `bh1 <- srFuns(type="BevertonHolt",param=1)`.

⁸If the model `bh1` was declared using `srFuns()`, then one would need to use `bh1nls <- nls(logR~log(bh1(stock,a,b)),data=LakeTroutGIS,start=bh1s)` to fit the model here.

```
> bh1nls <- nls(bh1,data=LakeTroutGIS,start=bh1s)
```

For comparative purposes the density-independence model is fit and saved to an object with

```
> bh0 <- logR~log(a*stock)           # declare model
> bh0s <- bh1s[1]                   # use the same starting value as above for a
> bh0nls <- nls(bh0,data=LakeTroutGIS,start=bh0s)
```

An “extra sums-of-squares” test and AIC calculations for determining whether the density independence or Beverton-Holt model “best” fits the data is computed with

```
> anova(bh0nls,bh1nls)
Analysis of Variance Table

Model 1: logR ~ log(a * stock)
Model 2: logR ~ log((a * stock)/(1 + b * stock))
  Res.Df Res.Sum Sq Df Sum Sq F value Pr(>F)
1      27      14.6
2      26      13.7  1  0.821    1.55  0.22
> AIC(bh0nls,bh1nls)
      df   AIC
bh0nls  2 65.16
bh1nls  3 65.53
```

With a large p-value ($p = 0.22$) for the ANOVA and a larger AIC value, it is clear that the Beverton-Holt model does NOT explain significantly more of the variability in recruitment than a simple density-independence model. Thus, the Beverton-Holt model with the density-dependent parameter does NOT appear to be a “better” fit for these data.

A graphic (Figure ??) depicting the relative fit of these two models can be constructed, from the “ground up”, as shown with

```
> plot(recruits~stock,data=LakeTroutGIS)
> curve((coef(bh1nls)[1]*x)/(1+coef(bh1nls)[2]*x),from=0,to=120,col="red",lwd=2,add=TRUE)
> curve(coef(bh0nls)[1]*x,from=0,to=120,col="blue",lwd=2,add=TRUE)
> legend("topleft",legend=c("density independent","density dependent"),
  col=c("blue","red"),lwd=2,cex=0.6)
```

The parameter estimates, along with other summary results, are obtained by submitting the saved `nls()` object to `overview()` from the `nlstools` package. Because the Beverton-Holt model was not a “better” fit, this is demonstrated below for the Beverton-Holt model for illustrative purposes only,

```
> overview(bh1nls)

-----
Formula: logR ~ log((a * stock)/(1 + b * stock))

Parameters:
  Estimate Std. Error t value Pr(>|t|)
a  0.38276   0.11470    3.34  0.0026
b  0.00736   0.00809    0.91  0.3711

Residual standard error: 0.727 on 26 degrees of freedom
```

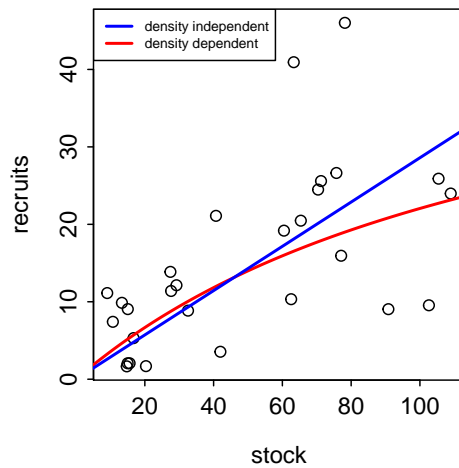


Figure 13. Plot of recruitment versus stock levels for the Gull Island Shoal Lake Trout data with the Beverton-Holt and simple density-independence stock-recruit models superimposed.

```
Number of iterations to convergence: 4
Achieved convergence tolerance: 2.9e-07
```

```
-----
Residual sum of squares: 13.7
```

```
-----
Asymptotic confidence interval:
      2.5%  97.5%
a  0.146988 0.61853
b -0.009262 0.02398
```

```
-----
Correlation matrix:
      a      b
a  1.0000  0.8887
b  0.8887  1.0000
```

