6.3.3 Growth Rates

Growth of fishes, as in many other poikilothermic animals, is indeterminate, meaning that individuals have no innate pattern of growth and can continue to increase in size throughout life. Because growth can be affected by food abundance, weather, competition, and many other factors, the measurement of growth rates is a common way fisheries biologists evaluate the effectiveness of management practices. Additionally, because the size of fish caught by recreational and commercial fishers greatly affects aesthetic and economic values of the catch, an understanding of growth dynamics in populations is important to predict fishery trends adequately. Mathematical models of fish growth are often incorporated into models of population dynamics to predict changes in stock biomass resulting from various harvest strategies.

Growth may be measured in terms of length (l) or weight (w) and is expressed in several ways:

1. absolute increase per unit time, that is, $l_2 - l_1$ or $w_2 - w_1$;
2. relative rate of increase per unit time, that is, $(l_2 - l_1)/l_1$ or $(w_2 - w_1)/w_1$; and
3. instantaneous rate of increase per unit time, that is, $\log_e l_2 - \log_e l_1$ or $\log_e w_2 - \log_e w_1$.

Estimates of these rates can be made from observations of length (or weight) of a cohort of fish at two or more points in time, from tagging studies, or from size-at-age data obtained from age and growth analyses.

These expressions assume linear increases of length or weight over time and should not be calculated for time periods where growth is typically nonlinear. Trends of length and weight of a cohort throughout life usually show an early period of rapid growth and a subsequent period of more gradual increase (Figure 6.5). Likewise, absolute, relative, and instantaneous growth rates computed from size at successive ages are initially low, increase to a maximum, and then decline with age.

6.3.3.1 Growth in Length

One useful model that mimics this pattern of declining growth rate with age was originally described by von Bertalanffy (1938). The von Bertalanffy model is based on the theory that the rate of change in length per unit of time (dl/dt) will get smaller and eventually become zero as a fish nears its maximum possible size (L_∞). Mathematically,

$$\frac{dl}{dt} = K(L_\infty - l_t), \tag{6.41}$$

where K is a growth parameter (not a rate in the sense defined earlier) and l_t is the length at time t. Equation (6.41) shows that the rate of increase in length is a constant proportion (K) of the difference between the maximum size and present length ($L_\infty - l_t$). Upon integration of equation (6.41), we obtain a predictive relationship:

$$l_t = L_\infty\left[1 - e^{-K(t-t_0)}\right], \tag{6.42}$$

where t is time (or age) in years and t_0 is the time at which l_t is 0.

A plot of this relationship shows a progressive increase in body size that asymptotically approaches L_∞ (Figure 6.6). Parameters of the model (L_∞, K, and t_0) are typically estimated from annual length-at-age data; procedures have been outlined by Gulland (1969) and Galluci and Quinn (1979).

A Walford plot provides a classical approach for obtaining values of L_∞ and K when fitting a von Bertalanffy growth model to a population's mean-length-at-age data. Across successive ages (usually excluding age 0), mean length at age $t + 1$ (vertical axis) is plotted against mean length at age t (horizontal axis). The plotted data should appear somewhat linear so that they can be well represented by a straight line by means of simple linear regression. The slope of the fitted line estimates e^{-K}, and

