values of the explanatory variables is then found by finding the 2.5% and 97.5% quantile for
the predicted values.

As an example, the 95% bootstrapped CI for the predicted mean number of cells on the fifth
day is found with,

```r
> B1.bc <- nl1.b[,1]
> B2.bc <- nl1.b[,2]
> B3.bc <- nl1.b[,3]
> pred.5 <- B1.bc/(1+exp(B2.bc+B3.bc*5))
> quantile(pred.5,c(0.025,0.975))
   2.5%   97.5%
  4.915366 5.677209
```

11.2.3 Von Bertalanffy Model

One of the most important models of individual fish growth is the Von Bertalanffy Growth
Model (VBGM). The VBGM has been shown to fairly represent size-at-age for a wide variety
of aquatic organisms (some citations here XXXX). In addition, because this was one of
the first growth models developed it has served as a sub-model in many other fisheries models,
including several important yield models.

Traditional Model Parameterization

The generalized VBGM is,

\[
E[S|t] = S_\infty \left(1 - e^{-K(t-t_0)}\right)^b
\]  

(11.2.5)

where

- \(E[S|t]\) is the expected or average size at time (or age) \(t\),
- \(S_\infty\) is the average size at the maximum age,
- \(K\) is the so-called Brody growth rate coefficient (units are \(yr^{-1}\)),
- \(t_0\) is the time or age when the average size is zero, and
- \(b\) is the power from the allometric length-weight relationship model (Section 6.1).

The generic “size” variable, \(S\), is used in this model but in practice \(S\) either represents the
length, \(L\), or weight, \(W\), of the fish at time, \(t\). However, when modeling length, the allometric
relationship term, \(b\), is not needed and is, thus, set to \(b = 1\). Thus, the generalized VBGM is
reduced to a specialized version of the VBGM for modeling length,
The parameters of (11.2.5) and (11.2.6) have strict meanings (described above) that have, unfortunately, been misunderstood in past work. The following items address some of these misunderstandings.

- $S_\infty$ is not the maximum size of the animal. Rather $S_\infty$ is the asymptote for the model of average size-at-age. As with any average, some individuals will be larger than average; thus, some animals will be larger than $S_\infty$. This is illustrated in Figure 11.6.

- $K$ is not a growth rate (Ricker, 1975, p. 221). The units of $K$ are in time$^{-1}$ rather than change in size per unit time as required by growth rates. The units of $K$ can be seen by algebraically solving (11.2.6) for $K$,

$$
1 - \frac{E[L|t]}{L_\infty} = -e^{-K(t-t_o)}
$$

$$
log\left(1 - \frac{E[L|t]}{L_\infty}\right) = -K(t-t_o)
$$

(11.2.7)

$$
K = \frac{log\left(\frac{L_\infty - E[L|t]}{L_\infty}\right)}{t - t_o}
$$

to notice that the units in the numerator disappear.

- ? offer two related interpretations of the meaning of $K$. First, $K$ “measures the exponential rate of approach to the asymptotic size.” Second, the value $e^{-K}$ is “the fixed fraction by which the annual growth increment is multiplied each year.” This last definition is seen by the relation

$$
E[L|t = i + 2] - E[L|t = i + 1] = e^{-K}(E[L|t = i + 1] - E[L|t = i])
$$

(11.2.8)

where because $K > 0$ the quantity $e^{-K}$ is a decimal. Thus, each succeeding growth increment is a constant fraction of the current growth increment indicating that growth slows as the fish gets older. The relation in (11.2.8) is proved in Appendix A.7.

- $t_0$, despite its definition above, is a modeling artifact and not a biological parameter (?). The $t_0$ is included in these models to adjust or “correct” the model for the initial size of the animal as most of the models do not pass through the origin. This is illustrated in Figure 11.6.

- $S_\infty$, $K$, and $t_0$ are highly related (or correlated). This can be seen in the solution for $K$ above where $K$ depends on the values of $L_\infty$ and $t_0$. For example, with all else held constant, $K$ will be larger for larger values of $L_\infty$. This dependency among parameters causes problems in interpretation and statistical analyses.
11.2. SIZE-AT-AGE MODELS

Figure 11.6: Example of the Von Bertalanffy growth function, \((11.2.6)\), fit to size-at-age Atlantic croaker data. The plot on the left is the fitted model expressed over the observed ages and lengths of the data. The plot on the right is same fitted model but expressed over a range of ages and lengths that allow illustrating the meaning of \(L_\infty\) and \(t_0\).

The mathematical derivations of \((11.2.5)\) and \((11.2.6)\) are in Appendices A.4-A.6.

**Review Exercises**

11.2 For each parameter of the VBGM for length model \((11.2.6)\), write a short paragraph describing what effect changing that parameter has on the model dynamics. For each parameter you should include a single graphic to support your conclusion. **Hint:** Use the `growmodel.sim()` function in the FSA package.

11.3 Write a short paragraph describing what effect changing \(b\) has on the VBGM for weight. You should include a single graphic to support your conclusion. **Hint:** use the `growmodel.sim()` function in the FSA package.

11.4 Write a short paragraph describing how the general shape of the VBGM for weight when \(b \neq 1\) differs from the general shape of the VBGM for length. You should include a single graphic to support your conclusion. **Hint:** use the `growmodel.sim()` function in the FSA package and make sure to include \(b \neq 1\) in the simulations.

11.5 The `VBGMlit` data frame in the FSA package (i.e., accessed with `data(VBGMlit)`) contains the estimated parameter values for the VBGM for several species of fish (based on ?). Choose three species from this data frame\(^2\) and model their growth in length using the `vb.comp()`

\(^2\)Create a new data.frame that contains your three species (e.g., rows 1,3, and 4) with \(v <- VBGMlit[c(1,3,4),]\).
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function in the FSA package\(^3\). The three species you choose should vary in terms of physical (e.g., shape, size), life history (e.g., top-level predator, anadromous), or other obvious characteristics. Model all three species over ages 1 to 50 even though the likely maximum age of your species is not near 50 (i.e., include \(t=1:50\) as an argument to \(\text{vb.comp}()\)). Write a short paragraph describing why you chose your three species (e.g., what were the characteristics that you considered when choosing the species and how do they differ) and a short paragraph describing how the VBGM compares among the three species. You should include a single graphic to support your conclusion (use \(\text{vb.comp}()\)).