The asymptotic confidence intervals and hypothesis tests in the results above should generally not be trusted. Instead 200 bootstrap samples are constructed with

```
> bootbh1 <- nlsBoot(bh1nls,niter=200) # B=200 is too low, should be nearer B=1000
Warning: NaNs produced
Warning: NaNs produced
Warning: NaNs produced
Warning: The fit did not converge 3 times during bootstrapping
```

and 95% bootstrap confidence intervals are obtained and visualized (Figure 14) with

```
> confint(bootbh1,plot=TRUE)
      95% LCI 95% UCI
a  0.247739 0.80408
b -0.001815 0.04037
```

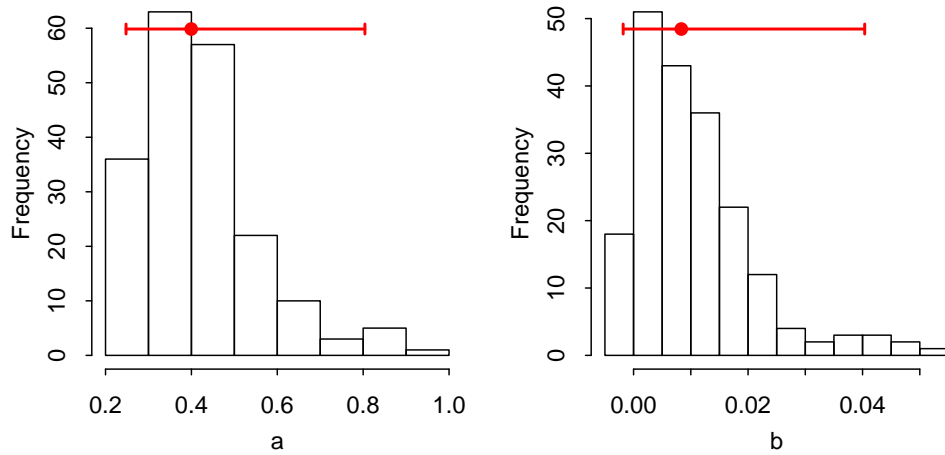


Figure 14. Histogram of the bootstrap results for the Beverton-Holt stock-recruit model fit to the Gull Island Shoal Lake Trout data. Red horizontal lines represent the 95% bootstrap confidence intervals.

The skewed distribution of the bootstrap results for both parameters suggests that the asymptotic CIs and tests in the `overview()` output are likely biased. In addition, note that the bootstrap CI for b suggests that b could be equal to zero, further suggesting that the density dependent parameter is not warranted for these data.

Finally, a scatterplot of the bootstrap estimates of the parameters, constructed below and seen in (Figure 15), shows a strong correlation between the two parameters.

```
> plot(bootbh1)
```

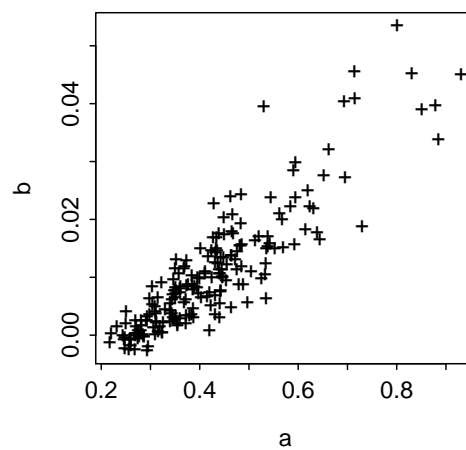


Figure 15. Scatterplot for the parameters of the bootstrap results for the Beverton-Holt stock-recruit model fit the Gull Island Shoal Lake Trout data.

