

9

Growth of Individuals

9.1 Growth in Size

9.1.1 uses of growth information

Ignoring immigration and emigration, stock production is a mixture of recruitment of new animals to the population and the growth of the individuals already in the population. This is one reason there is a huge literature on the growth of individuals in fisheries ecology. In addition, many aspects of a species' life history characteristics tend to be reflected in how it grows. Thus, long-lived species tend to be relatively slow growing, while short-lived species tend to grow more quickly (though exceptions exist; Ziegler et al., 2007). In this chapter, we will ignore the biology of growth and focus instead on the mathematical description of growth.

In ecology and fisheries, it is very common to gather information about how organisms grow in size (especially in terms of length- or weight-at-age). Besides recruitment of juveniles, increases in the stock biomass vulnerable to fishing come about by the growth of individuals already recruited to the stock. This aspect of production is used in many stock assessment analyses. For example, as discussed in Chapter 2, yield-per-recruit analyses ask: What average or minimum size or age at first capture leads to the optimal yield? This is a trade-off between the loss of biomass through the natural mortality of individuals and the gain to biomass through the growth of individuals. Without this sort of information and analysis there is a risk of growth overfishing (taking too many fish when they are still too small for optimum yield). Ecologically, growth information can also provide insights into how a species interacts with its environment. Mathematical relationships between age, length, and weight are often used to translate the outputs of models based upon animal numbers into outputs based upon biomass.

The literature on individual growth is too extensive (Summerfelt and Hall, 1987) to permit here anything other than a brief review of the most important aspects from a stock assessment point of view. In this chapter, we will introduce various models of individual growth and the methods used to estimate their parameters for particular populations. Very commonly, it is

useful to be able to compare growth curves (indeed, any set of nonlinear relationships). Strategies and methods for making such comparisons are also addressed in this chapter, including a randomization test that may improve matters when the ageing data are suboptimal.

9.1.2 The Data

Generally, data in studies of growth consist of estimates and measurements of age, size (often length or width), and weight. However, tagging data can also be collected and those, generally, consist of the dates of tagging and recapture, the initial length at tagging, and the length at recapture. It is unusual to have the age of the individuals in tagging studies. Different methods are required for fitting growth models to these two distinct types of data. It is also possible to describe the average growth within a population by following a series of model progressions assumed to represent cohorts through known time periods (using multiples of Example Box 3.14).

We are interested in the relationships formed between all three possible combinations of direct data: age vs. length, age vs. weight, and length vs. weight. Of these, the latter usually has the simplest model and is usually the most straightforward to fit to raw data. Obtaining data relating to length or weight is relatively simple, although weight may be affected by many things other than length (maturity and gonad development stage, gut contents, freshness, free water content, etc.). Obtaining data relating to age tends to be far more problematical.

Many methods have been suggested for ageing aquatic organisms, and the approach that best suites a particular species depends upon many factors. Many species do not grow at a uniform rate throughout the year. Instead, there tends to be a slowing of growth in the winter or less productive months. This can be relatively unmarked in tropical areas but tends to be very clear in cooler or freshwater environments. Many body parts can be affected by this differential growth, and these effects can be used to age the fish. Literal growth rings (analogous to annual tree rings) can be found in such body parts as the scales, the vertebrae, and fin-ray spines, but especially in the various ear bones known as otoliths (Summerfelt and Hall, 1987). As well as annual rings, there have been developments using daily growth rings. Analogous rings can be found in some invertebrates, and although these may not necessarily be annual, they can also be used to age the animals concerned (Moltschaniwskyj, 1995).

There is an enormous literature concerning the development and structure of otoliths. However, here all we need to know is that when a fish is to be aged is captured, it is first measured for length and weight, and then commonly its otoliths are removed (this can be a highly skilled art when done properly). There are a number of ways in which the otoliths (or other structures to be aged) can be treated to make the yearly rings more visible, but whatever method is used, the aim is to determine the age of the fish in years or

fractions of years. Using such methods relies upon many assumptions, the most important being that the rings can be clearly identified and that they are, in fact, annual; this latter can be validated using tagging experiments or a variety of other techniques (Summerfelt and Hall, 1987).

9.1.3 Historical usage

A variety of mathematical descriptions have been applied to growth. At the start of the twentieth century various people assumed either a constant proportional increase (equivalent to exponential growth) or a linear increase in size with age. In the 1930s the observed size-at-age was used, and later still, Ricker is reported as assuming an exponential increase in weight (Smith, 1988). In the 1950s, there was a search for a general mathematical model of growth with a biological basis, i.e., an explanatory model. Beverton and Holt (1957) introduced the idea of von Bertalanffy growth curves to fisheries. This was an approach in which growth was defined as the balance between positive and negative processes within organisms. Von Bertalanffy derived an equation that could be used to predict the length of an organism as a function of its age (von Bertalanffy, 1938). The cube (or close approximation to the cube) of this equation could then be interpreted as the weight of an organism in relation to age (changes in one dimension being reflected in three dimensions). The validity of applying this model to the average growth of collections of individuals, when it was designed to describe the growth of single individuals, was not attended to at the time (Sainsbury, 1980).

A common alternative to the von Bertalanffy equation is simply to have a lookup table of mean lengths (or weights) at a given age or the proportional distribution of numbers at different sizes for given ages. If sufficient information is available, such age-length keys permit estimates of the uncertainty around each mean length-at-age value. However, an empirical table does not readily permit interpolation of missing or underrepresented ages, so most models use some mathematical representation of average individual growth. Not all growth equations currently used have interpretable parameters; there are even examples of the use of polynomial equations to describe growth in fish empirically (Roff, 1980).

9.2 Von Bertalanffy Growth Model

9.2.1 Growth in Length

Despite a wide array of criticisms, the growth model of length with age most commonly used in fisheries remains the three-parameter equation developed by von Bertalanffy (1938):

© 2011 by Taylor & Francis Group, LLC

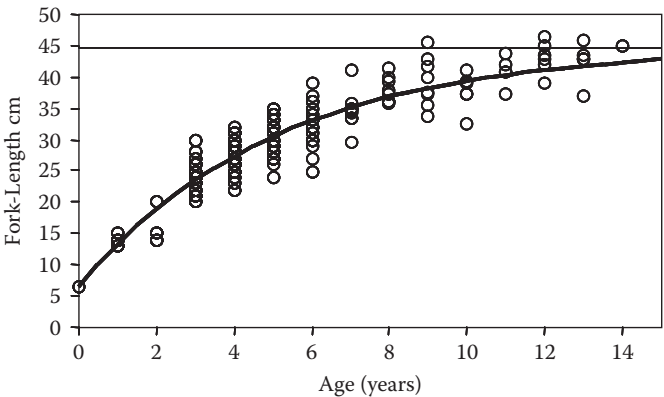


Figure 9.1
Von Bertalanffy growth curve for fish length against age, from a 1985 sample of snapper, *Pagrus auratus*, from the Bay of Plenty, New Zealand. The parameters are $L_{\infty} = 44.79$, $K = 0.196$, and $t_0 = -0.81$. The L_{∞} asymptote is illustrated by the fine horizontal line. Some points lie above this line because, with Equation 9.1, L_{∞} is interpreted as the average length at the maximum age. Notice also that most data occur where the curve is turning over (ages 3 to 6), that there are only few data points for the youngest ages, and the number of observations are also reducing for older fish; this is typical of many data sets. This lack of data points for the younger and older animals can distort or bias all of the estimated parameters (L_{∞} and K should be bigger, while the t_0 value should be closer to zero).

$$L_t = L_{\infty} \left(1 - e^{-K[t-t_0]} \right) + \epsilon \tag{9.1}$$

where L_t is the length-at-age t , L_{∞} (pronounced L -infinity) is the asymptotic average maximum body size, K is a growth rate coefficient that determines how quickly the maximum is attained, and t_0 is the hypothetical age at which the species has zero length (t_0 fixes the position of the curve along the x axis, and can affect the steepness of the curve; see Figure 9.1). It should be remembered that t_0 is an extrapolation from available data and can be difficult to interpret. The epsilon (ϵ) denotes the belief that residuals would be distributed normally about the expected growth line. When fitted using least squared residuals, this curve represents the average growth of the population members.

Continuous and serial spawning species add variation into the length-at-age relationship. To some extent the t_0 parameter glosses over uncertainties relating to the date of spawning and metamorphosis from larval forms to juveniles.

The parameter values derived from a single sample may not provide an adequate description of the growth properties of the sampled population (Figure 9.1). The L_{∞} and t_0 parameters are at the extremes of the curve, and this is where the data tend to be least adequate. As with all things, care must be taken to obtain a representative sample. The curve may be fitted to raw data using nonlinear least squares methods (Example Box 9.1). Whether the

EXAMPLE BOX 9.1

Fitting length- and weight-at-age von Bertalanffy growth curves to length data for female Pacific hake (Kimura, 1980). The weight-at-age data were invented. To calculate the expected lengths in column D, put $=B\$1*(1-\exp(-B\$2*(A5-B\$3)))$ into D5 and copy down to D17. Similarly, in F5 put $=F\$1*(1-\exp(-B\$2*(A5-B\$3)))^F\2 and copy down to F17. Finally, put $=\text{average}(D5:D17)$ into cell F3. Plot column C against A as a scattergram and add columns A against F as a line (cf. Figure 9.2) to observe the relation between age and weight. In addition, plot column B against A as a scattergram and add column D to the graph to relate length and age (cf. Figure 9.3). First use the solver to minimize D1 by altering B1:B3 (the values given here are close to but not the optimum). Then, minimize D2 by varying cells F1:F2. Copy and store the values from A1:F3 to the right of the workings below. Then minimize the total sum of squared residuals in D3 by varying B1:B3 and F1:F2 together (B1:B3,F1:F2). Do the answers differ? If you believe the variance of the residuals around the curve increases with age, we could use a constant coefficient of variation and not a constant variance. This means we need to increase the weight of the residuals for the smaller fish and decrease it for the larger. To do this, put $=(F\$3/D5)*(B5-D5)^2$ into E5, copy down, and re-solve. The curve fits the younger ages more closely than the older ages (the residuals are allowed to spread more widely with age).

	A	B	C	D	E	F	G
1	L_{∞}	61.2	SSq_L	$=\text{sum}(E5:E17)$	W_{∞}	4.85	
2	K	0.3	SSq_W	$=\text{sum}(G5:G17)$	b	3.078	
3	T_0	-0.06	Tot_SSq	$=D1+D2$	Avg Ex(L)	48.853	
4	Age	Obs(L)	Obs(W)	Ex(L)	SSqL	Ex(W)	SSqW
5	1	15.40	0.20	16.671	$=(B5-D5)^2$	0.0883	$=(C5-F5)^2$
6	2	28.03	0.35	28.212	$=(B6-D6)^2$	0.4466	$=(C6-F6)^2$
7	3.3	41.18	0.72	38.865	$=(B6-D6)^2$	1.1978	$=(C7-F7)^2$
8	4.3	46.20	1.70	44.654	Copy down	1.8370	Copy down
9	5.3	48.23	2.40	48.942	To row 17	2.4366	To row 17
10	6.3	50.26	3.12	52.119	3.4571	2.9574	0.0265
11	7.3	51.82	3.82	54.473	7.0378	3.3883	0.1864
12	8.3	54.27	3.93	56.216	3.7886	3.7336	0.0607
13	9.3	56.98	4.22	57.508	0.3342	4.0042	0.0466
14	10.3	58.93	3.88	58.465	0.2163	4.2129	0.1109
15	11.3	59.00	4.42	59.174	0.0302	4.3723	0.0023
16	12.3	60.91	4.13	59.699	1.4666	4.4929	0.1317
17	13.3	61.83	4.42	60.088	3.0345	4.5837	0.0268

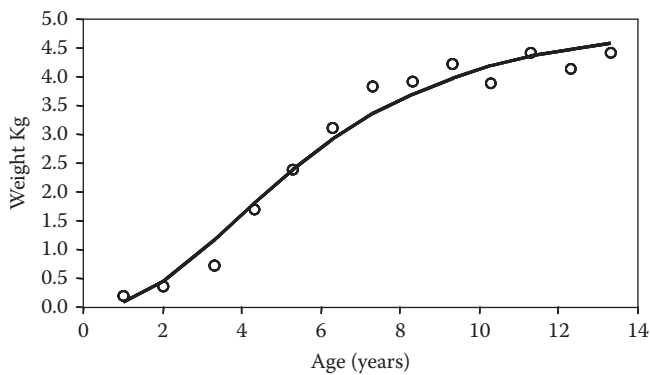


Figure 9.2
Von Bertalanffy growth curve of invented mean body weights against age in years for female Pacific hake (length and age data from Kimura, 1980; see Example Box 9.1). The shape of such curves is typically sigmoidal, which contrasts with that for growth in length ($w_\infty = 4.85$ and $b = 3.078$).