Second Parameterization

The most common version of the VBGM in the literature, and the version we will focus on, is (11.2.6). However, with different definitions, substitutions, and algebra, models can be equivalently cast with different parameters. One such useful alternative parameterization of the VBGM (from ?) is,

\[
E[S|t] = \left[ S_1^b + (S_2^b - S_1^b) \frac{1 - e^{-K(t-t_1)}}{1 - e^{-K(t_2-t_1)}} \right]^\frac{1}{b} \tag{11.2.9}
\]

where \(S_1\) is the average size at the youngest age, \(t_1\), and \(S_2\) is the average size at the oldest age, \(t_2\), in the sample. When modeling length \(b = 1\) as before and (11.2.9) reduces to,

\[
E[L|t] = L_1 + (L_2 - L_1) \frac{1 - e^{-K(t-t_1)}}{1 - e^{-K(t_2-t_1)}} \tag{11.2.10}
\]

The derivation of this model from (11.2.6) is shown in Appendix A.8.

It is important to note that this parameterization is not more parsimonious then (11.2.6) as it still has three parameters, \(S_1\), \(S_2\), and \(K\). However, it does have two major advantages over the first parameterization. First, the parameters in this parameterization are less correlated (Galucci and Quinn II, 1979) and, thus, more stable. Second, this parameterization is directly comparable to the general Schnute model to be discussed in Section 11.2.5. The major drawback of this parameterization is that comparison to results in the literature is difficult as the first parameterization is far more prevalent. ? did show, however, that the point estimate of \(L_\infty\) and \(t_0\) can be obtained from the parameters in the second parameterization as follows,

\[
L_\infty = \frac{L_2 - L_1 e^{-K(t_2-t_1)}}{1 - e^{-K(t_2-t_1)}} \tag{11.2.11}
\]

\[
t_0 = t_1 + \frac{1}{K} \ln \left( \frac{L_2 - L_1}{L_2 - L_1 e^{-K(t_2-t_1)}} \right)
\]

\(^3\text{Use } \text{vb.comp}(v)\).
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A common mistake in the interpretation of the second parameterization is to equate $S_2$ and $S_{\infty}$. However, $S_2 \neq S_{\infty}$ as $S_{\infty}$ is the average size at the theoretical maximum age and $S_2$ is the average size at the maximum age in the sample. Thus, $S_2 \leq S_{\infty}$ because the maximum age in the sample is either less than or equal to the theoretical maximum age (Figure 11.7).

**Review Exercises**

**11.6** For each parameter in the second parameterization of the VBGM for length model (11.2.10), write a short paragraph describing what effect changing that parameter has on the model dynamics. For each parameter you should include a single graphic to support your conclusion. **Hint:** Use the `growsim.growmodel.sim("vb2")` function in the FSA package.

**Galucci and Quinn II (1979) Parameterization**

Galucci and Quinn II (1979) noted that comparisons of “growth” between two groups should involve both $K$ and $L_{\infty}$. However, because of the general high correlation between these two parameters simultaneous hypothesis tests of these two parameters are compromised and difficult to interpret. To aid comparison between two groups they introduced a new parameter,
\( \omega = KL_\infty \) which, by solving this quantity for \( L_\infty \) and substituting into (11.2.6), yields yet another reparameterization of the von Bertalanffy model,

\[
E[L|t] = \frac{\omega}{K} \left( 1 - e^{-K(t-t_0)} \right) \tag{11.2.12}
\]

Galucci and Quinn II (1979) state that \( \omega \) can be thought of as a growth rate because the units are in length-per-time and, in fact, it is representative of the growth rate near \( t_0 \). Furthermore, they claim that \( \omega \) is the appropriate parameter to use to compare populations because of its statistical robustness.

**Review Exercises**

11.7 For each parameter in the Galucci and Quinn II (1979) parameterization of the VBGM for length model (11.2.12), write a short paragraph describing what effect changing that parameter has on the model dynamics. For each parameter you should include a single graphic to support your conclusion. **Hint:** Use the `growmodel.sim()` function in the FSA package.

**Fitting in R**

The von Bertalanffy, as well as most other growth models, are non-linear models that will require non-linear statistical methods to estimate parameter values. Recall from Section 11.2.2 that fitting non-linear models is a two-step process of first finding initial values for model parameters and, second, calling the `nls()` function with these starting values.

Knowledge of the meanings of the parameters in the Von Bertalanffy models can be used to identify appropriate starting values for the `nls()` function. In the first parameterization of the VBGM, the maximum length in the data will be used as an initial value for \( L_\infty \) and zero will be used as an initial value for \( t_0 \). Similarly, in the second parameterization of the VBGM, initial values for \( L_1 \) and \( L_2 \) are the average length at the youngest and oldest ages in the data, respectively. In all parameterizations of the VBGM, an initial value for \( K \) is obtained by estimating the instantaneous growth rate between two ages,

\[
K_{init} = \frac{ln(\bar{L}_2) - ln(\bar{L}_1)}{t_2 - t_1} \tag{11.2.13}
\]

where \( \bar{L}_j \) is the average length at a selected time, \( t_j \). A more robust method of finding an initial value for \( K \) is to average the \( K_{init} \) found using (11.2.13) for two pairs of ages. Finally, in the third parameterization, an initial value for \( \omega \) is obtained by multiplying the initial values of \( L_\infty \) and \( K \).

The selection of starting values for the Von Bertalanffy growth models can also be estimated with the `growmodel.sim()` function of the FSA package. This function produces a plot of
length-at-age with a VBGM model superimposed that is controlled with slider bars tied to the parameters of the VBGM. The slider bars are adjusted until a VBGM is produced that "roughly" fits the observed lengths-at-age. The parameters of the VBGM when this rough fit is found can then be used as the starting values for the \texttt{nls()} function.

For this purpose, the \texttt{growmodel.sim()} function has three arguments as described below,

- \texttt{model=} is a string that identifies which model and parameterization to use,
  - \texttt{"vb"} : traditional general von Bertalanffy (i.e., \texttt{(11.2.5)})
  - \texttt{"vb2"} : second general von Bertalanffy parameterization (i.e., \texttt{(11.2.9)})
  - \texttt{"vbgq"} : Galucci and Quinn II (1979) von Bertalanffy parameterization for lengths (i.e., \texttt{(11.2.12)})
- \texttt{x=} the vector of observed ages, and
- \texttt{y=} is the vector of observed lengths or weights.

Once the starting values have been chosen the growth model is fit by entering the growth model expression as the first argument and entering the starting parameter values identified with the \texttt{growmodel.sim()} function in the \texttt{start=} argument to \texttt{nls()}. The model fit should be assigned to an object for further analysis including producing a fitted line plot, residual plot, residual QQ plot, and residual histogram to check the assumptions of the model fit (as shown previously for the \texttt{lm()} function).

\textbf{Example 11.1 - Atlantic Croaker, males}

\begin{verbatim}
▽ The ageing of Atlantic croaker by Old Dominion University in conjunction with the Virginia Marine Resources Commission (VMRC) was introduced in Example 7.5. In addition to the precision analysis illustrated in that example, the VMRC, for management purposes, wanted to explore models for describing the growth of Atlantic Croaker and determine if sex-based differences in growth existed.