3.2 Fitting Beverton-Holt Model in R – Case II

Stock and recruitment data for the 1971-1991 year-classes of Lake Trout in Michigan waters of Lake Superior were recorded by Richards *et al.* (2004). The “stock” data was the geometric mean CPE of age-8 and older fish caught in gillnets (separated by whether the fish were of “wild” or “hatchery” (i.e., stocked) origin) whereas the “recruit” data was the geometric mean CPE of age-7 fish caught in gillnets. These data are loaded, the structure of the data frame is examined, the log of the recruits variable is created, the hatchery and wild CPE data are combined to one “stock” variable, and the data is reduced to just fish captured in the MI7 area with

```
> data(LakeTroutMI)
> str(LakeTroutMI)
'data.frame': 105 obs. of 5 variables:
 $ year      : int  1971 1972 1973 1974 1975 1976 1977 1978 1979 1980 ...
 $ recruits: num  1.1 2.1 4.2 6.3 3.8 5.7 14 10.8 2.3 7.4 ...
 $ wild      : num  0.2 0.5 12 3.1 3.2 4.8 11 16 4.9 14 ...
 $ stocked   : num  20 21 182 48 47.5 46 69 121 48 75 ...
 $ area      : Factor w/ 5 levels "MI3","MI4","MI5",...: 1 1 1 1 1 1 1 1 1 1 ...
> LakeTroutMI$logR <- log(LakeTroutMI$recruit)
> LakeTroutMI$stock <- LakeTroutMI$stocked + LakeTroutMI$wild
> MI7 <- Subset(LakeTroutMI,area=="MI7")
> str(MI7)
'data.frame': 21 obs. of 7 variables:
 $ year      : int  1971 1972 1973 1974 1975 1976 1977 1978 1979 1980 ...
 $ recruits: num  3.9 1.6 19 13.4 5.7 9.6 16.8 4.2 6.5 9 ...
 $ wild      : num  3.6 2 3.5 10.1 10 25.1 27.3 27 21.5 13.2 ...
 $ stocked   : num  122 10.1 18 101 82 100 51 48 26.5 22.8 ...
 $ area      : Factor w/ 1 level "MI7": 1 1 1 1 1 1 1 1 1 1 ...
 $ logR      : num  1.36 0.47 2.94 2.6 1.74 ...
 $ stock     : num  125.6 12.1 21.5 111.1 92 ...
```

The recruitment measure is missing from one year; thus, that year should be removed from the data with

```
> MI7 <- MI7[complete.cases(MI7),]
```

The second parameterization of the Beverton-Holt model is declared⁹ and starting values are found with

```
> bh2 <- srFuns(type="BevertonHolt",param=2)
> bh2s <- srStarts(recruits~stock,data=MI7,type="BevertonHolt",param=2)
> unlist(bh2s) # unlist use only to save space for display
      a      Rp
0.2153 19.0000
```

An attempt is then made to fit the model with

```
> bh2fit <- nls(logR~log(bh2(stock,a,Rp)),data=MI7,start=bh2s)
```

However, this code produces the error `In log(bh2(stock, a, Rp)) : NaNs produced`. This error typically occurs when the `nls()` algorithm “wanders” into a territory where the parameters produce a negative level of recruits. One way to avoid this error is to constrain the a and R_p parameters to be positive. However,

⁹The `srFuns()` function produces a function for all parameterizations of the Beverton-Holt and Ricker stock-recruit models discussed here. This is purely a convenience function and one should make sure they know how to enter functions “by-hand” into R so as not to be restricted to just those models found in `srFuns()`. The “by-hand” method was demonstrated in the previous example.

the default optimization algorithm in `nls()` does not support constrained parameters. Therefore, the optimization algorithm needs to be changed to the so-called “port” algorithm which does support constrained parameter choices. The optimization algorithm is changed with `algorithm="port"` and lower bounds of zero are set for both parameters with `lower=c(0,0)`. Thus, the constrained model is fit and saved to an object with

```
> bh2fit <- nls(logR~log(bh2(stock,a,Rp)),data=MI7,start=bh2s,algorithm="port",lower=c(0,0))
```

The density-independence model is fit to these data with

```
> bh0 <- logR~log(a*stock)
> bh0s <- bh2s[1]
> bh0fit <- nls(bh0,data=MI7,start=bh0s,algorithm="port",lower=c(0))
```