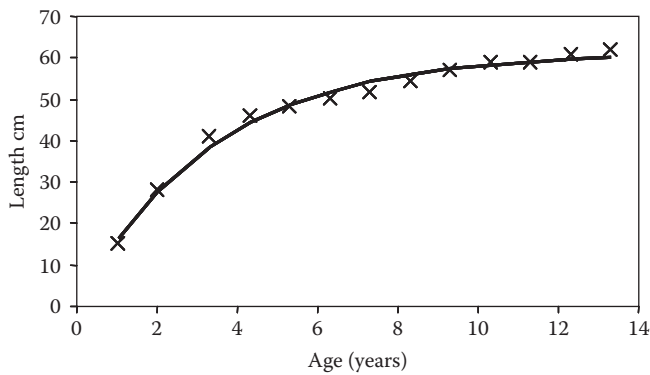


Figure 9.3
The optimal von Bertalanffy curve fitted to data for female Pacific hake (Kimura, 1980). The curve may be fitted using simple least squares with a constant variance for the residuals for all ages, or using weighted least squares to give rise to a constant coefficient of variation (Example Box 9.1).

least squares assumption of a constant variance of lengths across all ages is valid should always be considered.

9.2.2 g rowth in Weight

The relation between observed length (L_t) and predicted weight (w_t) for many animals is best described by a power function:

$$\hat{w}_t = aL_t^b \tag{9.2}$$

© 2011 by Taylor & Francis Group, LLC

where b is the allometric growth parameter and a is a scaling constant. The residual errors for such a curve can be either normal, ε , or lognormal, e^ε . If normal random errors are used, then how the variance changes with length would most likely need to be explicitly modelled, which would usually require maximum likelihood methods. By combining Equations 9.1 and 9.2, and defining the asymptotic maximum expected weight to be w_∞ , we can produce the von Bertalanffy growth equation for body weight:

$$\hat{w}_t = w_\infty \left[1 - e^{-K[t-t_0]} \right]^b \quad (9.3)$$

which is identical in form to the equation for length, Equation 9.1, but replacing L_∞ with the equivalent of Equation 9.2 at L_∞ (i.e., $w_\infty = a.L_\infty^b$) and the addition of the allometric growth parameter b (the two equations are identical if a and b are set to 1). As an approximation the constant b is often set equal to 3. The shape of the two curves is clearly different (cf. Figures 9.1 and 9.2). The curve describing growth in length has a rapid increase that slows down to reach the asymptote at the L_∞ . The curve describing growth in weight, however, can have two inflections producing a sigmoidal curve (Figure 9.2, Example Box 9.1).

As with the von Bertalanffy curve of length-at-age, one can use nonlinear least squares to fit this curve to a data set (Figure 9.2, Example Box 9.1). Of course, if the residuals were deemed to have a distribution that is anything other than a normal or lognormal distribution (this would be uncommon), then one would need to use maximum likelihood methods (Haddon et al., 2008). Where there may be a modification from the standard least squares strategy is with the variance of the residuals. It is possible that the variance of the residuals is not constant but increases with age. If this were so, it is possible to use residuals having a constant coefficient of variation rather than a constant variance (Example Box 9.1); this would be weighted least squares.

9.2.3 Seasonal growth

The growth of many organisms in highly seasonal waters does not necessarily proceed at the same rate throughout the year. Growth rings in otoliths and other hard parts come about through differences in the metabolism and growth rate of the species concerned. In the tropics, with reduced seasonal variation in the environment, annual rings are difficult to detect because growth is more continuous. This is one reason why age-related fisheries techniques can be less useful in tropical regions than in temperate or boreal systems (although there has been some progress using daily growth rings; Choat and Axe, 1996).

In nontropical regions, especially in freshwater systems, differences in growth rate within a year are sometimes so marked that modifications are required to growth models so that seasonal variation can be described

© 2011 by Taylor & Francis Group, LLC

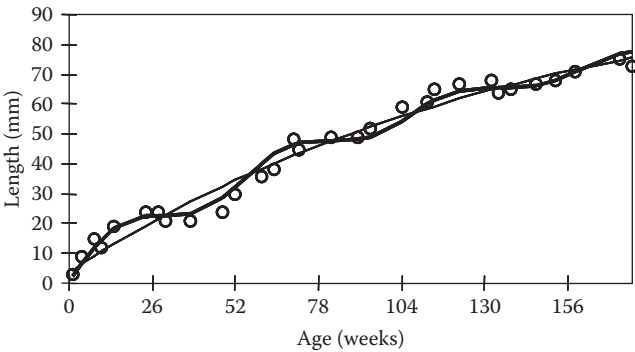


Figure 9.4
Data extracted from Pitcher and Macdonald (1973) for minnows. Note the x axis is in weeks and covers just over three years. The thick curve is from Equation 9.4, with $L_{\infty} = 106.89$, $t_0 = -5.2$, $K = 0.00768$, $C = 0.06$, and $s = 4.007$. The fine nonoscillatory curve is the same von Bertalanffy curve without the imposed oscillation (Example Box 9.2). Both t_0 and s are in units of weeks.

adequately. Once again, many different models have been proposed. Pitcher and MacDonald (1973) proposed a modification to the von Bertalanffy curve to include seasonality:

$$L_t = L_{\infty} \left(1 - e^{-\left[C \sin\left(\frac{2\pi(t-s)}{52}\right) + K(t-t_0) \right]} \right) \tag{9.4}$$

where C is related to the magnitude of the expected oscillations above and below the nonseasonal growth curve, s is the starting point in time for the sine wave (relates to the phase of the oscillation), and the other constants, K , L_{∞} , and t_0 , are defined as before (Figure 9.4). The variable t is the age at length L_t . The value of 52 in Equation 9.4 indicates that the timescale of events is that of weeks (thus, s , t , and t_0 will be measured in weeks). In effect, this equation is the von Bertalanffy curve with a sine wave added.

By changing the period to twelve, and adjusting the units of the parameters s , t , and t_0 , one could just as easily work with months (though obviously with less precision). Such seasonal adjustments to the growth model are less likely to be necessary in tropical areas, and are more likely to be required in freshwater environments where temperatures and the productivity of the habitat are highly seasonal.

As with all curve fitting, it is a good idea to examine the residuals after the optimum fit has been determined (Figure 9.5). When this is done with the minnow data, it is clear that the optimum fit is missing an obvious cycle in the data.

The pattern in the residuals approximates another sinusoidal wave, so one possible solution would be to add a further sine wave to the model and

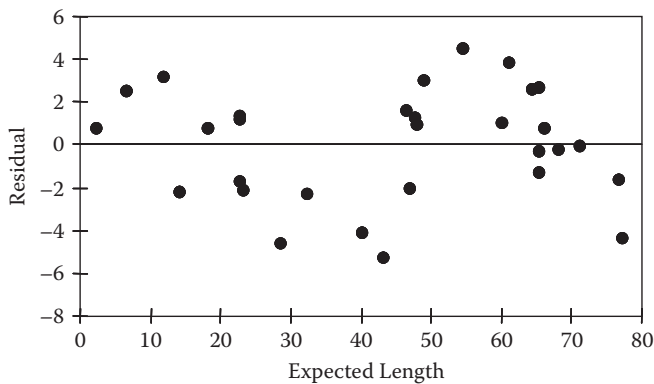


Figure 9.5
The residuals remaining after an optimum fitting seasonal growth curve has been fitted to the data in Table 9.1 (Figure 9.4). There remains a clear sine wave in the data. Inspection of Figure 9.4 suggests that it has a period of about two years, so it may be worthwhile to add a further sine wave to the model (Example Box 9.2).

refit to the data. Whether this pattern in the residuals reflects some natural phenomenon not noticed when the data were being collected would require further investigation.

The equation would become

$$L_t = L_{\infty} \left(1 - e^{-\left[C_1 \sin\left(\frac{2\pi(t-s_1)}{52}\right) + C_2 \sin\left(\frac{2\pi(t-s_2)}{p}\right) + K(t-t_0) \right]} \right) \tag{9.5}$$

where p is the period of the second cycle, and the other parameters are as before, only duplicated for each cycle (Example Box 9.2).

The addition of a further cycle to the model may appear arbitrary but illustrates a vital issue when attempting to model a natural process. The objective is generally to obtain the optimal balance between generating a realistic model of a process while at the same time obtaining an optimal fit to the data using the smallest number of parameters to do so. A regular pattern in the residuals indicates a trend remains undescribed by the model. Therefore, decisions need to be made about changing the model (usually to make it more complicated). Generally, one would only accept a more complex model if some criterion, such as Akaike’s information criterion (Burnham and Anderson, 2002) indicated that the improvement in the quality of fit outweighed the inclusion of an increased number of parameters. The second sine wave presumably represents a cycle of longer period than the annual cycle of seasons. In this way, the model has indicated a valuable research direction to be followed in future work (Example Box 9.2).

EXAMPLE BOX 9.2

A seasonal varying growth curve fitted to data extracted from Pitcher and MacDonald (1973) for minnows (Figure 9.4, Table 9.1). The data need to be copied into columns A and B, down to row 36. The model is relatively complicated being Equation 9.5; put the following into C7 and copy down to C36: $=B\$1*(1-\exp(-(\$B\$4*\sin((2*\pi())*(A7-\$B\$5))/52)+\$E\$1*\sin((2*\pi())*(A7-\$E\$2))/\$E\$3)+\$B\$2*(A7-\$B\$3)))$. When the amplitude parameters C_1 and C_2 are set to zero, then the sine wave terms collapse to zero, leaving the basic von Bertalanffy growth curve. Remember that each of the time-related parameters are in weeks. Plot column B against A as a scattergram and add column C to it as a thick line. Add column F to this as a thin line to mimic Figure 9.4. Minimize F5 by altering cells B1:B5. Then plot the residuals as column D against C to mimic Figure 9.5. Once the pattern in the residuals is apparent, refit the model but this time alter cells B1:B5, E1:E3. Observe the impact of this on the total sum of squares and on the residuals. Is there still a pattern in the residuals? Is there anything suggestive about the estimated period for the second curve? By how much does the SSQ get smaller? Is it worth adding three more parameters for the improved quality of fit? Look ahead to Equation 9.18 and put $=F4*\ln(F5/F4)+2*5$ into F1 to calculate the Akaike information criterion. The $2*5$ indicates five parameters, when you fit both cycles that would use eight parameters, leading to $2*8$, so the addition of the second cycle would need to reduce the first term by at least six for the bigger model to be preferable.