The first parameterization of the VBGM is fit to the male Atlantic croaker length data with,

\begin{verbatim}
> data(Croaker2)
> crm <- Croaker2[Croaker2$Sex=="M",]
> attach(crm) # Just males
> growmodel.sim("vb",Age,TL) # Find initial values
> svb <- list(Linf=380,K=0.3,to=-0.2) # Vector of initial values
> vbl1 <- nls(TL~Linf*(1-exp(-K*(Age-to))),start=svb)
\end{verbatim}

The fitted model is then visualized and the assumptions are assessed with,

\begin{verbatim}
> plot.fit(vbl1,crm); plot.resid(vbl1)
> qqp(residuals(vbl1)); hist(residuals(vbl1))
\end{verbatim}
\end{verbatim}
The non-linear model appears to adequately represent the data (Figure 11.8). However, there is an indication of a slight heteroscedasticity and non-normal residuals (Figure 11.8). The residuals, however, are not strongly skewed with most of the skewness the result of a few individuals that are much larger than would be expected for their age (Figure 11.8). Thus, interpretations should be made cautiously as there is some indication that the assumptions for fitting the model are not met.

Basic summary results for a non-linear model object are obtained with the `summary()` function as described in Section 11.2.2. This function will provide the usual parameter estimates, standard errors, and default t-tests with p-values and an estimate of the residual error. In addition, for non-linear models, an estimate of the correlation between each parameter is provided.

Example 11.2 - Atlantic Croaker, males (Continued)
The results from fitting the first parameterization of the VBGM model to the male Atlantic croaker data are obtained with

\begin{verbatim}
> summary(vbl1)
Parameters:
         Estimate Std. Error t value Pr(>|t|)
Linf     366.4148   16.7546  21.870  < 2e-16 ***
     K    0.3148     0.1076   2.924  0.00419  **
     to -1.7142    1.0486  -1.635  0.10493

Residual standard error: 33.42 on 111 degrees of freedom

Correlation of Parameter Estimates:
       Linf       K
Linf -0.9507
     K -0.8706  0.9718
     to -0.8706  0.9718
\end{verbatim}

Thus, point estimates of the parameters are: \( \hat{L}_\infty = 366.4154 \), \( \hat{K} = 0.3148 \), and \( \hat{t}_0 = -1.7142 \).

In addition, as expected, the parameter estimates are very highly correlated.

Confidence intervals for the parameter estimates are derived from the non-parametric bootstrap methods with the `boot.case()` and `ci.bc()` functions. The `boot.case()` function when supplied the results of a model as an argument will return a data frame of parameter estimates from \( B \) resamples of the data. If this data frame is saved to an object and submitted as an argument to `ci.bc()` then the 2.5% and 97.5% quantiles (or whatever quantiles desired) of the bootstrapped parameter estimates will be returned as the endpoints of a non-parametric 95% confidence interval.

\textbf{Example 11.3 - Atlantic Croaker, males (Continued)}

The results from fitting the first parameterization of the VBGM model to the male Atlantic croaker data are obtained, with confidence intervals for each parameter, using the bootstrap methods with\(^4\),

\begin{verbatim}
> library(alr3)
> coef.boot <- boot.case(vbl1)
> ci.bc(coef.boot)
     Linf        K        to
     2.5%  341.2125 0.09306553 -5.65467024
    97.5% 496.5094 0.64968519  0.05280673
\end{verbatim}

\(^4\)Bootstrap methods require patience as the algorithm continuously resamples the original data. Furthermore, the bootstrap methods rely on randomization; thus, the results shown below would likely be different upon a different “run” of the functions.
Thus, for example, one is 95% confident that the Brody growth coefficient ($K$) is between 0.093 and 0.649. ▲

The bootstrap results can also be used to construct a non-parametric bootstrap hypothesis test for a parameter. Specifically, the p-value for a one-sided test is found by computing the proportion of bootstrap parameter estimates more extreme (i.e., “less” or “greater” than depending on the alternative hypothesis) than the hypothesized value. The p-value for a two-sided test is found by doubling the minimum of the proportion less than or the proportion greater than the hypothesized value. The bootstrap p-values can be obtained by submitting the results of `boot.case()` to `ho.bc()`.

**Example 11.4 - Atlantic Croaker, males (Continued)**

▽ The p-value for testing the hypotheses $H_0 : K = 0.5$ versus $H_A : K > 0.5$, for example, is obtained from the bootstrap results with,

```r
> ho.bc(coef.boot,2,0.5,"gt")
   bo   p.value
[1,] 0.5 0.1021021
```

(note that $K$ is the second parameter in the model, thus the use of 2 as the second argument). Thus, there is only little or no evidence that $K$ is greater than 0.5. ▲

Predictions of the mean length of fish at a given age are obtained with the `predict()` function. Unfortunately, the `predict()` function for `nls()` does not support prediction or confidence intervals as of version 2.2.1 of R. However, a 95% confidence interval for the mean length at a given age can be found with the results of the `boot.case()` function.

The `boot.case()` function returns a data frame of parameter estimates for each bootstrap sample. A prediction at a given age can be made for each bootstrap sample by plugging the given age into the VBGM using the bootstrap sample parameter estimates. The 95% CI for the mean length at the given age is then found by finding the 2.5% and 97.5% quantile for the predicted values.

**Example 11.5 - Atlantic Croaker, males (Continued)**

▽ The mean predicted length for 8-year-old male Atlantic croakers is obtained with,

```r
> new <- data.frame(Age=8)
> predict(vbl1, new, level=0.95)
 [1] 349.2005
```