The “extra sum-of-squares” test and AIC results to compare these two models are computed with

```
> anova(bh0fit,bh2fit)
Analysis of Variance Table

Model 1: logR ~ log(a * stock)
Model 2: logR ~ log(bh2(stock, a, Rp))
  Res.Df Res.Sum Sq Df Sum Sq F value Pr(>F)
1      19      10.55
2      18       5.67  1   4.88   15.5 0.00097
> AIC(bh0fit,bh2fit)
      df  AIC
bh0fit  2 47.96
bh2fit  3 37.54
```

Both a “small” p-value ($p = 0.0010$) and the smaller AIC value suggest that the Beverton-Holt model with the density-dependent parameter provide a “better” fit to the data than the simple density-independence model. A supporting graphic (Figure ??) is constructed with

```
> plot(recruits~stock,data=MI7,pch=19)
> curve(bh2(x,coef(bh2fit)[1],coef(bh2fit)[2]),from=0,to=130,col="red",lwd=2,add=TRUE)
> curve(coef(bh0fit)[1]*x,from=0,to=130,col="blue",lwd=2,add=TRUE)
> legend("topright",legend=c("density independent","density dependent"),col=c("blue","red"),
      lwd=2,cex=0.6)
```

The parameter estimates, along with other summary results, are obtained with

```
> overview(bh2fit)
-----
Formula: logR ~ log(bh2(stock, a, Rp))

Parameters:
  Estimate Std. Error t value Pr(>|t|)
a      0.632     0.499   1.27  0.2213
Rp     10.691     3.107   3.44  0.0029

Residual standard error: 0.561 on 18 degrees of freedom
```

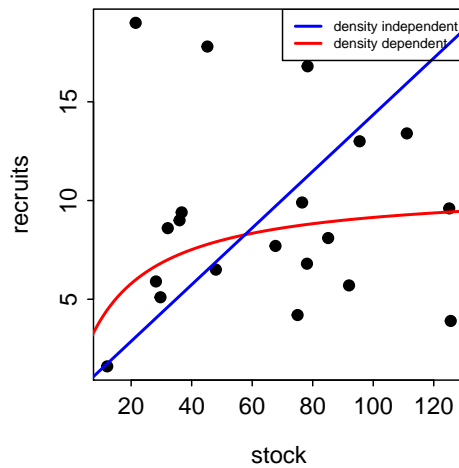


Figure 16. Plot of recruitment versus stock levels for the Lake Superior MI7 area Lake Trout data with the Beverton-Holt and simple density-independence stock-recruit models superimposed.

```
Algorithm "port", convergence message: relative convergence (4)
```

```
-----
```

```
Residual sum of squares: 5.67
```

```
-----
```

```
Asymptotic confidence interval:
```

```
2.5% 97.5%
```

```
a -0.4163 1.681
```

```
Rp 4.1634 17.218
```

```
-----
```

```
Correlation matrix:
```

```
      a      Rp
```

```
a  1.0000 -0.8219
```

```
Rp -0.8219 1.0000
```

The 95% bootstrap confidence intervals are obtained and visualized (Figure 17) with

```
> bootbh2 <- nlsBoot(bh2fit,niter=200) # B=200 is too low, should be nearer B=1000
```

```
Warning: The fit did not converge 41 times during bootstrapping
```

```
> confint(bootbh2,plot=TRUE)
```

```
95% LCI 95% UCI
```

```
a 0.309 8.005
```

```
Rp 7.218 17.088
```

The bootstrap results show a strongly skewed distribution for a . The R_p distribution is less skewed and approximate 95% confidence intervals for R_p is between 7.2 and 17.1.