	A	B	C	D	E	F
1	L_∞	106.9		C_2	0	
2	K	0.0068		s_2	-20	
3	t_0	-5.2		Period2	70	
4	C_1	0.06			N	=count(E7:E36)
5	s_1	4.0			SSQ	=sum(E7:E36)
6	T	Obs_ L_t	Model	Resid	Resid ²	Nonseasonal
7	1	3	2.19	=B7-C7	=D7^2	=B\$1*(1-exp(-B\$2*(a7-B\$3)))
8	4	9	6.46	=B8-C8	=D8^2	=B\$1*(1-exp(-B\$2*(a8-B\$3)))
9	8	15	11.84	=B9-C9	=D9^2	=B\$1*(1-exp(-B\$2*(a9-B\$3)))
10	10	12	14.24	Copy	Down	Copy down to row 36
11	14	19	18.18	To	Row 36	13.056
12	24	24	22.64	1.363	1.857	19.210
13	28	24	22.78	1.221	1.491	21.557

TABLE 9.1

A Subset of Length-at-Age Data for Minnows Measured from a Figure in Pitcher and Macdonald (1973)

Weeks	Obs L	Weeks	Obs L	Weeks	Obs L
1	3	52	30	114	65
4	9	60	36	122	67
8	15	64	38	132	68
10	12	70	48	134	64
14	19	72	45	138	65
24	24	82	49	146	67
28	24	90	49	152	68
30	21	94	52	158	71
38	21	104	59	172	75
48	24	112	61	176	73

Note: The ages are in weeks and the lengths are in millimeters. These data are illustrated in Figure 9.4 and used in Example Box 9.2.

9.2.4 Fitting to Tagging Data

So far, we have only considered fitting the von Bertalanffy curve to data where one has each fish's length at particular ages. Obviously, for this, one would need to be able to age the fish accurately. But there are other forms of data available that can be used to fit a von Bertalanffy curve. When one conducts a tagging experiment, it is common to obtain lengths when animals are first tagged and to remeasure them on recapture with the time interval between recaptures known. If the von Bertalanffy curve could be reformulated in terms of size increments after a given time from a given initial size, it would be possible to use such data to fit the growth curve.

Fabens (1965) transformed the von Bertalanffy curve so it could be used with the sort of information obtained from tagging programs (see Appendix 9.1 for the full derivation). By manipulating the usual von Bertalanffy curve (Equation 9.1) Fabens produced

$$\Delta \hat{L} = (L_{\infty} - L_t)(1 - e^{-K\Delta t})$$
$$\Delta \hat{L} = L_{t+\Delta t} - L_t$$

(9.6)

where, for an animal with an initial length of L_t , $\Delta \hat{L}$ is the expected change in length through the period of Δt . By minimizing the squared differences between the observed ΔL and the expected $\Delta \hat{L}$ for each point, using Equation 9.6, estimates can be derived for the K and L_{∞} parameters. The average length at a known age would be required to include an estimate of t_0 , so often, no estimate can be generated and the exact location of the growth curve along an age axis is not determined. In these cases, the t_0 parameter is often set to zero (Figure 9.6, Example Box 9.3).

© 2011 by Taylor & Francis Group, LLC

Copyright © 2011. CRC Press LLC. All rights reserved.

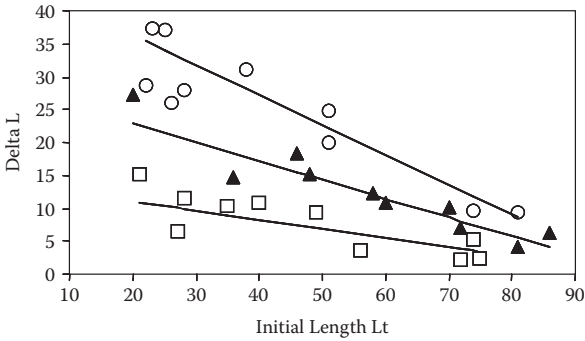


Figure 9.6
Plot of artificial data for tag returns from three different time intervals (squares = 170 days, filled triangles = 385 days, and circles = 690 days); each time interval has its own expected ΔL for a given starting length L_t illustrated by the three solid lines. If the lines were projected, they would meet the x axis at L_∞ (Table 9.2, Example Box 9.3).

9.2.5 extensions to Fabens Method

The use of the Fabens method appears straightforward (Example Box 9.3), but there are difficulties that are easily overlooked. Sainsbury (1980) pointed out that, as originally developed, both Equations 9.1 and 9.6 relate to the growth of individuals and thus do not predict the average length-at-age t or the average growth increment for a given initial length and time passed, Δt . Instead, it is just assumed that these curves can be applied to collections of individuals. This ignores the fact that there will be variation in the growth of individuals.

An inspection of the distribution of the length increments relative to the initial size at tagging (Figure 9.6) indicates that the variation around the expected length increments appears to be greater at the smaller initial lengths, L_t . Thus, as the expected ΔL declines with increasing initial size, the variability of the residuals appears to decline. One could use either a weighted least squares approach to fitting the model (having a constant coefficient of variation instead of a constant variance), or one could use a maximum likelihood method and directly estimate the variance. Francis (1988a) described just such a maximum likelihood approach that fitted the model to the data assuming the residuals were distributed normally, and he suggested a number of different functional forms for the relationship between residual variance and expected ΔL . Thus, normal errors are used, but the variance of the residuals is determined separately. Using ordinary normal random errors (i.e., constant variance) would provide identical answers to a least squares approach. The negative log-likelihood in this case would be

$$-veLL = -\sum L_n \left(\frac{1}{\sqrt{2\pi}\sigma} e^{-\frac{(\Delta L - \hat{\Delta L})^2}{2\sigma^2}} \right) \tag{9.7}$$

EXAMPLE BOX 9.3

The Fabens method of fitting a growth curve to tagging data extended using ideas from Francis (1988a). The t_0 is redundant (but could be used to plot a growth curve from a length-at-age perspective). Enter the data from Table 9.2 into columns A to C, down to row 35. In E4 put $=\text{sum}(H6:H35)$. To obtain the number of years at liberty put $=A6/365.25$ into D6. In E6 put $=(B\$1-B6)*(1-\text{EXP}(-B\$2*D6))$. Copy D6:E6 down to row 35. In column H put $=-\text{Ln}(\text{normdist}(C6,E6,G6,\text{false}))$ and copy down to row 35 to obtain the negative log-likelihoods. The first model fit can be generated using least squares by getting the solver to minimize B4 while changing B1:B2. Record the answer somewhere else on the sheet. If you were to put $=E\$3$ into cell G6 and copy down, you could obtain the same result via maximum likelihood as from least squares, by minimizing E4, by changing (B1:B2, E3). This is not particularly stable and you may need to try a number of starting points to obtain an answer. If it does fail and generate a #NUM error, look for the reason why it happened. Alternatively, you could put $=E\$1*E6$ into G6 and copy down to obtain Equation 9.8, the linear relation between residual standard deviation and the expected ΔL (minimize E4 by modifying B1:B2, E1). Finally, try the two other residual structures: $=E\$1*E6^{\wedge}E\2 and $=E\$2*(1-\text{exp}(-E\$1*E6))$. Compare the parameter estimates and the total log-likelihood. Which is the best fitting model? Examine the residuals in a graphical plot. Compare the various fits using the likelihood ratio test or using Akaike's information criterion ($\text{AIC} = 2\text{LL} + 2p$), where LL is the negative log-likelihood and p is the number of parameters. The smallest AIC wins.

	A	B	C	D	E	F	G	H
1	L_{∞}	100.39		Nu	0.5			
2	K	0.31		tau	0.5			
3	t_0	0		Sigma	3			
4	SSq	$=\text{sum}(F6:F35)$		-veLL	75.5175			
5	ΔT	Lt	ΔL	ΔT Yrs	$E(\Delta L)$	Resids ²	StDev	LL
6	170	21	15.1	0.465	10.62	$=(C6-E6)^2$	3.00	3.133
7	170	27	6.4	0.465	9.82	$=(C7-E7)^2$	3.00	2.666
8	170	28	11.5	0.465	9.68	$=(C8-E8)^2$	3.00	2.201
9	170	35	10.3	0.465	8.75	Copy down	3.00	2.151
10	170	40	10.8	0.465	8.08	To F35	3.00	2.429
11	170	49	9.4	0.465	6.87	6.379	3.00	2.372

TABLE 9.2

Artificial Example Tagging Data Simulated from $L_{\infty} = 100$ and $K = 0.3$

Δt	L_t	ΔL	Δt	L_t	ΔL	Δt	L_t	ΔL
170	21	15.1	385	20	27.2	690	22	28.6
170	27	6.4	385	36	14.8	690	23	37.3
170	28	11.5	385	46	18.3	690	25	37.2
170	35	10.3	385	48	15.2	690	26	26.1
170	40	10.8	385	58	12.2	690	28	27.9
170	49	9.4	385	60	10.8	690	38	31
170	56	3.6	385	70	10.2	690	51	24.7
170	72	2.1	385	72	7.1	690	51	19.9
170	74	5.2	385	81	4.1	690	74	9.7
170	75	2.3	385	86	6.2	690	81	9.3

Note: Each set of three relates to different days at liberty, Δt , L_t relates to the initial size at tagging, and ΔL is the change in length during Δt . These data are illustrated in Figure 9.6 and are used in Example Box 9.3.

where σ^2 is the constant variance of the residuals between the observed and expected ΔL values. Francis (1988a) provided a number of different formulations for describing this variance, including an inverse linear relationship between the standard deviation and the expected ΔL :

$$\sigma = v(\Delta \hat{L}) \tag{9.8}$$

where v (nu) is a constant multiplier on the expected ΔL , and would need to be estimated separately. The likelihood becomes

$$L(\Delta L | Data) = \sum_i \left(\frac{1}{\sqrt{2\pi v \Delta \hat{L}}} e^{-\frac{(\Delta L - \Delta \hat{L})^2}{2(v \Delta \hat{L})^2}} \right) \tag{9.9}$$

Francis (1988a) also suggested exponentially declining residual standard deviations:

$$\sigma = \tau(1 - e^{-v \Delta \hat{L}}) \tag{9.10}$$

where τ is an extra estimable constant. Finally, Francis (1988a) suggested that the residual standard deviation might follow a power law:

$$\sigma = v \Delta \hat{L}^{\tau} \tag{9.11}$$

Francis (1988a,b) took his extensions of the Fabens method further with suggestions for how to account for consistent bias in the measurement of length,

with additions to the model to estimate seasonal variation in growth rates and to account for outlier contamination. All of these extensions constitute valuable improvements over the simple Fabens method. With each different formulation of the relationship between the variance of the residuals and the expected ΔL , the constants τ and ν would change in their interpretation. As seen before, the parameter estimates obtainable from the same model can vary if different error structures are assumed (Example Box 9.3).

Unfortunately, how we select which error structure is most appropriate is not a question that is simple to answer. One could use a likelihood ratio test (see Equation 9.21) to compare the quality of fit obtained with the different numbers of parameters. Thus, if there were an improvement to the log-likelihood of the order of 1.92 (a χ^2 value of 3.84 divided by 2) from fitting the model using Equation 9.11 instead of Equation 9.8 (adding a parameter), this would constitute a statistically significant improvement. However, ideally, one would have other reasons for preferring one error structure over another for the residual variance.

9.2.6 Comparability of g growth Curves

The Fabens version of the von Bertalanffy equation derives directly from the classical equation (Appendix 9.1), and yet the parameters generated from size-at-age data have been given different interpretations than those generated from tagging data (Sainsbury, 1980; Francis, 1988b). This may appear paradoxical until it is realized that the curves are being fitted using very different residual error structures.

With size-at-age data, the residuals are between observed size-at-age and expected size-at-age in a snapshot sample from the population. With tagging data the residuals are between the observed size increment and the expected for possibly different time intervals, for data collected at least some time after the initial observations. The net result is that the estimation of L_∞ tends to be biased upwards with tagging data, while the reverse seems true for the size-at-age data. That the estimates of the parameters obtained from length-at-age data and from tagging data are different (as claimed by Sainsbury, 1980; Francis, 1995) can be seen directly by simulating a population where the individuals each grow with their own particular von Bertalanffy growth parameters. If a population is set up with individuals each having their own L_∞ and K values (assume a t_0 of zero) varying normally about overall mean parameter values, then this hypothetical population could be sampled for both size-at-age data and time increment growth data. Note that the same population is being sampled. If there were no difference between the two methods, then, on average, we would expect their parameter estimates to coincide (Figure 9.7). In fact, the parameter estimates do not coincide and both show biases, with the tagging approach appearing to be more biased than the size-at-age approach. Clearly, care must be taken if comparisons are to be made between growth curves estimated differently.