$$K = -\log_e(\text{slope}). \tag{6.43}$$

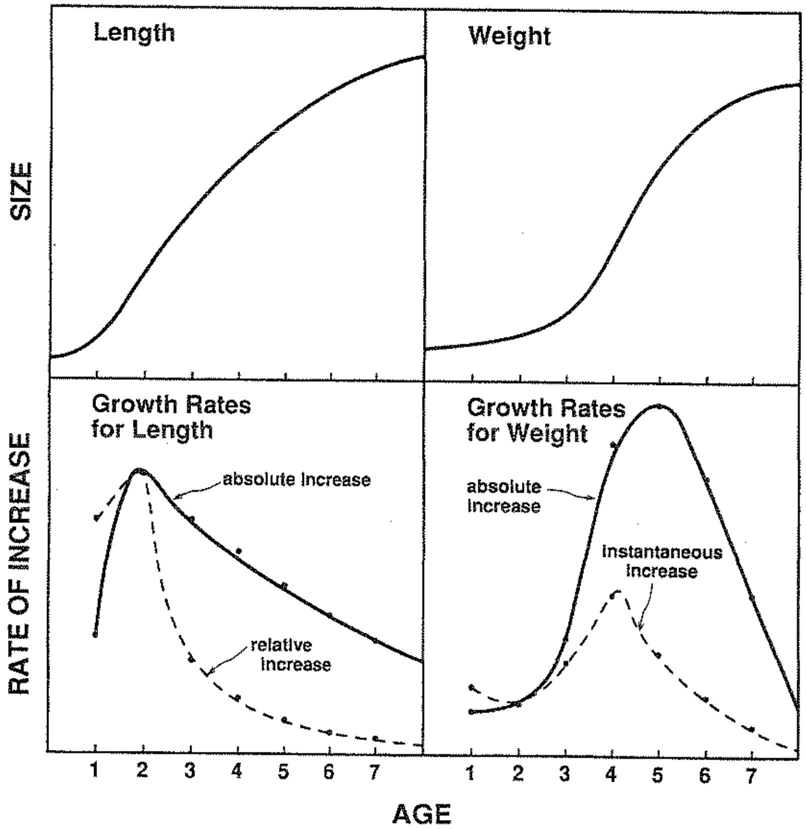

Figure 6.5 Typical trends of length, weight, and growth rates throughout the life of a fish.

The point of intersection between the fitted line and a 45° line (where l_t equals l_{t+1}) estimates L_∞, the theoretical upper length that fish in the population approach but never quite reach, even if they live many years. This upper length is determined from the fitted regression line as

$$L_\infty = \frac{\text{intercept}}{1-\text{slope}}. \tag{6.44}$$

Because the value of L_∞ is obtained using mean-length-at-age data, the estimate represents the length that the average fish in the population would reach if it lived to age infinity. Accordingly, one might occasionally find a fish longer than the estimated L_∞.

To determine t_0, a second regression analysis is done. Consider the linear form of the von Bertalanffy model, which is acquired by taking the natural logarithm of both sides of equation (6.42):

$$\log_e(L_\infty - l_t) = \log_e(L_\infty) + Kt_0 - Kt. \tag{6.45}$$

Using the value of L_∞ determined from equation (6.44) and the mean-length-at-age data, values of t are plotted (on the horizontal axis) against corresponding values of $\log_e (L_\infty - l_t)$; a linear pattern with negative slope should be observed. The slope that results when linear regression analysis is run on these data provides another estimate of K (this value may differ slightly from the previous value of K estimated from equation (6.43). The intercept from the regression analysis will estimate $\log_e (L_\infty) + Kt_0$. Consequently, t_0 can be estimated as

$$t_0 = \frac{\text{intercept} - \log_e L_\infty}{K}. \tag{6.46}$$

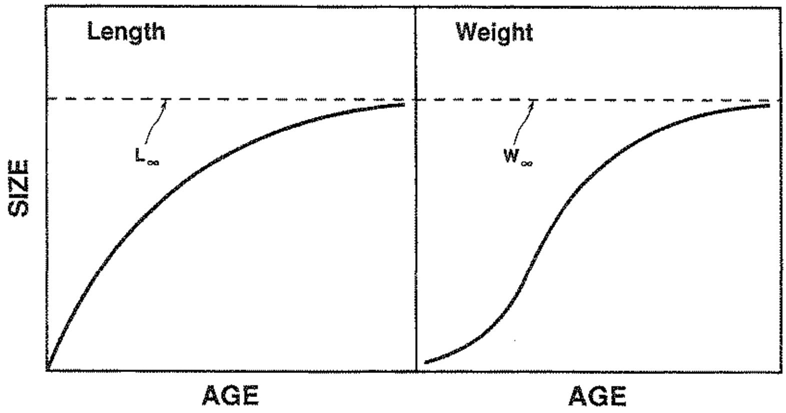

Figure 6.6 Growth trends predicted from von Bertalanffy models of length and weight.

As an example, consider the following mean-length-at-age data for a cohort of gizzard shad.