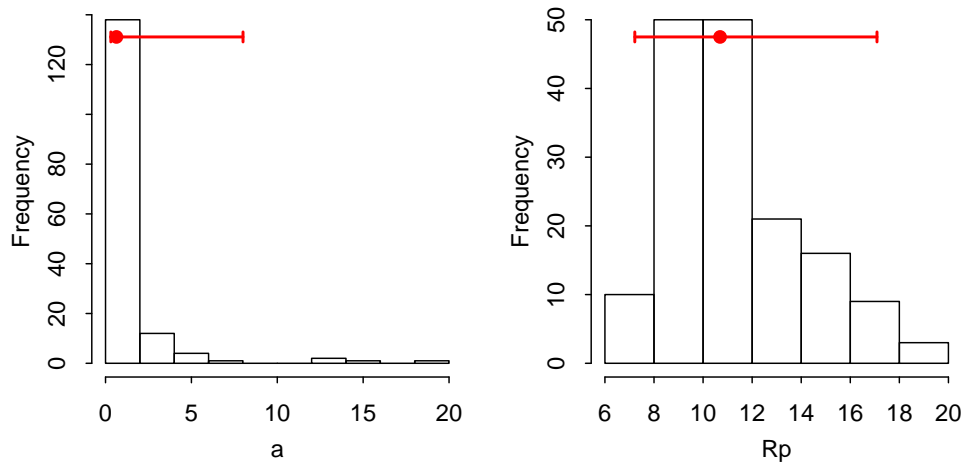


Figure 17. Histogram of the bootstrap results for the Beverton-Holt stock-recruit model fit to the Lake Superior MI7 area Lake Trout data. Red horizontal lines represent the 95% bootstrap confidence intervals.

3.3 Fitting the Ricker Model in R

The fitting of the third parameterization of the Ricker model is illustrated with Lake Trout data from Lake Superior's MI7 area. The third parameterization of the Ricker model is declared and starting values are found with

```
> r3 <- srFuns(type="Ricker",param=3)
> r3s <- srStarts(recruits~stock,data=MI7,type="Ricker",param=3)
> unlist(r3s)      # unlist use only to save space for display
      a      Rp
0.3901 9.3217
```

The model is then fit and saved to an object with

```
> r3fit <- nls(logR~log(r3(stock,a,Rp)),data=MI7,start=r3s,algorithm="port",lower=c(0,0))
```

The density-independence model is fit and the “extra sum-of-squares” test and AIC results computed with

```
> r0 <- logR~log(a*stock)
> r0s <- r3s[1]
> r0fit <- nls(r0,data=MI7,start=r0s,algorithm="port",lower=c(0))
> anova(r0fit,r3fit)
```

Analysis of Variance Table

```
Model 1: logR ~ log(a * stock)
Model 2: logR ~ log(r3(stock, a, Rp))
  Res.Df Res.Sum Sq Df Sum Sq F value Pr(>F)
1      19      10.55
2      18       5.15 1    5.39   18.9 0.00039
```

```
> AIC(r0fit,r3fit)
```

```
      df  AIC
r0fit  2 47.96
r3fit  3 35.63
```

Both a “small” p-value ($p = 0.0004$) and the smaller AIC value suggest that the Ricker model with the density-dependent parameter provide a “better” fit to the data than the simple density-independence model. A supporting graphic (Figure ??) is constructed with

```
> plot(recruits~stock,data=MI7,pch=19)
> curve(r3(x,coef(r3fit)[1],coef(r3fit)[2]),from=0,to=130,col="red",lwd=2,add=TRUE)
> curve(coef(r0fit)[1]*x,from=0,to=130,col="blue",lwd=2,add=TRUE)
> legend("topright",legend=c("density independent","density dependent"),col=c("blue","red"),
      lwd=2,cex=0.6)
```

The parameter estimates, along with other summary results, are obtained with

```
> overview(r3fit)

-----
Formula: logR ~ log(r3(stock, a, Rp))
```

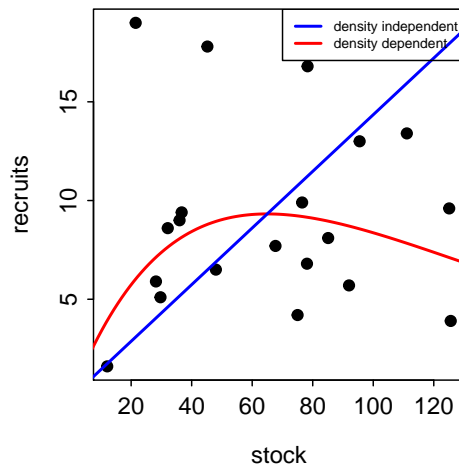


Figure 18. Plot of recruitment versus stock levels for the Lake Superior MI7 area Lake Trout data with the Ricker and simple density-independence stock-recruit models superimposed.