© 2011 by Taylor & Francis Group, LLC

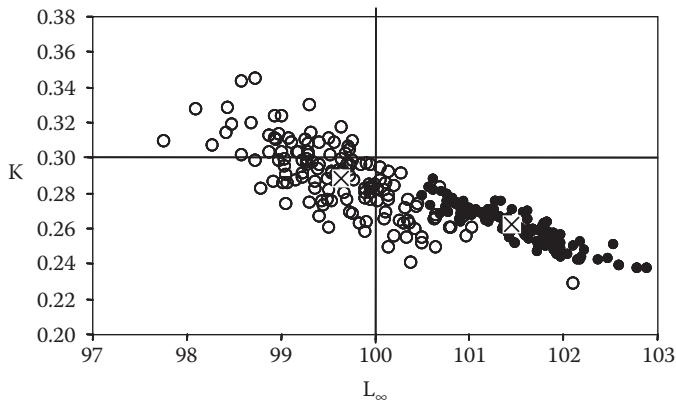


Figure 9.7

Growth curve parameters estimated from two hundred Monte Carlo simulations of sampling a single hypothetical population of individuals, each individual with its own von Bertalanffy growth parameters. Growth curves were fitted as with size-at-age data (open circles) and tagging data (small, solid circles). The two crosses indicate the mean of each set of parameter estimates. The mean values for L_{∞} and K were 100 and 0.3, respectively, as indicated by the crossed lines. Generally, the estimates from tagging data were biased high for the L_{∞} and low for the K parameter. From size-at-age data, both parameter estimates were biased slightly low.

9.2.7 Growth from Modal Progression

If the size distribution of a population is measured through time, then the average growth of the animals surviving through time can be estimated in the form of a growth curve. Such curves would not be directly comparable to growth curves estimated using size-at-age or tagging data. Modal progression relates to the average growth of a surviving population, whereas the other two methods relate to the growth of individuals. If there are any size-selective mortality processes occurring, then the growth curve produced using modal analysis will differ significantly from the other methods. Nevertheless, modal analysis has been used for a long time in fisheries science (Fournier and Breen, 1983) and has the advantage that the collection of data is simple and cheap.

Example Box 3.14 illustrates how to fit modes directly to length frequency data. Given a time series of such data, a growth curve can be fitted by including growth curve parameters that give rise to predicted mean lengths at time instead of estimating these modal means directly. The modal means are taken to represent different cohorts growing within the population.

This approach to describing average population growth is most useful with juvenile and small animals. Generally, as animals become mature, their growth tends to slow significantly and any modes begin to overlap and become difficult to distinguish correctly. Nevertheless, modal analysis remains a useful approach for characterizing early growth.

© 2011 by Taylor & Francis Group, LLC

9.3 Alternatives to Von Bertalanffy

9.3.1 A generalized Model

Virtually every fishery paper concerned with growth uses the von Bertalanffy growth equation, but this does not mean that it is the only possible growth function or even necessarily the best in a given situation.

A very general model has been proposed by Schnute and Richards (1990). This starts as a four-parameter model of growth, which generalizes the classical logistic model, as well as those by Gompertz (1825), von Bertalanffy (1938), Richards (1959), Chapman (1961), and Schnute (1981). It also generalizes the Weibull (1951) distribution, which has been used with applied problems. All of these papers contain equations, which could easily be used as alternatives to the von Bertalanffy growth function (VBGF). They all share the property of permitting a description of increasing size, leading to an asymptotic maximum, but have alternative shapes, depending on their parameters. Schnute and Richards's (1990) model has the form

$$y^{-b} = 1 + \alpha e^{-ax^c} \quad (9.12)$$

By altering the parameters (a , b , c , and α), and the formal structure of the model, Equation 9.12 can take the form of many of the popular growth models (Figure 9.8). For example, if $b = c = 1$, then Equation 9.12 becomes the classical logistic relationship

$$y = \frac{1}{1 + \alpha e^{-ax}} \quad (9.13)$$

Schnute and Richards (1990) implicitly assumed that the y variable was scaled in units of y_∞ . If this asymptote is included, the model finishes with five parameters and becomes extremely flexible:

$$y_t = y_\infty \left(1 + \alpha e^{-at^c} \right)^{-\frac{1}{b}} \quad (9.14)$$

where the parameters are as before, t is age, and y_∞ is the average maximum value of the variable y . When parameter $c = 1$, the model becomes equivalent to Schnute's (1981) generalized growth model. The Schnute and Richards (1990) model generalizes the Schnute (1981) model when the age t is replaced with t^c :

$$Y_t = \left[y_1^b + (y_2^b - y_1^b) \frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \right]^{1/b} \quad (9.15)$$

© 2011 by Taylor & Francis Group, LLC

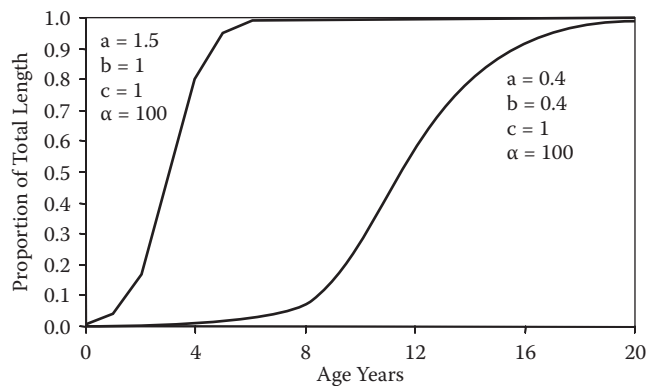


Figure 9.8
Two curves generated by substituting different sets of values for α , a , b , and c , in Equation 9.12. The general equation generates a curve of relative size against age. Construct a worksheet to illustrate this growth curve.

where t is age, y_i is the size-at-age t , and the other parameters are as before. Once again, by varying the various parameters, a wide range of curves can be generated, some of which are not necessarily asymptotic. Schnute’s (1981) model appears to have been used more in the literature than the more general Schnute and Richards (1990) model (Gillanders et al., 1999, although strictly, they used Francis’s (1995) mark-recapture analogue to Schnute’s Equation 9.15; Ziegler et al., 2007). Different model designs are still being developed (Francis, 1995; Wang and Thomas, 1995). This area of research remains open for further development (Haddon et al., 2008).

9.3.2 Model Selection—AiC and BiC

With four parameters, Equation 9.12 has one more parameter than most other growth models, which is one reason why it can embody so many models with fewer parameters as special cases. Such an equation is mathematically general and is useful for providing a unified analytical framework for a diverse literature. Knowing that all these growth models constitute special cases of a single general model should make it clear that they may be regarded solely as descriptions of growth with no explanatory power. This is a very valuable lesson. What it means is that even if we manage to obtain a very good fit of a particular growth model to a data set, the interpretation of its parameters is not necessarily meaningful. For example, just because a model implies an asymptotic maximum mean length (because it calculates one) does not force the species concerned to actually have such a maximum. We will discuss this point further when considering the many criticisms directed against von Bertalanffy curves.

Whether one would use Schnute and Richards’s (1990) general model when selecting an equation to describe growth, instead of one of the special

cases, is a difficult question to answer. The special cases might be preferred to the general equation because having fewer parameters, fitting them to real data might be more straightforward, as would using them in an assessment model. However, if these growth models truly are just descriptive black boxes, having an input to provide a particular output, then, with available computing power, it would make very little difference which equation was used. Presumably, one should use the equation that provides the best description of the growth process being described. Unfortunately, deciding what constitutes “best” is not as simple as one might hope. If one simply wants the closest description of one’s growth data (according to some criterion such as likelihood ratio or AIC), then one could try fitting a wide range of models and error structures and proceed with the one producing the best fit. As mentioned before, the AIC attempts to balance the trade-off between improving the quality of fit for a model and minimizing the number of parameters used. The AIC is calculated using

$$AIC = 2LL + 2p \quad (9.16)$$

where LL is the negative log-likelihood and p is the number of parameters. The model fit with the smallest AIC provides the best trade-off between fit and number of parameters. An alternative is the so-called Bayesian information criterion (BIC), which includes the natural log of the sample size (N) in its calculation (Burnham and Anderson, 2002). Where the sample size is greater than seven ($(\ln(7.389) = 2)$) the BIC tends to penalize the addition of parameters more than the AIC (Haddon et al., 2008).

$$BIC = 2LL + p \log(N) \quad (9.17)$$

Burnham and Anderson (2002) provide an alternative when using least squared residuals:

$$AIC = N \log(\hat{\sigma}^2) + 2p \quad (9.18)$$

where $\hat{\sigma}^2$ is the maximum likelihood estimate of the variance

$$\hat{\sigma}^2 = \frac{\sum \epsilon^2}{N} \quad (9.19)$$

where ϵ^2 is the sum of squared residuals. However, if one really wants to obtain biologically sensible interpretations when fitting a model, then model selection cannot be solely dependent upon quality of statistical fit. Instead, it should reflect the theoretical viewpoint (for example, of growth) that is being considered for reasons independent of its statistical fit to data.

© 2011 by Taylor & Francis Group, LLC

9.3.3 Polynomial equations

Polynomial functions, of three or four parameters, have been suggested as alternatives to the von Bertalanffy growth function. These polynomials are explicitly empirical, as there is little to be gained from trying to interpret the parameters. Comparisons between curves would be reliant on them each having the same number of parameters. However, Chen et al. (1992) made an explicit comparison of a variety of polynomials against the VBGF and concluded that the VBGF performed better than any of the polynomial equations considered. In the process of doing this, they also suggested a neat way of comparing growth curves of any type (see later) to determine whether they differed statistically.

If all that is required is a description of how growth has occurred, there is no reason not to use polynomial equations. However, while the interpolation of growth within the range observed is possible, attempts to extrapolate beyond the observed data could possibly lead to large errors.

9.3.4 Problems with the von Bertalanffy growth Function

With the wide range of alternative growth equations available, the ongoing use of the VBGF to represent fish growth has been questioned by a number of people. Knight (1968) criticized the VBGF as often being more like fiction than a useful model of growth. His major complaint was that L_{∞} was generally estimated through extrapolation, and sometimes extreme extrapolation (Figure 9.9).

The estimation of L_{∞} is especially a problem with fish species that do not exhibit an asymptotic maximum length (Figure 9.9). The best fit von Bertalanffy curve to the minimal data provided by Knight (1968) suggests an L_{∞} of 453 cm, that is, a cod 4.5 meters in length, which is biological nonsense. The validity of such extrapolation depends almost completely on the appropriateness of the assumptions of the von Bertalanffy model of growth for the species concerned. Roff (1980) was critical of a number of people, including Beverton and Holt (1957), who applied the curve in an apparently unthinking manner. He also emphasized its inapplicability to fish species that do not appear to have an asymptotic maximum length. The same argument against extrapolation could have been expressed about the estimation of t_0 .