Age (years)	1	2	3	4	5	6	7	8	9
Mean length (mm)	133	176	202	240	249	256	268	271	276

A regression of l_{t+1} on l_t (Walford plot) gives a slope of 0.71 and an intercept of 83.2 mm. By applying equations (6.43) and (6.44), we find values of 0.34 for K and 286.8 mm for L_∞. Next, a regression of $\log_e (L_\infty - l_t)$ on t (using 286.8 mm for L_∞) gives a slope of -0.34 ($K = 0.34$) and an intercept of 5.36. Applying equation (6.46) leads to an estimate of -0.88 for t_0. Therefore, the fitted von Bertalanffy model is

$$l_t = 286.8\left[1 - e^{-0.34(t+0.88)}\right].$$

6.3.3.2 Growth in Weight

In many stock analyses, it is more desirable to model growth in weight because stock biomass is the product of population size times mean weight. The von Bertalanffy model can be converted to an expression for weight by first using the allometric relationship

$$W = aL^b, \tag{6.47}$$

where the parameters a and b describe the form of the weight–length relationship. Methods for estimating these parameters are outlined in Carlander (1969) and Ricker (1975). In many cases, b is near 3.0, and for computational ease a value of 3 for b is often used, so that only the parameter a is estimated. This produces a simple form of the von Bertalanffy weight model:

$$w_t = W_\infty\left[1 - e^{K(t-t_0)}\right]^3, \tag{6.48}$$

where W_∞ is $aL_\infty^{\,3}$, and the other parameters are the same ones used in the length model.

A plot of w_t versus age shows an initial period of accelerating growth, an intermediate period when growth is approximately linear, and a final phase of decelerating growth as w_t approaches W_∞ (Figure 6.6). Ricker (1975) presents methods of predicting w_t when the value of b (equation 6.47) is not equal to 3.

6.3.3.3 The Gompertz Model

A second expression that can be used to describe fish growth in either length or weight over many years of life is the Gompertz model, which represents fish growth in weight quite well across all life stages, including age 0. The model for weight is

$$w_t = w_0 e^{G\left(1-e^{-gt}\right)}, \qquad (6.49)$$

where w_t is weight at age t, w_0 is the weight of a fish at the beginning of the growth period, G is the instantaneous growth rate when t is 0 and w is w_0, and g is the instantaneous rate at which G decreases as t increases. Estimates of w_0, G, and g can be made using observations of fish weight for a series of age-groups (Ricklefs 1967; Hilborn and Walters 1992).

The Gompertz model has been used less frequently than the von Bertalanffy model. Ricker (1975) suggested that this is not due to its inferiority but because the von Bertalanffy model became more well-known after it was adopted for use in yield models. However, the Gompertz model is gaining popularity for describing growth in length of larval fishes (Michaletz 1997), which often slows as the juvenile stage is approached. When used to describe growth in length, only the upper portion of the S-shape Gompertz curve (beyond the inflection point) is used. Consequently, the model appears as

$$l_t = L_\infty e^{-e^{(G-gt)}}, \qquad (6.50)$$

where L_∞ is the theoretical asymptotic upper length (as in the von Bertalanffy model), and G and g are as previously described (but for growth in length).

To fit this model to length-at-age data, equation (6.50) can be linearized as

$$\log_e\left(\log_e \frac{L_\infty}{l_t}\right) = G - gt, \qquad (6.51)$$

and a regression of $\log_e[\log_e(L_\infty / l_t)]$ versus age (t) is used to estimate G from the intercept and g from the slope. An iterative procedure can then be used whereby values of L_∞ are selected until the best linear fit to the data is acquired. A Gompertz model for weight can also be linearized so that linear regression can be applied.

6.4 PREDICTION OF FISHERY TRENDS

A major activity of fisheries managers has been to predict the effects of different amounts of fishing effort on the numbers and sizes of fish obtained on a continuing basis from a stock. Models are developed within constraints imposed by data availability, types of predictions desired, and mathematical and computational complexity. Models are tools that should be as simple as possible while providing appropriate types of predictions—emphasis should be placed on making decisions regarding feasible management practices rather than impossible ones. Formulation of any mathematical representation of population dynamics will require certain assumptions, and the validity of the assumptions will affect the accuracy and meaning of predictions from a model. Evidence of failure of assumptions does not necessarily mean that the model