A 95% CI for the mean length of all age 8 male Atlantic croaker is obtained with,
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```r
> pv <- coef.boot[,1]*(1-exp(-coef.boot[,2]*(8 coef.boot[,3])))
> quantile(pv,c(0.025,0.975))
  2.5%   97.5%
337.5335 362.0466
```

Thus, the mean length of all age 8 male Atlantic croakers is between 337.5 and 362.0 mm.

Review Exercises

11.8 Load the Atlantic croaker data, create a data frame of just MALES, and fit the second parameterization of the von Bertalanffy model. Write a short paragraph comparing the results from the second parameterization to the results from the first parameterization shown in the text. In addition, assume that interest rests solely in estimating $K$ and comment on which parameterization is preferred (if either) and why.

11.2.4 Gompertz Model

The Gompertz model is a general model that can be used to model either the length, $L$, or weight, $W$ of an animal at age $t$. In contrast to the VBGM for length, the Gompertz model allows an inflection point in the growth curve. Because of this characteristic, Ricker (1975) notes that the Gompertz model usually describes the weight-at-age quite well and is usually only used on length-at-age data for the years after the inflection point in the model. The three most common parameterizations of the Gompertz model are,

$$E[S|t] = S_0 e^{G(1-e^{-gt})}$$ (11.2.14)

$$E[S|t] = S_\infty e^{-e^{-g(t-t^*)}}$$ (11.2.15)

$$E[S|t] = S_\infty e^{-\frac{1}{2}(e^{-g(t-t_0)})}$$ (11.2.16)

where $S_\infty$ is as defined for the VBGM and

- $S_0$ is the theoretical average size at $t = 0$;
- $G$ is the instantaneous rate of growth at $t = 0$;
- $g$ has two interpretations (Ricker, 1975),
  - the instantaneous growth rate at the inflection point, $t^*$, and
  - the instantaneous rate of decrease of the instantaneous rate of growth;
- $t^*$ is the time or age where the inflection in the Gompertz growth curve occurs; and
Figure 11.9: Example of the Gompertz growth functions fit to size-at-age Atlantic croaker data. The plot on the left is the fitted model expressed over the observed ages and lengths of the data. The plot on the right is the same fitted model but expressed over a range of ages and lengths that allow illustrating the meaning of $S_\infty$, $S_0$, $t^\ast$, and $t_0$.

- $t_0$ is still a modeling artifact that has the same purpose but not the same meaning as described for the VBGM because the Gompertz curve has a lower horizontal asymptote at $S = 0$.

As with the VBGM, these alternative parameterizations produce the exact same curve (Figure 11.9). The mathematical derivations of (11.2.15) and (11.2.16) are in Appendices A.9 and A.10, respectively.

**Review Exercises**

11.9 For each parameter of the first parameterization of the Gompertz growth model (11.2.14), write a short paragraph, referring to a single graphic, describing what effect changing that parameter has on the model dynamics. **Hint:** Use the `growmodel.sim()` function in the FSA package.

11.10 For each parameter of the second parameterization of the Gompertz growth model (11.2.15), write a short paragraph, referring to a single graphic, describing what effect changing that parameter has on the model dynamics.

11.11 For each parameter of the third parameterization of the Gompertz growth model (11.2.16), write a short paragraph, referring to a single graphic, describing what effect changing that parameter has on the model dynamics.
Starting values for the Gompertz model do not follow directly from the meanings of the parameters as was seen with the Von Bertalanffy model. Thus, starting values for the Gompertz model are obtained by “roughly fitting” the model to data with the `growmodel.sim()` function as was described for the Von Bertalanffy model. The `model=` argument, however, must be set to "gomp1", "gomp2", or "gomp3" for choosing either the first, second, or third parameterization of the Gompertz model (in the order presented above).

The methods for fitting and interpreting the Gompertz models is exactly the same as for the Von Bertalanffy models except that the specific Gompertz model must be entered into the model formula for the `nls()` function.

**Review Exercises**

11.12 The R commands below were applied to the FEMALE Atlantic Croaker data. Use the results under each command to answer the following questions.

(a) What model (including specific parameterization) was fit to these data?
(b) What is the best estimate of \( g \)?
(c) What is the interval estimate of \( G \)?
(d) What hypothesis test is computed with the `ho.bc` code below? Interpret the results of this hypothesis test.
(e) Interpret the results of the `quantile()` code below?

```r
> summary(GF1fit)
Parameters:
   Estimate Std. Error t value Pr(>|t|)
So  191.51942  24.70978  7.751 4.45e-13 ***
G   0.81370   0.09666  8.418 7.15e-15 ***
g   0.28320   0.07468  3.792 0.000198 ***
---
Residual standard error: 45.68 on 201 degrees of freedom

Correlation of Parameter Estimates:
   So   G
So 1.000
G -0.9439

> coef.boot <- boot.case(GF1fit)
> ci.bc(coef.boot)

   So   G   g
2.5% 130.7852 0.7041649 0.08179562
97.5% 247.0880 1.2937751 0.50317906

> ho.bc(coef.boot,2,1,"two.sided")