Roff (1980) reviewed the problems associated with using the VBGF and suggested that people stop using it and turn to different functions instead. To his credit, Roff (1980) did not advocate any particular equation but stated that the choice should be dictated by circumstances. He also pointed out that the equation was very hard to fit to data in a statistically satisfactory manner, meaning, presumably, either that there was no simple or deterministic way of fitting the curve or that the comparison of growth curves was difficult. It is common to fit growth curves even with little data available for younger and older animals, and when the sampled population is fished and has a

© 2011 by Taylor & Francis Group, LLC

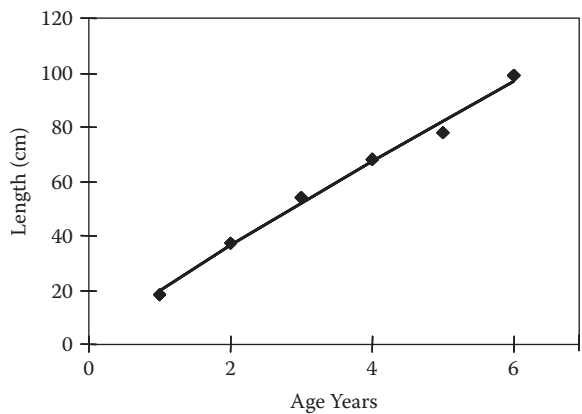


Fig ur e 9.9
Plot of the growth of Atlantic cod through the first six years of life. (After Knight, 1968.) Shows the best von Bertalanffy curve fit with $K = 0.0391$, $t_0 = -0.126$, and $L_\infty = 453$ cm, which is clearly an exaggeration of possible reality.

legal minimum size. In these cases, the data are not really representative of the population, and care must be taken with the generality of any resulting curves and comparisons with other populations.

Very obviously, there are many problems with using the VBGF; nevertheless, fisheries scientists continue to use it in their models. Given a model, although fitting the curve is no longer the technical problem it was, there is rarely any discussion about how the residuals are expected to be distributed about the expected curve. Generally, they are assumed to be normal random and additive, but there is rarely consideration of whether they are symmetrical or otherwise, or whether the variance of the residuals is constant or varies with size. Analytical and statistical computer programs routinely have procedures for generating nonlinear fits to particular models (e.g., SAS, R, Excel's nonlinear solver). Putting aside Sainsbury's (1980) and Francis's (1988a,b) problem of different concepts having the same name, the major difficulty is that of statistically comparing growth curves, for example, from different stocks or sexes of the same species.

9.4 Comparing Growth Curves

9.4.1 Nonlinear Comparisons

Because of the nonlinear nature of the von Bertalanffy growth function (VBGF), we cannot use a standard analysis of covariance with which we might usually compare regression lines. Many early methods of comparing

© 2011 by Taylor & Francis Group, LLC

growth curves relied upon linearizing the VBGF and comparing the linear regressions produced. These methods often only produced approximate fits of the VBGF to the data and will not be discussed further. Misra's (1980) approach was rather more complicated but still used a linearized reparameterization of the VBGF, fitting it to data using multiple regression, and tested for differences between growth curves using ANOVA on the separate parameters. Alternatively, Bernard (1981) used a multivariate test, Hotelling's T , to compare all three VBGF parameters at once.

A summary and consideration of methods was provided by Cerrato (1990), who compared the ability of the t , univariate χ^2 , likelihood ratio, and Hotelling's T tests to provide valid comparisons of VBGF curves. The last two methods are generally considered better than the others, not least because they consider all parameters at once. Because there are strong correlations between the parameters of the von Bertalanffy equation, one should never compare individual parameters in isolation.

Cerrato (1990, p. 416) provided a clear statement of the problems faced when attempting to compare nonlinear growth curves using the likelihood ratio or Hotelling's T tests:

Both approaches are approximate ones. They are taken from linear statistical theory, and their validity when applied to the von Bertalanffy equation depends on the degree of bias and non-normality in the parameter estimates caused by the non-linearity of the model. In addition, both are characterized in terms of asymptotic properties for which no exact small sample theory exists. Finally, at least as commonly practised, both approaches handle unequal and unknown error variances in an approximate way.

Despite these problems, Cerrato (1990), in an empirical test, found that the likelihood ratio comparison most often, and most accurately, reflected the true state of affairs and recommended that this should be the approach of choice. Moulton et al. (1992) went slightly further in that they recommended reparameterizing the VBGF as recommended by Francis (1988a,b), and then using the likelihood ratio for comparative tests between the reparameterized curves.

9.4.2 An Overall Test of Coincident Curves

A method of comparing a number of curves at once was proposed by Chen et al. (1992) and is called the analysis of residual sum of squares (AoRSS). The method is different from the likelihood ratio approach, but it is useful in itself, and because there are analogies between the two approaches, the AoRSS is a useful way to introduce the principle behind likelihood ratios. Only curves fitted using the same residual error structures can be compared using these methods.

© 2011 by Taylor & Francis Group, LLC

The analysis of residual sum of squares is a total comparison, meaning that it does not compare the parameters separately but simply tests whether two or more curves are statistically different (are coincident curves). A linear version of this test was described by Zar (1984) as an overall test for coincident regressions. Equation 9.20 is simply an extension to the nonlinear case. There are four steps to the AoRSS:

1. For each data set i , fit a curve and calculate the sum of squared residuals, RSS_i , and an associated degree of freedom, DF_i .
2. The resultant RSS_i and DF_i for each curve are added to give the ΣRSS_i and ΣDF_i .
3. Data for all curves are pooled, a new curve is fitted to the combined data, and the total or pooled RSS_p and DF_p are calculated.
4. Using these statistics, an F statistic is calculated as in Equation 9.20:

$$F = \frac{\frac{RSS_p - \sum RSS_i}{DF_p - \sum DF_i}}{\frac{\sum RSS_i}{\sum DF_i}} = \frac{\frac{RSS_p - \sum RSS_i}{3.(K-1)}}{\frac{\sum RSS_i}{N - 3.K}} \quad (9.20)$$

where F is the F statistic with $3.(K-1)$ and $(N-3.K)$ degrees of freedom, K is the number of curves being compared, and N is the total or pooled sample size. This test can be applied to all classes of curve, not just the VBGF. This is a test of the hypothesis that the curves being compared are all equivalent descriptions of the data available; an example may serve to make this clear.

Kimura (1980) provides a table of age length data relating to Pacific hake with separate data for both males and females (Figure 9.10, Table 9.3). The question is whether the male and female Pacific hake exhibit different growth throughout their lives. In this case $K = 2$ and $N = 24$.

As listed above, one first has to find the best fitting curves for the males and females separately. For the von Bertalanffy curve this leads to: females, $L_\infty = 61.23$, $K = 0.2963$, and $t_0 = -0.0573$, with 10 df, and $RSS = 48.224$; males, $L_\infty = 55.98$, $K = 0.3856$, and $t_0 = 0.1713$, with 8 df, and $RSS = 19.423$. Then the male and female data are treated as one population and the pooled growth curve fitted, which leads to $L_\infty = 59.29$, $K = 0.3205$, and $t_0 = 0.0104$, with 21 df, and $RSS = 79.764$. When these figures are substituted into Equation 9.20, the resulting $F = 3.915$ is just significant ($P = 0.0258$). This analysis certainly indicates that the two curves (Figure 9.10) are different but does not indicate in which way. A different test would be necessary if more details were required.

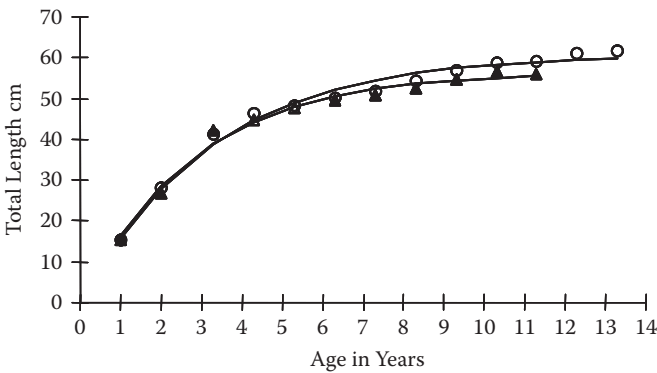


Figure 9.10
Average length-at-age for the Pacific hake for females (circles; $L_{\infty} = 61.23$, $K = 0.296$, and $t_0 = -0.057$) and males (triangles; $L_{\infty} = 55.98$, $K = 0.386$, and $t_0 = 0.171$). (Data from Kimura, 1980.) The lines illustrated are the maximum likelihood best fitting curves (Table 9.3, Example Box 9.6).

TABLE 9.3
Average Length-at-Age for Male and Female Pacific Hake from the U.S. West Coast

Age Years	Female Sample Size	Female Mean Length, cm	Male Sample Size	Male Mean Length, cm
1.0	385	15.40	385	15.40
2.0	36	28.03	28	26.93
3.3	17	41.18	13	42.23
4.3	135	46.20	83	44.59
5.3	750	48.23	628	47.63
6.3	1,073	50.26	1,134	49.67
7.3	1,459	51.82	1,761	50.87
8.3	626	54.27	432	52.30
9.3	199	56.98	93	54.77
10.3	97	58.93	21	56.43
11.3	44	59.00	8	55.88
12.3	11	60.91		
13.3	6	61.83		

Source: Data from Table 1 in Kimura, 1980.
Note the change to the years of age after age 2.

9.4.3 Likelihood ratio Tests

The general principle when using the AorSS involves comparing the outcome (RSS_p) of the hypothesis that all the curves are coincident (each data set is effectively a sample from the same population) with the outcome (ΣRSS_i) of the hypothesis that all data sets are from independent populations

© 2011 by Taylor & Francis Group, LLC

(Example Box 9.4). The method of likelihood ratios does something very similar in that it sets up the outcome of the hypothesis of two or more independent curves as a base case against which to compare all alternative hypotheses. For the von Bertalanffy curve the alternative hypotheses would be: (1) that all curves were coincident, as with the AoRSS test, (2) that the L_∞ values were equal, (3) that the K values were equal, (4) that the t_0 values were equal, (5) that the L_∞ and K values are equal, (6) that the L_∞ and t_0 values are equal, and finally, (7) that the K and t_0 values are equal. Strictly, if the test of coincident curves (hypothesis 1) were not rejected, one would not need to test hypotheses 2 to 7.

However, if one were testing multiple curves for equivalence and the test of coincident curves proved false, then one would have to proceed by making subsequent pair-wise comparisons between individual growth curves to discover the details of which aspects of the curves in question differed.

The standard description of the likelihood ratio methodology was given by Kimura (1980), who dealt exclusively with the von Bertalanffy growth curve. The method is more general than this, however, and can be applied to comparing any nonlinear equations fitted to data as long as the residuals used are additive and normally distributed (Barrett et al., 2007). The necessity for this restriction is illustrated in the derivation of the method (see Appendix 9.2). The important thing for our discussion is to determine how to calculate the likelihoods for each hypothesis to be compared. The test calculates a statistic that is compared with the χ^2 distribution with degrees of freedom equal to the number of constraints (i.e., the number of parameters being assumed equal). The method turns out to be extremely simple, and to start with the conclusion, the test is based on the following equation:

$$\chi_k^2 = -N \times \ln \left(\frac{\sum RSS_i}{RSS_p} \right) = -N \times \ln \left(\frac{RSS_\Omega}{RSS_\omega} \right) \quad (9.21)$$

where k is the degrees of freedom (equals the number of constraints placed upon the fit), N is the total number of observations from both curves combined, RSS_Ω is the total sum of squared residuals derived from fitting both curves separately (i.e., the minimum sum of squares from each curve added together), and RSS_ω is the total sum of squared residuals derived from fitting the curves with one of the hypothesized constraints (e.g., the K s are equal, or the L_∞ s are equal; hypotheses 1 to 7 above). The base case (RSS_Ω) will always provide the smallest residual sum of squares because it has the largest number of independent parameters (all parameters are assumed to be independent). When any of the possible constraints are tested, the number of independent parameters will obviously decrease so the fit will be somewhat less precise. The question to be answered in each test is whether the decline in fit (i.e., the difference between the two residual sums of squares) is greater than would

© 2011 by Taylor & Francis Group, LLC

EXAMPLE BOX 9.4

The implementation of the analysis of residual sum of squares. The data are in Table 9.3. Put =sum(H14:H24) into C5. In cell B6 put =count(B14:B26)–3 or the female df, in C6 put =count(F14:F26)–3, and in D6 put =count(B14:B26, F14:F26)–3. In B10 put =abs((C8–B8)/(C9–B9))/(B8/B9), and in C10 put =abs((C8–B8)/(3*(2–1)))/((B8/(24–(3*2)))); they should give the same F value. In B11 put =fdist(B10,3,B9). To calculate the expected lengths put =\$B\$2*(1–exp(–\$B\$3*(A14–\$B\$4))) into C14 and =(B14–C14)^2 into D14. Copy C14:D14 down to row 26. Similarly, put =(F14–G14)^2 into cell H14 and put =\$C\$2*(1–exp(–\$C\$3*(E14–\$C\$4))) into G14, and copy G14:H14 down to row 24. Using the solver, in turn, minimize B5 by altering B2:B4, and C5 by altering C2:C4. Copy B5:C6 into F2:G3 as values. Put =D2 into B2 and C2, and copy down to row 4. Then minimize cell D5 by altering D2:D4; copy D5:D6 into H2:H3, and the answer should be determined. Plot column B against A as points and add column C as a line; add columns E and F as points and column G as a further line to mimic Figure 9.10.