Parameters:

	Estimate	Std. Error	t value	Pr(> t)
a	0.390	0.101	3.85	0.0012
Rp	9.322	1.115	8.36	1.3e-07

Residual standard error: 0.535 on 18 degrees of freedom

Algorithm "port", convergence message: both X-convergence and relative convergence (5)

Residual sum of squares: 5.15

Asymptotic confidence interval:

	2.5%	97.5%
a	0.1773	0.6029
Rp	6.9790	11.6644

Correlation matrix:

	a	Rp
a	1.0000	0.4613
Rp	0.4613	1.0000

The 95% bootstrap confidence intervals are obtained and visualized (Figure 19) with

```
> bootr3 <- nlsBoot(r3fit,niter=200) # B=200 is too low, it should be nearer B=1000
> confint(bootr3,plot=TRUE)
      95% LCI 95% UCI
a      0.2478 0.6228
Rp     7.6325 11.8094
```

The bootstrap results show a moderately skewed distribution for both a and R_p . Approximate 95% confidence intervals for R_p is between 7.6 and 11.8.

One can compute a confidence interval for the stock level that corresponds to the peak recruitment level by

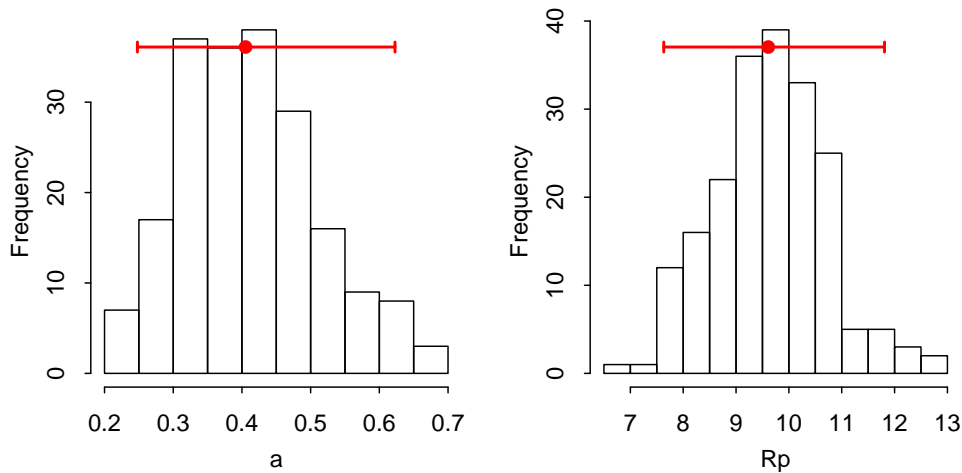


Figure 19. Histogram of the bootstrap results for the Ricker stock-recruit model fit to the Lake Superior MI7 area Lake Trout data. Red horizontal lines represent the 95% bootstrap confidence intervals.

applying the formula provided previously to the a and R_p results from each of the bootstrap samples found in the `coefboot` object of the `bootr3` object. Thus, the S_p value for each bootstrap sample is computed with

```
> Sp <- bootr3$coefboot[, "Rp"]*exp(1)/bootr3$coefboot[, "a"]
```

The median value and 95% confidence interval for S_p can be found by supplying those results to the `quantile` function as follows

```
> ( qSp <- quantile(Sp,c(0.5,0.025,0.975)) )
 50%  2.5% 97.5%
63.74 45.46 99.57
```

Thus, one is 95% confident that the stock level that produces the peak recruitment level is between 63.7 and 99.6. An interesting plot (Figure ??) of these results, along with the peak level of recruitment results, is constructed with

```
> plot(recruits~stock,data=MI7,pch=19,col="gray")
> curve(r3(x,coef(r3fit)[1],coef(r3fit)[2]),from=0,to=130,lwd=2,add=TRUE)
> ( cRp <- coef(r3fit)["Rp"] )
  Rp
9.322
> plotCI(x=qSp[1],y=cRp,li=qSp[2],ui=qSp[3],err="x",lwd=2,pch=19,col="red",add=TRUE)
> plotCI(x=qSp[1],y=cRp,li=confint(bootr3,param="Rp")[1],ui=confint(bootr3,param="Rp")[2],
  err="y",lwd=2,pch=19,col="red",add=TRUE)
```