  param p.value
```
`new <- data.frame(Age=6)
> predict(GF1fit, new)
[1] 372.3814
> pv <- coef.boot[,1]*exp(coef.boot[,2]*(1-exp(-coef.boot[,3]*6)))
> quantile(pv,c(0.05,0.95))
    5%  95%
363.3058 379.1448

11.13 Load the Atlantic croaker data, create a data frame of just FEMALES, and fit the second parameterization of the Gompertz model. Write a short paragraph comparing the results from the second to the results from the first parameterization shown in the text. In addition, assume that interest rests solely in estimating $g$ and comment on which parameterization is preferred (if either) and why.

11.14 An empirical method to show that two models fit data identically is to fit both models to a given data set, use each model to make a series of predictions at the same values of the explanatory variable (i.e., age in growth models), and then subtract the predictions from each other. If the difference between all of the predictions is zero then the models are equivalent.

Use this strategy to show that two different parameterizations of the Gompertz growth model, e.g., (11.2.14) and (11.2.15), are equivalent when fit to the Vermillion Lake cisco data (found in cisco.txt). Hint: Fit a model and save to an object and then use that object to make a series of predictions for the given data.frame with `G1pv <- predict(object)` . Repeat this for a second model. Then summarize the differences between the two sets of predictions (i.e., `summary(G1pv-G2pv)`).

11.2.5 Schnute Model

? proposed a general model for growth with the following four parameters,

- $S_1$ is size at some time (or age) $t_1$,
- $S_2$ is size at some time (or age) $t_2$,
- $c$ is a shape parameter that is related to the time or age of the inflection point in the growth curve, and
- $d$ is another shape parameter that is related to the ratio of the size at the inflection point to the asymptotic size.

where $S_2 > S_1 > 0$ and $t_2 > t_1$. Most presentations of the Schnute model will appear to have six parameters; the four above along with $t_1$ and $t_2$. However, $t_1$ and $t_2$ are two ages, usually the minimum and maximum age respectively, set by the user and the data. Again, note that the generic $S$ could represent either $L$ or $W$. This particular growth model was considered
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“general” because special cases of parameter selections reduce the model to several well-known growth models including the Von Bertalanffy and Gompertz models.

The specific Schnute growth model is dependent on choices for the $c$ and $d$ parameters. Thus, the model is usually represented specifically for four different “cases” of parameter choices,

- **Case 1.** $c \not= 0, d \not= 0$:
  \[
  E[S|t] = \left[ S_1^d + \left( S_2^d - S_1^d \right) \frac{1 - e^{-c(t-t_1)}}{1 - e^{-c(t_2-t_1)}} \right]^{\frac{1}{d}}
  \] (11.2.17)

- **Case 2.** $c \not= 0, d = 0$:
  \[
  E[S|t] = S_1 e^{\ln \left( \frac{S_2}{S_1} \right) \frac{1 - e^{-c(t-t_1)}}{1 - e^{-c(t_2-t_1)}}}
  \] (11.2.18)

- **Case 3.** $c = 0, d \not= 0$:
  \[
  E[S|t] = \left[ S_1^d + \left( S_2^d - S_1^d \right) \frac{t - t_1}{t_2 - t_1} \right]^{\frac{1}{d}}
  \] (11.2.19)

- **Case 4.** $c = 0, d = 0$:
  \[
  E[S|t] = S_1 e^{\ln \left( \frac{S_2}{S_1} \right) \frac{t - t_1}{t_2 - t_1}}
  \] (11.2.20)

It will be important in the analysis of these models to note that Case 1 is the most general version of this model with four parameters. Cases 2 and 3 are three parameter models that are each nested or simplified models of Case 1. Finally, Case 4 is a two parameter model, that is nested within Case 2 or Case 3. Because of the nested nature of these models, comparison of the fit of these different “cases” to data can be examined with an extra-sum-of-squares or AIC summary (to be described later).

It can also be shown that the Von Bertalanffy and the Gompertz growth models are special cases of the Schnute general growth model. In particular, we have these special cases,

- **Special Case 1.** If $c = K > 0$ and $d = b$ then the Schnute model is exactly the second parameterization of the **generalized VBGM model** (11.2.9).
- **Special Case 2.** If $c = K > 0$ and $d = 1$ then the Schnute model is exactly the second parameterization of the **VBGM for length model** (11.2.10).
- **Special Case 3.** If $c > 0$ and $d = 0$ then the Schnute model resembles the **Gompertz growth model**. Notice that this is exactly Case 2 (11.2.18) with the further restriction that $c > 0$.
- **Special Case 4.** If $c = K > 0$ and $d = -1$ then the Schnute model resembles the **logistic growth model** (i.e., $E[S|t] = \frac{S_\infty}{1 + e^{-K(t-t_\ast)}}$; which we have not discussed).
- **Special Case 5.** If $c = K > 0$ and $d < 0$ then the Schnute model resembles the **Richards growth model** (i.e., $E[S|t] = S_\infty \left( 1 + de^{-K(t-t_0)} \right)^{-\frac{1}{d}}$; which we have not discussed).
Depending on parameter choices, a Schnute model can represent a wide variety of growth trajectories including an increasing power function to a horizontal asymptote, a sigmoidal shape to a horizontal asymptote, and an “exponential” shape that does not reach an asymptote, all with varying rates and points of inflection (Figure 11.10).

Figure 11.10: Left-Set of eight regions in the $c,d$-plane defined by the $c$-axis, $d$-axis, $d = 1$, and $d = -c \frac{t_2 - t_1}{\ln(S_2) - \ln(S_1)}$ (modified from ?). Right-Set of eight characteristic growth curves corresponding to the $(c,d)$ parameter pair shown in the left plot. Each plot on the right assumes constant $S_1 = 1$ and $S_2 = 100$.

The mathematical derivations of the Schnute models are provided in the readily available ?.

**Review Exercises**

11.15 For each parameter of the Schnute growth models ((11.2.17)-(11.2.20)), write a short paragraph describing what effect changing that parameter has on the model dynamics. We suggest choosing more than three values of the variable that you are varying so as to cover the broad range of dynamics that can be expressed by this model. Furthermore, for simplicity, we suggest that you choose $-1 \leq c \leq 1$ and $-3 \leq d \leq 3$. For each parameter you should include a single graphic to support your conclusion. **Hint:** Use the `growmodel.sim()` function in the FSA package.

Initial values for the Schnute function must be found using the iterative plotting routine implemented with the `growmodel.sim()` function as described for the Von Bertalanffy and Gompertz models. The `model=` argument must be set to "Schnute" to fit with the Schnute model.

Fitting the Schnute model is slightly more complicated because each case of the model should be fit and then an extra-sum-of-squares test or AIC should be used to determine which case is most
parsimonious while still adequately representing the data. The analysis should begin by fitting the most general case first (i.e., Case 1, (11.2.17)) to make sure that the model assumptions (fit, homoscedasticity, and normality) are met. If there are no assumption problems then Cases 2-4 ((11.2.18)-(11.2.20)) are fit to the data.

Example 11.6 - Atlantic Croaker, males (Continued)

Case 1 of the Schnute model was fit with,

```r
> attach(crm)
> growmodel.sim("Schnute",Age,TL)
> sschn1 <- list(S1=,S2=,c=,d=)
> t.min <- min(Age); t.max <- max(Age)
> S41fit<-nls(TL~(S1^d+(S2^d-S1^d)*((1-exp(-c*(Age-t.min)))/
+ (1-exp(-c*(t.max-t.min)))))^(1/d),start=sschn1)
```

where `t.min` and `t.max` are the minimum and maximum ages, respectively, and are needed to simplify the look of the `nls()` call. As with the von Bertalanffy fit (Example 11.1) the non-linear model appears to adequately represent the data (Figure 11.11). However, there is an indication of a slight heteroscedasticity and non-normal residuals (Figure 11.11).

With the assumptions at least adequately met the models for the other three cases can be fit. However, because each of the other cases is missing at least one of the parameters (e.g., `d` is removed from Case 2) the list of starting values must be modified by removing the starting value for the missing parameter.