	A	B	C	D	E	F	G	H
1		Female	Male	Total		Female	Male	Total
2	Linf	61.233	55.978	59.294	SSq	28.800	19.423	79.765
3	K	0.296	0.386	0.320	df	10	8	21
4	t0	–0.057	0.171	0.010				
5	SSQ	=sum(D14:D26)	19.423	=B5+C5				
6	df	10	8	21				
7		Individual	Pooled					
8	SSQ	=F2+G2	=H2					
9	df	=F3+G3	=H3					
10	F	3.924	3.924					
11	P	0.026						
12	Fem	Fem	Fem	Fem	Male	Male	Male	Male
13	Age	Length	E(L)	Resid2	Age	Length	E(L)	Resid2
14	1	15.4	16.47	1.14	1	15.4	15.31	0.01
15	2	28.03	27.94	0.01	2	26.93	28.32	1.94
16	3.3	41.18	38.58	6.73	3.3	42.23	39.22	9.03
17	4.3	46.2	44.39	3.27	4.3	44.59	44.58	0.00
18	5.3	48.23	48.71	0.23	5.3	47.63	48.23	0.36

be expected by chance. If the χ^2 value calculated from Equation 9.21 is not significant, then the decline in the quality of fit is assumed to be no more than if the parameters being compared were random selections from the same origin (i.e., those parameters are not significantly different).

Equation 9.21 is relatively simple to calculate because, as with the AoRSS method, it only requires the calculation of various sums of squares. Kimura's (1980) paper provides a brief description of why we can successfully use the specified residual sum of squares as likelihood estimates in this likelihood ratio test (demonstrated in detail in Appendix 9.2). In practice, the likelihood ratio requires separately calculating the total residual sum of squares for the base case and for the hypothesis of interest (e.g., the K values are equal) and substituting the values into Equation 9.21. The likelihood ratio is then compared with a table of the χ^2 distribution with k degrees of freedom (k is the number of constraints placed upon the fit; Example Box 9.5).

9.4.4 Kimura's Likelihood Ratio Test

Kimura (1980) provided a set of test data and the analytical outcomes so that anyone attempting to implement a likelihood ratio test would be able to ensure the computer program worked. He provided data relating to the average length-at-age for Pacific hake for each sex with the objective of determining whether the two sexes differed significantly in their overall growth pattern (Table 9.3, Figure 9.10). The data were used in the AoRSS statistic example above and the curves were not found to be coincident. We will use the likelihood ratio test to determine how the curves differ (Example Box 9.5).

The method is simple. First, find the best fitting separate curves for each data set separately. Then, in sequence, compare the total residual sum of squares from this base case with that obtained by adding various constraints. Perhaps the best order in which to impose these tests is to first assume the hypothesis that both data sets can best be described by a single line (coincident curves). If this indicates that a significant difference exists, then one should sequentially assume that single parameters are the same between the two lines and determine whether significant differences arise. If differences are found, then one would conclude that evidence exists that the curves do differ and be able to identify which parameters are different between the curves for each data set (Table 9.3).

When the likelihood ratios were calculated for Kimura's data, a difference between the curves was indicated by the comparison of the base case with the assumption of the same curve fitting both data sets. With the more detailed analyses, a difference between the L_∞ was strongly indicated, while there was some slight evidence that the K parameter might be different; however, there was no indication that the t_0 parameters differed significantly (Table 9.4).

EXAMPLE BOX 9.5

Kimura’s (1980) likelihood ratio test. Copy the data from Table 9.3 into columns B and C, female data followed by the male. In D14 put $=B\$1*(1-\exp(-B\$2*(B14-B\$3)))$ and copy down to D26. In D27 put $=B\$4*(1-\exp(-B\$5*(B27-B\$6)))$ and copy down to D37. In B8 put $=\text{sum}(E14:E26)$ and in C8 put $=\text{sum}(E27:E37)$. Put $=\text{count}(B14:B26)$ into B12 and $=\text{count}(B27:B37)$ into C12. In D12 put $=B12+C12$ for the total N. In D9 calculate the likelihood ratio $=-D12*\text{Ln}(F8/D8)$. In D10 manually put the degrees of freedom = number of constraints being considered. In D11 put $=\text{chidist}(D9,D10)$. In D9, note the reference to F8, which is merely the stored result of minimizing D8 by altering B1:B6 and storing B1:B6 into F2:F7 and B8 into F8 as values. This sets up the sheet ready for hypothesis testing. To test for coincident curves, put $=B1$ into B4 and copy down to B6. This sets the same parameters for both data sets. Then minimize D8 by altering B1:B3. Copy the answers as values from B1:B6 and from D8:D11 into G2:G11 for later reference. To test if the L_{∞} are different put $=B1$ into B4 and minimize D8 by altering (B1:B3,B5:B6). Remember to alter the degrees of freedom in D10 to 1. Copy the results to the right of column G. Try the other hypotheses by similar manipulations of which cells are set equal to which and by altering the cells to be altered by the solver. Try changing the analysis by restricting the sum of squares residuals for females to the first 11, like the males, by putting $=\text{sum}(E14:E24)$ into B8 and $=\text{count}(C14:C26)$ into B13. Are the results of the analysis the same?

	A	B	C	D	E	F	G
1	Linf-f	61.23			Results	BaseCase	Coincident
2	K-f	0.296			Linf-f	61.2331	59.2938
3	T0-f	-0.057			K-f	0.2963	0.3205
4	Linf-m	55.98			t0-f	-0.0573	0.0104
5	K-m	0.386			Linf-m	55.9779	59.2938
6	T0-m	0.171			K-m	0.3856	0.3205
7		Female	Male	Total	t0-m	0.1713	0.0104
8	SSQ	28.800	19.423	=B8+C8	SSQ	48.2238	79.7645
9			χ^2	0	χ^2		12.077
10			df	3	Df		3
11			P	1	P		0.0071
12	Count	13	11	24			
13		Age	Length	E (L)	Resid2		
14	Fem	1	15.4	15.54	=(C14-D14)^2		
15	Fem	2	28.03	27.70	=(C15-D15)^2		
16	Fem	3.3	41.18	38.76	Copy down		
17	Fem	4.3	46.2	44.68	To row 37		

TABLE 9.4
Likelihood Ratio Test for the Pacific Hake Data from Table 9.3

	BaseCase	Coincident	=Linf	=K	=t0
$L_{\infty f}$	61.233	59.294	59.404	60.140	60.767
Kf	0.296	0.320	0.337	0.330	0.313
$t_0 f$	-0.057	0.010	0.087	0.095	0.057
$L_{\infty m}$	55.978	59.294	59.404	57.435	56.454
Km	0.386	0.320	0.297	0.330	0.361
$t_0 m$	0.171	0.010	-0.111	-0.021	0.057
RSS_{ω}	48.224	79.765	71.602	56.337	50.758
χ^2	—	12.077	9.487	3.732	1.229
df	—	3	1	1	1
P	—	0.0071	0.0021	0.0534	0.2676

Source: Data from Kimura, 1980.
Note: The top three rows of parameters relate to the female fish, while the middle set of parameters refer to the male fish. The base case is where two separate curves are fitted independently, the coincident column is where the lines are assumed identical, and the remaining three columns are where the listed parameter is assumed equal between the two lines. RSS_{ω} refers to the total residual sum of squares for both curves together given the constraint ω . In the BaseCase column, the 48.224 refers to the unconstrained RSS_0 , against which all the RSS_{ω} are compared. N in all these cases is 24, 13 females and 11 males (Example Box 9.5, Figure 9.10).

9.4.5 Less than Perfect Data

Unfortunately, it is quite common with real fisheries to only obtain ageing data from a sample of fish obtained from commercial operations. Such a sample may be influenced by the existence of a legal minimum length, and there may be low numbers of animals taken in the younger or older age classes. Finally, with size-selective fishing, the larger, faster growing fish of all ages may have been differentially removed from the population through fishing pressure (Figure 9.11).

Growth curves fitted to samples from a commercial fishery can have many biases, and the parameters obtained may be very wide of the values obtained from a more representative sample (Figure 9.11). However, if such data are all that is available, it would be useful to know whether it was valid to compare growth curves derived from such imperfect data.

For example, in Example Box 9.5 two curves are compared where one data set covered the ages 1 to 13.3 while the other only covered ages from 1 to 11.3 years. In that example, a significant difference was found between the two curves, driven primarily by differences in the L_{∞} parameter. However, if the comparison is restricted to the first eleven data points in both data sets, the hypothesis that the two curves are coincident is not proved incorrect (this can be tried in Example Box 9.5). However, in that example only average length-at-age data were used; in reality, one would now use the unsummarized data, so the results may differ, but the methods remain the same.

© 2011 by Taylor & Francis Group, LLC

Copyright © 2011. CRC Press LLC. All rights reserved.

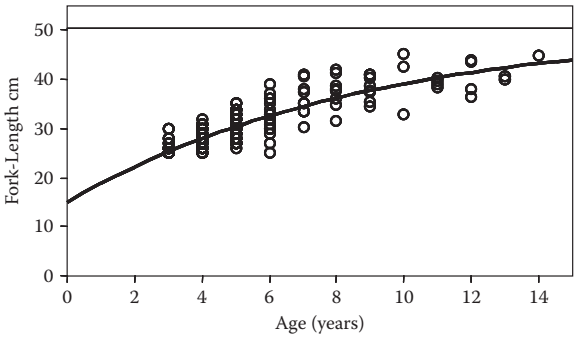


Figure 9.11

The same data as in Figure 9.1, for snapper, *Pagrus auratus*, from the Bay of Plenty, New Zealand, but with all animals less than 25 cm excluded as being below the legal size, and fewer older animals, as taken by the commercial fleet. Instead of $L_{\infty} = 44.79$, $K = 0.196$, and $t_0 = -0.81$, the best fitting von Bertalanffy growth curve was for $L_{\infty} = 50.45$, $K = 0.115$, and $t_0 = -3.06$; the L_{∞} line is now well above the data and the t_0 is obviously unrealistic. Clearly, there are many potential impacts of limiting the data in this way. It also makes drawing conclusions from curve comparisons dangerous.

The von Bertalanffy curve is strongly determined by the values for L_{∞} and t_0 , which are at the extremes of the curve and usually have the least data. This is why so many people have spent time trying to reparameterize the curve (Sainsbury, 1980; Frances, 1988a,b) to have parameters closer to the data from which they are estimated. If the data we use to construct growth curves is biased or not representative (e.g., samples from commercially caught fish), then extra care needs to be taken when comparing growth curves. When comparing growth curves derived from nonrepresentative data, it seems intuitively reasonable to conduct tests only over equivalent ranges of data. Thus, if we were to compare the data from Figures 9.1 and 9.11, we would be likely to find differences. But if we restricted the data from Figure 9.1 to those sizes greater than 25 cm and ages greater than 2, we would be much more likely to find no differences (because, along with removing some of the older animals, that was how the data in Figure 9.11 were generated). We are assuming there are no errors in the ageing, so we should only compare ages with like ages. If there is an obvious difference, such as a legal minimum length influencing only one of the samples, then this must also be taken into account.