Finally, one may ask the question of whether the Beverton-Holt or Ricker model is a “better” fit to these data. This can be answered by submitting the fitted objects of these two models to `AIC()` as follows

```
> AIC(r3fit,bh2fit)
      df  AIC
r3fit  3 35.63
bh2fit  3 37.54
```

With a lower AIC value, the Ricker model appears to be a “better” fit to these data.

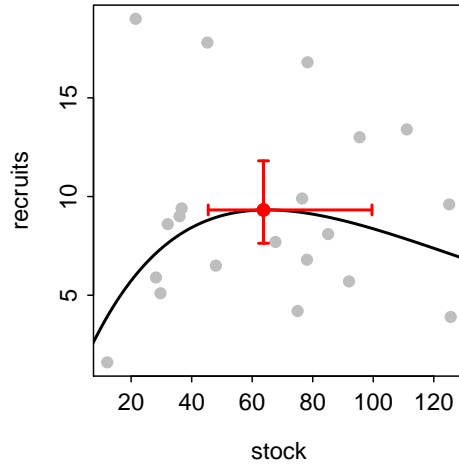


Figure 20. Plot of recruitment versus stock levels for the Lake Superior MI7 area Lake Trout data with the Ricker stock-recruit model and 95% bootstrapped confidence intervals for the predicted peak level of recruitment (vertical) and the stock level that would produce the predicted peak level of recruitment (horizontal) superimposed.

4 Spawning Potential Ratio

NEED TO WORK ON THIS

$$SPR = \frac{P_{fished}}{P_{unfished}}$$

$$P = \sum_{i=1}^n \mu_i E_i \prod_{j=0}^{i-1} S_{ij}$$

where

- n is the maximum age
- μ_i is the proportion mature at age i
- E_i is the mean fecundity (number of eggs produced) by females of age i in the absence of density-dependent growth
- S_{ij} is the annual survival rate (probability) of age i females when they were age j (for $j < i$) and is $e^{-(F_{ij}+M_{ij})}$
- F_{ij} is the instantaneous fishing mortality rate of age i females when they were age j
- M_{ij} is the instantaneous natural mortality rate of age i females when they were age j

Mace and Sissenwine (1993), Goodyear (1993),

References

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Reproducibility Information

Version Information

- **Compiled Date:** Tue Dec 17 2013
- **Compiled Time:** 8:36:34 AM
- **Code Execution Time:** 8.82 s

R Information

- **R Version:** R version 3.0.2 (2013-09-25)
- **System:** Windows, i386-w64-mingw32/i386 (32-bit)
- **Base Packages:** base, datasets, graphics, grDevices, methods, stats, utils
- **Other Packages:** diagram_1.6.1, FSA_0.4.3, FSAdata_0.1.4, gdata_2.13.2, knitr_1.5.15, nlstools_0.0-15, plotrix_3.5-2, shape_1.4.0, xtable_1.7-1
- **Loaded-Only Packages:** bitops_1.0-6, car_2.0-19, caTools_1.16, cluster_1.14.4, evaluate_0.5.1, formatR_0.10, Formula_1.1-1, gplots_2.12.1, grid_3.0.2, gtools_3.1.1, highr_0.3, Hmisc_3.13-0, KernSmooth_2.23-10, lattice_0.20-24, MASS_7.3-29, multcomp_1.3-1, mvtnorm_0.9-9996, nlme_3.1-113, nnet_7.3-7, quantreg_5.05, sandwich_2.3-0, sciplot_1.1-0, SparseM_1.03, splines_3.0.2, stringr_0.6.2, survival_2.37-4, tools_3.0.2, zoo_1.7-10
- **Required Packages:** FSA, FSAdata, nlstools, plotrix and their dependencies (car, gdata, gplots, Hmisc, knitr, multcomp, nlme, quantreg, sciplot, stats)