```r
> sschn2<-sschn1[-4]  # remove starting d
> S42fit<-nls(TL~S1*exp(log(S2/S1)*(1-exp(-c*(Age-t.min)))/
+ (1-exp(-c*(t.max-t.min)))),start=sschn2)
> sschn3<-sschn1[-3]  # remove starting c
> S43fit<-nls(TL~(S1^d+(S2^d-S1^d)*(Age-t.min)/
+ (t.max-t.min)))^(1/d),start=sschn3)
> sschn4<-sschn1[-c(3,4)]  # remove starting c,d
> S44fit<-nls(TL~ S1*exp(log(S2/S1)*(Age-t.min)/
+ (t.max-t.min)),start=sschn4)
```

The results of the four case fits are then compared with the `anova()` function to determine which, if any, is the simplest case that is significantly different from Case 1. First, compare Case 1 to Case 4 with `anova(S44fit,S41fit)` . If the two models are not significantly different (i.e, `p-value < α`) then Case 4 is the simplest model of all four cases (and you are done!). Otherwise, Case 1 is then compared to Case 2 and Case 3 with `anova(S43fit,S41fit)` and `anova(S42fit,S41fit)` . If both results are significant then Case 1 is the best-fit model (and you are done!). If both results are insignificant then the best-fit of Cases 2 and 3 is the model
Figure 11.11: Fitted line plot, residual plot, residual QQ plot, and residual histogram from fitting model (11.2.17) to the male Atlantic croaker data.

with the lowest residual standard errors. If one result is significant and the other is insignificant then the insignificant case is the best-fit case.

Example 11.7 - Atlantic Croaker, males (Continued)

\[ \text{The extra-sums-of-squares test for comparing Case 4 to Case 1 is,} \]

\[ > \text{anova(S44fit,S41fit)} \quad \# \text{ANOVA comparison of cases 4,1} \]
\[ \text{Model 1: } TL \sim S1 * \exp(\log(S2/S1) * (Age - t.min)/(t.max - t.min)) \]
\[ \text{Model 2: } TL \sim (S1^d + (S2^d - S1^d) * ((1 - \exp(-c * (Age - t.min)))/ ...} \]
\[ \text{Res.Df Res.Sum Sq Df Sum Sq F value Pr(>F)} \]
\[ 1 \quad 112 \quad 140968 \]
\[ 2 \quad 110 \quad 123349 \quad 2 \quad 17619 \quad 7.856 \quad 0.000647 \quad *** \]

These results indicate that Case 1 fits the data significantly better than Case 4. Thus, Case 4 is removed as a candidate and Case 2 is compared to Case 1 with,
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\[
\begin{align*}
\text{Model 1: } TL & \sim S1 \times \exp\left(\log(S2/S1) \times (1 - \exp(-c \times (Age - t.min)))\right)/ \ldots \\
\text{Model 2: } TL & \sim (S1^d + (S2^d - S1^d) \times ((1 - \exp(-c \times (Age - t.min))))/ \ldots \\
\text{Res.Df Res.Sum Sq Df Sum Sq F value Pr(>F)}
\end{align*}
\]

1  111  123699
2  110  123349 1  350 0.3117 0.5777

which indicates no significant difference between Case 2 and Case 1. Thus, because Case 2 is simpler, it would be preferred over Case 1. Case 3 is compared to Case 1 with

\[
\begin{align*}
\text{Model 1: } TL & \sim (S1^d + (S2^d - S1^d) \times (Age - t.min)/(t.max - t.min))^{(1/d)} \\
\text{Model 2: } TL & \sim (S1^d + (S2^d - S1^d) \times ((1 - \exp(-c \times (Age - t.min))))/ \ldots \\
\text{Res.Df Res.Sum Sq Df Sum Sq F value Pr(>F)}
\end{align*}
\]

1  111  126557
2  110  123349 1  3208 2.8607 0.0936

which indicates that Case 1 is weakly significantly “better” than Case 3. If a researcher does not believe that weak significance is significant enough then the conclusion would be that Case 3 is better to use than Case 1 because it is simpler. However, overall, Case 2 is the best model because either (i) it is “better” than Case 1 which was better than the other two cases or (ii) it is “better” than Case 3 based on a smaller RSS (i.e., 123699 compared to 126557). ▲

The Akaike Information Criterion discussed in Section ?? can also be used to choose the “best case” of the Schnute model.

Example 11.8 - Atlantic Croaker, males (Continued)

\[\text{\narrowleft} \text{The AIC values for each of the four cases can be found with,}\]

\[
\begin{align*}
\text{> AIC(S41fit,S42fit,S43fit,S44fit)}
\text{df AIC}
S41fit 4 1127.988
S42fit 3 1126.310
S43fit 3 1128.915
S44fit 2 1139.208
\end{align*}
\]

These results also indicate the Case 2 is the “best” case for these data. ▲

\[\text{\narrowleft} \text{accurately point out that if it is determined that Case 1 of the Schnute model is the “best” case then a hypothesis test should be performed to see if } d = 1. \text{ If } d = 1 \text{ then Special Case 2 of the Schnute model holds and the model essentially reduces to fitting a VBGM for length. This} \]

hypothesis test is performed by finding the results from the S41fit object and then using the boot.case() and ho.bc() functions as described for the VBGM.

**Review Exercises**

11.16 The R commands below were applied to the FEMALE Atlantic Croaker data. Use the results to determine which case of the Schnute model best fits these data.

```r
> anova(S44fit,S41fit) # ANOVA comparison of cases 4,1
Model 1: TL ~ S1 * exp(log(S2/S1) * (Age - t.min)/(t.max - t.min))
Model 2: TL ~ (S1^d + (S2^d - S1^d) * ((1 - exp(-c * (Age - t.min)))/ ... 
  Res.Df Res.Sum Sq Df Sum Sq F value Pr(>F) 
 1 202  439841
 2 200  415193 2  24648 5.9366 0.003129 **

> anova(S43fit,S41fit) # ANOVA comparison of cases 3,1
Model 1: TL ~ (S1^d + (S2^d - S1^d) * (Age - t.min)/(t.max - t.min))^(1/d)
Model 2: TL ~ (S1^d + (S2^d - S1^d) * ((1 - exp(-c * (Age - t.min)))/ ... 
  Res.Df Res.Sum Sq Df Sum Sq F value Pr(>F)
 1 201  415194
 2 200  415193 1  1 5e-04 0.9817