What these suggestions mean is that we are not comparing complete growth curves but, instead, the growth of the species over the ranges of ages (or lengths) for which we have data in each of the data sets being compared. Obviously, when reporting such comparisons, it is vital to be explicit about exactly what was compared with what.

9.4.6 A randomization Version of the Likelihood ratio Test

When low-quality data are compared, the assumption that the likelihood ratio adheres to the χ^2 distribution becomes invalid and alters the risk of

type I errors (claiming a difference where one does not exist) and type II errors (claiming no difference when one exists). If, in Example Box 9.7, one restricts the comparison of curves to ages 1 to 11.3, the coincident curve comparison indicates no statistical difference ($\chi^2 = 6.398$, $P = 0.0938$, $df = 3$). However, if one then continued and compared the two curves with the L_∞ constrained to be identical, a slightly significant difference is found ($\chi^2 = 4.359$, $P = 0.0368$, $df = 1$). Thus, one test concludes no difference while the other concludes a difference exists. An assumption in the analysis, that the likelihood ratio will approximate the χ^2 distribution, appears to be failing.

With inadequate data, instead of using the likelihood ratio test as it stands, it is possible to arrange the data so that we can generate a randomization version of the likelihood ratio test that will generate its own empirical sampling distribution for the test statistic. What is being suggested is that the length-at-age data need to be randomized in some way between the two groups to test the hypothesis that the two data sets are equivalent to two random samples from the same statistical population. This has previously been suggested by Weinberg and Helser (1996), where they made the comparisons by randomizing age and length data pairs between different populations of surfclams. Unfortunately, with their design of randomization, if there are low numbers of the extreme age classes, it would be quite possible to include tests where all the younger or older individuals were selected by chance into one of the randomized data sets. This would have the effect of overestimating the number of times large likelihood ratios would be expected to occur. This design appears to be including a comparison of the proportional catch-at-age as well as the growth curves from the two populations. If the data sets were large and the numbers at age were relatively evenly distributed, this may not be a great problem.

With Kimura's (1980) data (for ages 1 to 11.3), when a randomization test is conducted in the manner described above, the test of coincident curves suggests that likelihood ratios greater than that observed (6.3986) occurred 223 times out of 1,000 (i.e., a $P = 0.223$), which is overly conservative. If we were to plot the proportion of the different likelihood ratio χ^2 values along with the hypothetical proportions from the χ^2 distribution, we would be able to see how closely the empirically determined statistic mimics the hypothetical (Figure 9.12, Example Box 9.6).

Clearly, the randomization of data pairs between the sexes would lead to a greater number of type II errors than expected. The test is too conservative and would have trouble detecting a difference even when one existed. If we are to use a randomization test, some other randomization schema would need to be adopted.

The ages are assumed to have been measured without error, and each age has an associated range of lengths observed in each population; in the Kimura example this is reduced to just a single length per age per sex, but with real data there would be a number of observations per age class.

© 2011 by Taylor & Francis Group, LLC

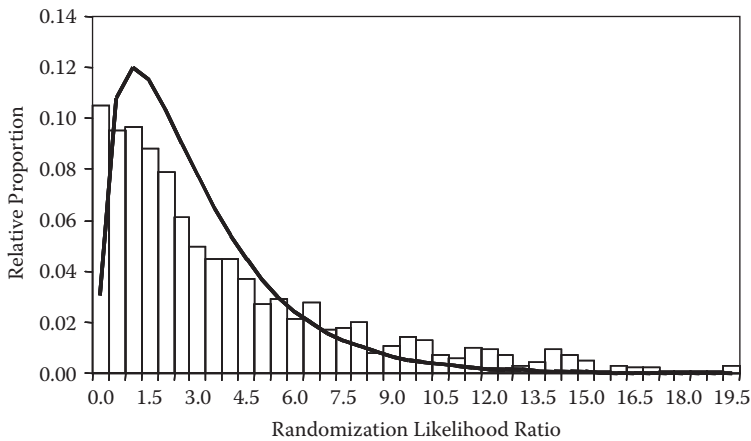


Figure 9.12
A comparison of the relative proportion of different χ^2 values obtained from a randomized likelihood ratio test (open columns) with the expected proportions derived from the χ^2 distribution (solid curve). The test was of whether the growth curves for Pacific hake were coincident for males and females when the ages being compared were restricted to ages 1 to 11.3 (Table 9.2, Figure 9.12, Example Box 9.6). The randomization test, in this case, involved the randomization of age and length data pairs between the two sexes (not recommended if relative numbers are uneven or proportional catch-at-age is variable). If the critical value chosen is 0.05, then the empirical statistic would require a larger likelihood ratio than the true χ^2 . In other words, the empirical statistic would claim not to have found a difference more often than it should (Example Box 9.6).

This structure to the data should be recognized, and instead of randomizing data pairs, the randomizations should be of lengths within age classes between sexes. Thus, for each randomization test one would need to conduct the same number of randomizations of data as one had age classes. With the Kimura data this would entail conducting eleven randomizations before fitting the models, one for each age class. In that case it would be merely deciding which data point was associated with which age. Clearly, this routine would be more complicated to implement (Example Box 9.7) than randomizing data pairs, and the Kimura data are an extreme case.

By randomizing within age classes but between sexes, the randomization test can avoid problems with the relative number of observations present in each age class. These now remain the same as in the original data set, and the proportional age structure of each data set remains the same as the original. The only thing that changes is the distributions of lengths at age in each of the two data sets. In fact, with the Kimura data there are only ten pairs of data points that differ, as the data for the one-year-old fish are the same for both sexes. By having so few data points that differ, the randomization test is relatively limited in the number of likelihood ratio values it can produce randomly. The upper and lower limits and the relative distribution did not alter after the first four thousand replicates (Figure 9.13).

© 2011 by Taylor & Francis Group, LLC

EXAMPLE BOX 9.6

The simplistic randomization algorithm can be introduced into Example Box 9.5 by adding some columns to the right of the calculations. Start in row 1. In one column put a series of =rand(); next to that put the female data pairs of age and length for containing ages 1 to 11.3, and under the female data put the male data for ages 1 to 11.3. Conduct the randomization as illustrated in Chapter 5. Sort the three new columns on the column of random number to randomize the data pairs between the two sexes. Then copy, as values, the randomized ages and associated lengths into columns B and C of Example Box 9.5. Repeat that at least one thousand times, conducting the likelihood ratio test each time, and recording the χ^2 value each time, perhaps into column K. Put =countif(\$K\$1:\$K\$1000,">="&M1)-countif(\$K\$1:\$K\$1000,">="&M2) in N2 and copy down to count the frequency of randomization χ^2 values into column N, using the bins defined in column M. Convert the cumulative χ^2 distribution into the standard distribution as shown in columns O and P. Plot columns P and Q against column L to mimic Figure 9.12. If you do more than one thousand replicates, be sure to alter columns N and Q.

L	M	N	O	P	Q
Average Class	0	Obs Freq	χ^2 Cumulative	χ^2	Prop Freq
=average(M1:M2)	1	197	=chidist(L2,3)	=1-O2	=N2/1000
=average(M2:M3)	2	173	=chidist(L3,3)	=O2-O3	=N3/1000
2.5	3	144	0.4753	=O3-O4	=N4/1000
3.5	4	73	0.3208	0.1545	0.073
4.5	5	51	0.2123	0.1085	0.051

There are clearly some distortions away from the ideal χ^2 distribution for the test statistic. It illustrates that the reliance of the likelihood ratio test on the χ^2 statistic is only approximate, especially when the data are not as representative as one would wish them to be. When the data used are of better quality (Figure 9.1), then the match between the empirical distribution and the hypothetical ideal can become closer.

9.5 Concluding Remarks

The study of individual growth is fascinating for many people, and this can lead them to draw strong conclusions from the form of the equations

© 2011 by Taylor & Francis Group, LLC

EXAMPLE BOX 9.7

A randomization of Kimura’s (1980) Pacific hake data. The age data are set out into eleven columns with columns of random numbers (=rand()) beside them. Row 41 relates to female lengths and row 42 to males. The test first randomizes the row in which each data point sits. The age-structured data are reconstituted in columns A and B. How the age length data are reconstructed can vary, but in the end one must be able to copy and paste the values into the required cells (C14:C35) prior to conducting the likelihood ratio test (assumes the females aged 12.3 and 13.3 have been removed). Age 1 is unchanged. For the rest, one first has to randomize the lengths between sexes within ages. Of course, one would create a macro to do all of the separate sorts, first D41:E42 on column D, then F41:G42 on column F, and so on. Once completed, the data in columns A and B would have been randomized. These data are copied and pasted as values into the correct cells for the likelihood ratio test to proceed. All this is repeated at least one thousand times and the results compared with the original analysis (Figure 9.13).

	A	B	C	D	E	F	G
40	Age	Length	Age 1	Age 2	Age 2	Age 3.3	Age 3.3
41	1	=C41	15.4	=rand()	28.03	=rand()	41.18
42	2	=E41	15.4	=rand()	26.93	=rand()	42.23
43	3.3	=G41					
44	4.3	=I41					
45	5.3	=K41					
46	6.3	=M41					

used to describe the growth of their favourite organism. Hopefully, it has been shown that growth equations are principally just descriptions of how growth proceeds; they are not explanations for the process of growth. Just because the equation has an asymptote does not imply that the fish species has such a thing. The move toward reparamaterized growth curves should assist in avoiding this error.

Comparisons between growth curves are difficult to conduct in a valid manner, and care must be exercised in any conclusions drawn from such tests. In many publications, the data presented constitute only a subsample of the true population. While this is better than no data, it should be recognized for what it is, which is a potentially nonrepresentative sample from the population. The difficulties of sampling marine populations are such that this will be a persistent problem for fisheries biologists. It is quite possible to obtain representative samples of what is caught by commercial fishers. This must be recognized, and its implications for comparisons of growth between different populations

© 2011 by Taylor & Francis Group, LLC

Copyright © 2011. CRC Press LLC. All rights reserved.

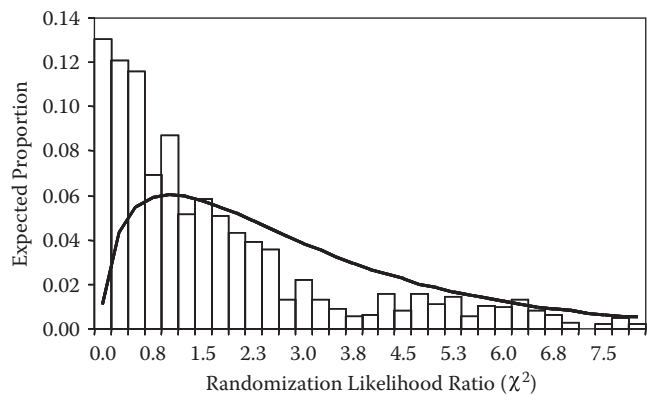


Figure 9.13
A comparison of the relative proportion of different χ^2 values obtained from a randomized likelihood ratio test (open columns) with the expected proportions derived from the χ^2 distribution (solid curve). The test was of whether the growth curves for Pacific hake were coincident for males and females when the ages being compared were restricted to ages 1 to 11.3 (Table 9.2, Figure 9.12, Example Box 9.7). The randomization test, in this case, involved the randomization of length data within ages but between sexes. Despite the distortions below a ratio of 5.0, the cumulative distribution leads to similar decisions when comparing the two curves. The empirical distribution suggests that there is some evidence that the curves are not coincident (Example Box 9.7).

should be considered before such comparisons are made. The randomization test suggested in this chapter is complex to implement (but is possible even in Excel), but it permits one to conduct the test required while testing the validity of the assumption of the test statistic being equal to the χ^2 statistic. Where the representativeness of the data is at all suspect, it is recommended that some version of the randomization test be implemented. With a great deal of data this can be relatively slow, but it is a case of computer-intensive statistics answering the questions for which answers are needed.