> anova(S42fit,S41fit) # ANOVA comparison of cases 2,1
Model 1: TL ~ S1 * exp(log(S2/S1) * (1 - exp(-c * (Age - t.min)))/ ... 
Model 2: TL ~ (S1^d + (S2^d - S1^d) * ((1 - exp(-c * (Age - t.min)))/ ... 
  Res.Df Res.Sum Sq Df Sum Sq F value Pr(>F)
 1 201  419482
 2 200  415193 1  4290 2.0663 0.1521
```

11.2.6 Comparing Growth Curves Among Groups

A fairly common analysis in fisheries research is to compare parameters from a growth model between two groups or populations. The statistical methods for making these comparisons will follow the general strategy outlined in Section 6.4.1 when indicator and interaction variables were discussed. However, the actual modelling is a bit more cumbersome with non-linear than linear models. In this section we will illustrate the methods for comparing parameters among two groups with the Von Bertalanffy length model. The methods will extend to the other growth models.

**The Models**

Comparisons among groups requires the use of an indicator variable. In contrast to the general strategy outlined for linear models, however, when using non-linear models we will have as many indicator variables as groups. Thus, for two groups, we will have the indicator variables,
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$G_1 = 1$ if an individual belongs to group 1 and 0 otherwise and $G_2 = 1$ if the individual belongs to group 2 and 0 otherwise.

Additionally, parameters specific to one of the groups must be defined by adding a subscript for the group to the parameter. For example, $L_{\infty 1}$ is the asymptotic mean length for individuals in group 1 and $K_2$ is the Brody growth coefficient for individuals in group 2. Parameters without a subscript, which will appear in some models, are the same or are common to both groups. For example, $L_{\infty}$ is the asymptotic mean length for all individuals, regardless of group.

With these modifications, several separate models will be considered,

- **General Model**: Separate parameter estimates for individuals in each group.
  \[
  L(t) = G_1 \left[ L_{\infty 1} \left( 1 - e^{-K_1(t-t_{01})} \right) \right] + G_2 \left[ L_{\infty 2} \left( 1 - e^{-K_2(t-t_{02})} \right) \right]
  \]

- **One parameter in common between groups**.
  - **Common $L_{\infty}$ Model**.
    \[
    L(t) = G_1 \left[ L_{\infty} \left( 1 - e^{-K_1(t-t_{01})} \right) \right] + G_2 \left[ L_{\infty} \left( 1 - e^{-K_2(t-t_{02})} \right) \right]
    \]
  - **Common $K$ Model**.
    \[
    L(t) = G_1 \left[ L_{\infty 1} \left( 1 - e^{-K(t-t_{01})} \right) \right] + G_2 \left[ L_{\infty 2} \left( 1 - e^{-K(t-t_{02})} \right) \right]
    \]
  - **Common $t_0$ Model**.
    \[
    L(t) = G_1 \left[ L_{\infty 1} \left( 1 - e^{-K_1(t-t_{0})} \right) \right] + G_2 \left[ L_{\infty 2} \left( 1 - e^{-K_2(t-t_{0})} \right) \right]
    \]

- **Two parameters in common between groups**.
  - **Common $L_{\infty}$ and $K$ Model**.
    \[
    L(t) = G_1 \left[ L_{\infty} \left( 1 - e^{-K(t-t_{01})} \right) \right] + G_2 \left[ L_{\infty} \left( 1 - e^{-K(t-t_{02})} \right) \right]
    \]
  - **Common $L_{\infty}$ and $t_0$ Model**.
    \[
    L(t) = G_1 \left[ L_{\infty} \left( 1 - e^{-K_1(t-t_{0})} \right) \right] + G_2 \left[ L_{\infty} \left( 1 - e^{-K_2(t-t_{0})} \right) \right]
    \]
  - **Common $K$ and $t_0$ Model**.
    \[
    L(t) = G_1 \left[ L_{\infty 1} \left( 1 - e^{-K(t-t_{0})} \right) \right] + G_2 \left[ L_{\infty 2} \left( 1 - e^{-K(t-t_{0})} \right) \right]
    \]

- **Common Model**: Same parameter estimates for both groups. This is (11.2.6).
  \[
  L(t) = L_{\infty} \left( 1 - e^{-K(t-t_{0})} \right)
  \]

Each “one parameter in common” model is a subset of the General Model, each “two parameters in common” model is a subset of two of the “one parameter in common” models, and the Common Model is a subset of each “two parameters in common” model. Thus, determining which is the best model is a matter of fitting each model and interpreting several anova() calls or interpreting the AIC() results.
Fitting The Models

The analysis of these models should begin by fitting and checking the assumptions for the General Model. If the assumptions are met with this model then they should be met for all other subset models. Thus, assumption checking only needs to take place on the most complex model.

Fitting the General Model requires finding starting values for six parameters. Starting values can generally be determined by fitting the Common Model to the data and assuming common parameter values for each group. Thus, starting values can be found using `growmodel.sim()` as described in Section 11.2.3. If these starting values do not work properly in R then the data may be split into two separate data frames corresponding to groups and then using `growmodel.sim()` on both data frames to find separate starting values.

Example 11.9 - Atlantic Croaker (Continued)

```
> croaker$G1<--croaker$G2<-rep(0,length(croaker$Age)) # Initially fill w/ 0s
> croaker$G1[croaker$Sex=="M"]<-1 # Replaces 0s w/ 1s when sex is male
> croaker$G2[croaker$Sex=="F"]<-1 # Replaces 0s w/ 1s when sex is female
> attach(croaker)
> growmodel.sim("vb",Age,TL)) # Find starting values
> sLinf<-500; sK<-0.075; sto<-0 # Store starting values
> mGen<-nls(TL~G1*Linf1*(1-exp(-K1*(Age-to1))) + G2*Linf2*(1-exp(-K2*(Age-to2))),
+ start=list(Linf1=sLinf,K1=sK,to1=sto,Linf2=sLinf,K2=sK,to2=sto))
```

with diagnostics from,