Appendix 9.1: Derivation of the Fabens Version of the von Bertalanffy Growth Equation

This is the version that is used when attempting to estimate the growth curve parameters from tagging data. With such data, one tends to have the dates of tagging and recapture, the initial length at tagging, and the length at recapture. It would be unusual to have the age of the tagged organisms. Hence, the standard length-at-age formulation cannot be used. Instead, we need an equation that generates an expected length increment in terms of the von Bertalanffy parameters, the length at time t (not age t), and the

© 2011 by Taylor & Francis Group, LLC

elapsed time, Δt . The standard formulation of the von Bertalanffy growth equation is given by Equation A9.1:

$$L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right) \quad (\text{A9.1})$$

where L_t is the length at time t , L_∞ is the average maximum length of individuals in the population, K is a growth rate parameter, t is the age of the animals, and t_0 is the hypothetical age at length zero. The brackets can be expanded thus:

$$L_t = L_\infty - L_\infty e^{-K(t-t_0)} \quad (\text{A9.2})$$

The expected length of an animal of age t after the passage of time, Δt , is given by Equation A9.3:

$$L_{t+\Delta t} = L_\infty - L_\infty e^{-K(t+\Delta t-t_0)} \quad (\text{A9.3})$$

Extract the Δt term from the exponential term:

$$L_{t+\Delta t} = L_\infty - L_\infty e^{-K(t-t_0)} e^{-K\Delta t} \quad (\text{A9.4})$$

The change in length over the time Δt is simply the difference between Equations A9.4 and A9.2:

$$\Delta L = L_{t+\Delta t} - L_t = L_\infty - L_\infty e^{-K(t-t_0)} e^{-K\Delta t} - L_\infty + L_\infty e^{-K(t-t_0)} \quad (\text{A9.5})$$

The order of the two exponential terms can be reversed:

$$\Delta L = L_\infty - L_\infty + L_\infty e^{-K(t-t_0)} - L_\infty e^{-K(t-t_0)} e^{-K\Delta t} \quad (\text{A9.6})$$

The $L_\infty e^{-K(t-t_0)}$ term can be extracted:

$$\Delta L = \left(L_\infty - L_\infty + L_\infty e^{-K(t-t_0)}\right) \left(1 - e^{-K\Delta t}\right) \quad (\text{A9.7})$$

The final change is to recognize that, in the first brackets, the second and third terms combined are equivalent to the standard von Bertalanffy equation (Equation A9.2):

$$\Delta L = \left(L_\infty - \left(L_\infty - L_\infty e^{-K(t-t_0)}\right)\right) \left(1 - e^{-K\Delta t}\right) \quad (\text{A9.8})$$

so we can substitute an L_t to leave the standard Fabens version of the von Bertalanffy growth equation:

$$\Delta L = (L_\infty - L_t) \left(1 - e^{-K\Delta t}\right) \quad (\text{A9.9})$$

© 2011 by Taylor & Francis Group, LLC

Appendix 9.2: Derivation of the Maximum Likelihood Estimator for the von Bertalanffy Curve

Kimura (1980) starts by writing out the maximum likelihood estimator for a von Bertalanffy curve. We will do the same here, but with a few more details to ensure clarity of exposition. With the usual notation the length of the u th individual at age t_u is defined as

$$L_u = L_\infty \left(1 - e^{(-K(t_u - t_0))}\right) + \varepsilon_u \quad (\text{A9.10})$$

Let L_∞ be the, possibly hypothetical, asymptotic length; K the constant relating to the rate of growth; t_0 the hypothetical age at length zero; and the ε_u s the independent, additive, normal random errors ($N(0, \sigma^2)$). For brevity in the following equations, the expected values of L_u can be regarded simply as a function of L_∞ , K , and t_0 :

$$\hat{L}_u = f(L_\infty, K, t_0, t_u) \quad (\text{A9.11})$$

In the following description, the $f(L_\infty, K, t_0, t_u)$ referred to is the von Bertalanffy equation, but it should be noted that the argument holds irrespective of which growth or nonlinear equation is used and compared. It should be remembered that there is more than one way in which the von Bertalanffy curve can be estimated (e.g., to individual fish data, to mean lengths at age, with or without constant variance), and this will influence the form of the residuals used. Of course, one can only compare like with like. As Kimura states, the optimum way to fit a von Bertalanffy curve to a set of data is to use a maximum likelihood estimator, and because we would be using normal random errors, this means the likelihood function would derive from the normal distribution:

$$L(L_u | L_\infty, K, t_0, \sigma^2) = \frac{1}{\sigma\sqrt{2\pi}} e^{\left(\frac{[-L_u - f(L_\infty, K, t_0, t_u)]^2}{2\sigma^2}\right)} \quad (\text{A9.12})$$

which is the likelihood of the single observation L_u . This is simply the usual normal distribution equation with the observed and expected lengths at t_u as the numerator in the major term. Note that the term involving the observed and expected values is identical to that which would be used in a least squares estimation. Given N different observations of age and length, the overall likelihood \tilde{L} is obtained by multiplying N by the separate likelihoods:

$$L(\tilde{L} | L_\infty, K, t_0, \sigma^2) = \prod_{i=1}^{i=N} \frac{1}{\sigma\sqrt{2\pi}} e^{\left(\frac{[-L_i - f(L_\infty, K, t_0, t_i)]^2}{2\sigma^2}\right)} \quad (\text{A9.13})$$

© 2011 by Taylor & Francis Group, LLC

This can be simplified by noticing that if we raise the $1/[\sigma\sqrt{(2\pi)}]$ term to the power N , square it, and invert it, we can take it outside of the product and the remaining product can be converted to a summation term:

$$L\left(\tilde{L}\left|L_{\infty}, K, t_0, \sigma^2\right.\right) = (2\pi\sigma^2)^{-\frac{N}{2}} \prod_{i=1}^N e^{\left(\frac{[-L_i - f(L_{\infty}, K, t_0, t_i)]^2}{2\sigma^2}\right)} \quad (\text{A9.14})$$

Equation A9.14 is a form that can be used for making maximum likelihood comparisons. However, Equation A9.14 can be simplified by using log-likelihoods that serve to replace the product with a summation. This acts to reduce the chance of rounding errors occurring due to the very small likelihoods that can arise. The logarithmic transformation also has the effect of reducing the e term to its exponent. To make the impact of the transformation explicit, note that

$$\begin{aligned} L\ln\left(\prod_1^N \frac{1}{\sqrt{2\pi\sigma^2}}\right) &= L\ln\left(\left(\frac{1}{\sqrt{2\pi\sigma^2}}\right)^N\right) \\ &= L\ln\left((2\pi\sigma^2)^{-N/2}\right) = -\frac{N}{2} L\ln(2\pi\sigma^2) \end{aligned} \quad (\text{A9.15})$$

and that

$$\begin{aligned} L\ln\left(\prod_{i=1}^N e^{\left[\frac{[-L_i - f(L_{\infty}, K, t_0, t_i)]^2}{2\sigma^2}\right]}\right) &= \sum_{i=1}^N \frac{[-L_i - f(L_{\infty}, K, t_0, t_i)]^2}{2\sigma^2} \\ &= \left(-\frac{1}{2\sigma^2} \sum_{i=1}^N [L_i - f(L_{\infty}, K, t_0, t_i)]^2\right) \end{aligned} \quad (\text{A9.16})$$

We can then see that the log-likelihood estimator is the combination of Equations A9.15 and A9.16:

$$LL\left(\tilde{L}\left|L_{\infty}, K, t_0, \sigma^2\right.\right) = -\frac{N}{2} L\ln(2\pi\sigma^2) - \frac{1}{2\sigma^2} \sum_{i=1}^N [L_i - f(L_{\infty}, K, t_0, t_i)]^2 \quad (\text{A9.17})$$

The maximum likelihood estimate of σ^2 , denoted σ_{ϕ}^2 , is obtained from the log-likelihood estimator by calculating the partial derivative with respect to σ^2 , and equating that to zero. Using Equation A9.17,

© 2011 by Taylor & Francis Group, LLC

$$\frac{\partial \text{LL}(\tilde{L}|L_{\infty}, K, t_0, \sigma_{\phi}^2)}{\partial \sigma_{\phi}^2} = -\frac{N}{2\sigma_{\phi}^2} + \frac{\sum_{i=1}^N [L_i - f(L_{\infty}, K, t_0, t_i)]^2}{2(\sigma_{\phi}^2)^2} = 0 \quad (\text{A9.18})$$

which leads by algebra to

$$\sum_{i=1}^N [L_i - f(L_{\infty}, K, t_0, t_i)]^2 = \frac{2(\sigma_{\phi}^2)^2 N}{2\sigma_{\phi}^2} \quad (\text{A9.19})$$

and, thereby,

$$\sigma_{\phi}^2 = \frac{\sum_{i=1}^N [L_i - f(L_{\infty}, K, t_0, t_i)]^2}{N} \quad (\text{A9.20})$$

The numerator in this relation is the sum of squared residuals; thus, the problem of maximum likelihood estimation for the von Bertalanffy curve is reduced to finding the least square estimates of L_{∞} , K , and t_0 (Kimura, 1980). N is used instead of $N - 1$ because this is a maximum likelihood estimate of variance. The exact details of the structure of the numerator (the structure of the residuals) will be related to the form of the data available. As described in Chapter 3 on parameter estimation, this is a general property of the maximum likelihood estimator for any linear or nonlinear equations that are fitted using additive, normal random errors. The form of Equation A9.20 is that required for the determination of the likelihoods of different hypotheses to be compared. This is done by substituting the maximum likelihood estimate of the variance, i.e., Equation A9.20, into Equation A9.16, which is equivalent to Equation 9.30 in the main text:

$$\begin{aligned} L(\tilde{L}|L_{\infty}, K, t_0, \sigma^2) &= (2\pi\hat{\sigma}^2)^{-\frac{N}{2}} e^{\left(\frac{-\sum (L_i - f(L_{\infty}, K, t_0, t_i))^2}{2\sum (L_i - f(L_{\infty}, K, t_0, t_i))^2} \right)} \\ &= (2\pi\hat{\sigma}^2)^{-\frac{N}{2}} e^{\left(\frac{-N}{2} \right)} \end{aligned} \quad (\text{A9.21})$$

When comparing two or more curves using likelihood ratios, one first sets up the general model against which all alternative simplified hypotheses are to be tested. This statistic is determined by comparing the ratio of the two likelihoods (Kimura, 1980):

© 2011 by Taylor & Francis Group, LLC

$$\Lambda = \frac{(2\pi\hat{\sigma}_\omega^2)^{-\frac{N}{2}} e^{\left(\frac{-N}{2}\right)}}{(2\pi\hat{\sigma}_\Omega^2)^{-\frac{N}{2}} e^{\left(\frac{-N}{2}\right)}} = \left(\frac{\hat{\sigma}_\Omega^2}{\hat{\sigma}_\omega^2}\right)^{\frac{N}{2}} \quad (\text{A9.22})$$

Kimura (1980) states that under the hypothesis that the linear constraint ω is true (e.g., the K s are equal), the test statistic

$$-2Ln(\Lambda) = -2Ln\left(\left(\frac{\hat{\sigma}_\Omega^2}{\hat{\sigma}_\omega^2}\right)^{\frac{N}{2}}\right) = -2\frac{N}{2}Ln\left(\frac{\hat{\sigma}_\Omega^2}{\hat{\sigma}_\omega^2}\right) = -NLn\left(\frac{\hat{\sigma}_\Omega^2}{\hat{\sigma}_\omega^2}\right) \quad (\text{A9.23})$$

will have, asymptotically, a χ^2 distribution. This means that the larger the sample size, the more likely the conclusions are to be valid. However, it should be clear that Equation A9.22 is equivalent to Equation 9.21 (the N s inside the brackets cancel to leave the RSS_χ), leading to Equation 9.23.