```
> plot.fit(mGen,croaker,Sex); plot.resid(mGen)
> qqp(residuals(mGen)); hist(residuals(mGen))
```

The model appears to fit the data appropriately, with slight heteroscedasticity, but approximately normal residuals (Figure 11.12). Overall, the assumptions are adequately met with this model. ▲

If the assumptions of the general model are met then each model should be fit to the data with the results from each saved in an appropriately named R object. The models should then be compared in a hierarchical manner as was done when sorting through the cases of the Schnute model. In other words, each “one parameter in common” model should be compared to the General Model. Any “one parameter in common” models that is not statistical different from the General Model is considered “better” then the General Model. If two “one parameter in common” models are better than the General Model then the one with the smallest RSS is chosen as the “best” “one parameter in common” model. Then each “two parameters in
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Figure 11.12: Fitted line plot, residual plot, residual QQ plot, and residual histogram from fitting the most general VBGM to the combined male and female Atlantic croaker data. Age axis on the fitted line plot was jittered to make the symbols more separate.

common" model is compared to the "best" "one parameter in common" model with the same rationale. Finally, if needed, the COMMON MODEL is compared to the "best" "two parameters in common" model. This process stops when a more complex model is significantly different then every simpler model it was compared to. Alternatively, the model with the lowest AIC is the "best" model.

Example 11.10 - Atlantic Croaker (Continued)

\( \bigtriangledown \) The other seven models for comparing among groups are fit to the entire Atlantic croaker data with,

\texttt{> m1KT<-nls(TL~Linf*(G1*(1-exp(-K1*(Age-to1))) + G2*(1-exp(-K2*(Age-to2)))),}
\texttt{+ start=list(Linf=sLinf,K1=sK,to1=sto,K2=sK,to2=sto))}
\texttt{> m1LT<-nls(TL~G1*Linf1*(1-exp(-K*(Age-to1))) + G2*Linf2*(1-exp(-K*(Age-to2)))),}
\texttt{+ start=list(Linf1= sLinf,K=sK,to1=sto,Linf2=sLinf,to2=sto))}
> m1LK<-nls(TL~G1*Linf1*(1-exp(-K1*(Age-to))) + G2*Linf2*(1-exp(-K2*(Age-to))),
+ start=list(Linf1=sLinf,K1=sK,to=sto,Linf2=sLinf,K2=sK))
> m2T<-nls(TL~Linf*(G1*(1-exp(-K*(Age-to1))) + G2*(1-exp(-K*(Age-to2)))),
+ start=list(Linf=sLinf,K=sto,to1=sto,to2=sto))
> m2K<-nls(TL~Linf*(G1*(1-exp(-K1*(Age-to))) + G2*(1-exp(-K2*(Age-to)))),
+ start=list(Linf=sLinf,K1=sK,to=sto,K2=sK))
> m2L<-nls(TL~G1*Linf1*(1-exp(-K*(Age-to))) + G2*Linf2*(1-exp(-K*(Age-to)) ),
+ start=list(Linf1=sLinf,K=sK,to=sto,Linf2=sLinf))
> mCom<-nls(TL~Linf*(1-exp(-K*(Age-to))),start=list(Linf=sLinf,K=sto,to=sto))

Each of the “one parameter in common” models is then compared to the GENERAL MODEL
with,

> anova(m1L,mGen)

Res.Df Res.Sum Sq Df Sum Sq F value Pr(>F)
1 313 546067
2 312 541854 1 4213 2.4257 0.1204

> anova(m1K,mGen)

Res.Df Res.Sum Sq Df Sum Sq F value Pr(>F)
1 313 542566
2 312 541854 1 712 0.4097 0.5226

> anova(m1T,mGen)

Res.Df Res.Sum Sq Df Sum Sq F value Pr(>F)
1 313 542055
2 312 541854 1 200 0.1153 0.7344

These results indicate that each of the “one parameter in common” models fits the data
as well as the more complex GENERAL MODEL. Thus, because each “one parameter
in common” model is simpler then the GENERAL MODEL, the GENERAL MODEL will be
removed from consideration as the “best model.” Thus, at this point, we know that we
do not need separate values of all three parameters for the two groups.

Of the “one parameter in common” models, the model with \( t_0 \) in common is the “best”
model because it has the lowest RSS (=542055) of the three “one parameter in common”
models. Thus, the two “two parameters in common” models that have \( t_0 \) in common will
be compared to this model with,

> anova(m2L,m1LK)

Res.Df Res.Sum Sq Df Sum Sq F value Pr(>F)
1 314 545239
2 313 542055 1 3184 1.8385 0.1761

> anova(m2K,m1LK)

Res.Df Res.Sum Sq Df Sum Sq F value Pr(>F)
1 314 557513
2 313 542055 1 15458 8.9261 0.003034 **

The first results suggest that the model with \( K \) in common fits the data as well as the
model without \( K \) in common. The second results indicate that the model without \( L_\infty \)
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in common fits better than the model with \( L_\infty \) in common. Thus, the separate \( L_\infty \) parameters should “stay” in the model at this point but a common \( K \) parameter can be used.

Finally, the model with \( K \) and \( t_0 \) in common should be compared to the COMMON MODEL to clarify that \( L_\infty \) differs between the groups. This comparison is done with,

\[
\begin{align*}
> \text{anova(mCom,m2L)} \\
\text{Res.Df Res.Sum Sq Df Sum Sq F value Pr(>F)} \\
1 & 315 & 647329 & & & & & \\
2 & 314 & 545239 & 1 & 102090 & 58.793 & 2.211e-13 ***
\end{align*}
\]

These results are very strong evidence that the COMMON MODEL does NOT fit the results better then the model with separate \( L_\infty \). Thus, the model with common \( K \) and \( t_0 \) but separate \( L_\infty \) is the model that best fits the data. We conclude that \( L_\infty \) but not \( K \) or \( t_0 \) differs between male and female Atlantic croakers.

Similar results can be obtained by computing the AIC for each model with,

\[
> \text{AIC(mGen,m1KT,m1LT,m1LK,m2T,m2K,m2L,mCom)}
\]

\[
\begin{align*}
\text{df} & \quad \text{AIC} \\
mGen & 6 \quad 3280.588 \\
m1KT & 5 \quad 3281.051 \\
m1LT & 5 \quad 3279.005 \\
m1LK & 5 \quad 3278.705 \\
m2T & 4 \quad 3293.224 \\
m2K & 4 \quad 3285.647 \\
m2L & 4 \quad 3278.568 \\
mCom & 3 \quad 3331.146
\end{align*}
\]

Making Predictions

Predictions of the mean length of fish at a given age are obtained in a similar but somewhat more complicated manner as what was described for the Von Bertalanffy model in Section 11.2.3. The process is more complicated because you must include values for \( G1 \) and \( G2 \) to identify whether your predictions are for individuals in group 1 or group 2 (unless the common model is the best-fit model). In addition, when using the results from \texttt{boot.case()} to make bootstrapped intervals it is critical that you know which column each parameter is in. The \texttt{boot.case()} will put the parameters in the columns in the same order that you put them in the \texttt{start=} argument of the \texttt{nls()} call for the best-fit model. However, you can easily double-check the order by using \texttt{names(coef.boot)} where \texttt{coef.boot} is the object in which the \texttt{boot.case()} results were saved (i.e., the examples in this chapter have all used \texttt{coef.boot}
CHAPTER 11. INDIVIDUAL GROWTH

Example 11.11 - Atlantic Croaker (Continued)

The predicted average length for age-8 male Atlantic croakers is found with,

```r
> new <- data.frame(Age=8,G1=1,G2=0) # predict MALE at age 8
> predict(m2L, new)
[1] 354.0889
> coef.boot<-boot.case(m2L) # Bootstrap the model results
> pv<-1*coef.boot[,1]*(1-exp(-coef.boot[,2]*(8-coef.boot[,3]))) +
  0*coef.boot[,4]*(1-exp(-coef.boot[,2]*(8-coef.boot[,3])))
> quantile(pv,c(0.025,0.975))
   2.5%   97.5%
345.3563 363.7076
```

Thus, an average age-8 male Atlantic croaker is between 345.4 and 363.7 mm.

The predicted average length for age-8 female Atlantic croakers is found with,

```r
> new <- data.frame(Age=8,G1=0,G2=1) # predict FEMALE at age 8
> predict(m2L, new)
[1] 395.1362
> pv<-0*coef.boot[,1]*(1-exp(-coef.boot[,2]*(8-coef.boot[,3]))) +
  1*coef.boot[,4]*(1-exp(-coef.boot[,2]*(8-coef.boot[,3])))
> quantile(pv,c(0.025,0.975))
   2.5%   97.5%
385.9993 404.1877
```

Thus, an average age-8 female Atlantic croaker is between 386.0 and 404.2 mm.

Review Exercises

11.17 ? examined the age and growth of troutperch in the southeaster portion of Lake Michigan. The data(TroutPerch) file contains the assigned age (by scales) and total length (mm) of a large sample of both male and female troutperch. Use these data to answer the following questions.

(a) Is there a significant difference between male and female troutperch in any of the parameters of the traditional Von Bertalanffy growth model? Show your work.

(b) Predict the mean lengths of age-2 male and female troutperch in this population.

11.18 The age and growth of longjaw cisco at two locations in Lake Michigan was examined by ?. The data(LJCisco) file contains the assigned ages (by scales) and total length (mm) of cisco from both sites. Use these data to answer the following questions.