Reverse Lee's phenomenon occurs when back-calculated lengths at age are larger for older fish than for younger fish in the sample; potential explanations are opposite to those presented above for Lee's phenomenon (e.g., fast-growing individuals escaped predation or fishing mortality). Lee's phenomenon and its reverse are common in growth analyses and should be investigated in detail when observed (Ricker 1992).

15.4.3.3 Growth Models

Fisheries scientists have modeled fish growth, especially of marine species, for over 100 years. Modeling fish growth has become increasingly popular, probably because of the prevalence of daily growth investigations of larval fish, increased use of otoliths, fin rays, and spines for assessing growth, and technological advancements that allow for better data handling and estimation procedures (e.g., computers and readily available statistical analysis programs). Growth models relate the age of fish in a population to their length or weight and are often viewed as final products of growth analyses (Jones 2000). The output of these models is an equation that describes growth of fish in a population and provides parameter estimates that can be used to make comparisons both among and within populations (Quist et al. 2003; He et al. 2005) and in population models (Quinn and Deriso 1999; Haddon 2001; Scholten and Bettoli 2005). The most common growth models are the von Bertalanffy, Gompertz, and logistic models.

The von Bertalanffy growth model. The von Bertalanffy growth function has been widely used in fisheries, and although it has been criticized over the years (e.g., Roff 1980), it remains one of the most popular growth models in fisheries science (e.g., Haddon 2001). Several alternative forms of the model are available, but the traditional and most common form of the von Bertalanffy function is

$$L_t = L_\infty[1 - e^{-K(t-t_0)}], \tag{15.5}$$

where L_t is the estimated length at time t, L_∞ is the asymptotic or theoretical maximum length, K is a growth coefficient, and t_0 is the theoretical age when length equals zero. The growth coefficient K describes how quickly the maximum length is attained; it is often misinterpreted as an absolute growth rate. The parameter t_0 is an extrapolation of the data and merely serves to fix the position of the curve along the x-axis. As such, the parameter has few, if any, real biological interpretations. Weight data are also commonly used in the von Bertalanffy model: $W_t = W_\infty[1 - e^{-K(t-t_0)}]^b$, where W_t, W_∞, and K are interpreted as above and b is the slope of the length–weight relationship (Chapter 14). Data used to estimate the von Bertalanffy growth function, and other growth functions, may include mean length at age (Brennan and Cailliet 1989; Nitschke et al. 2001; Alves et al. 2002) or back-calculated length at age (Jones 2000; Williamson and Garvey 2005; Isely and Grabowski 2007). Using back-calculated length-at-age data from individual fish may cause bias in parameter estimates because growth estimates of the same fish at different ages are not independent. To help account for these biases, repeated-measures models have been proposed to fit the von Bertalanffy model (Jones 2000). This concern is not unique to von Bertalanffy growth models; therefore, similar model-fitting practices should be investigated for other growth models when using data that are not independent measures of growth.

The von Bertalanffy model allows for easy comparisons of growth among populations or between sexes and provides parameter estimates that are used in other applications, such as Beverton–Holt yield models (Ricker 1975) or calculation of mortality caps (Miranda 2002). The von

Bertalanffy curve describing growth in length typically exhibits a rapid increase that begins to level off as L_∞ is approached (Figure 15.19). This pattern generally fits annual growth data for fish in stable systems but not growth of fish in highly variable environments or growth of larval

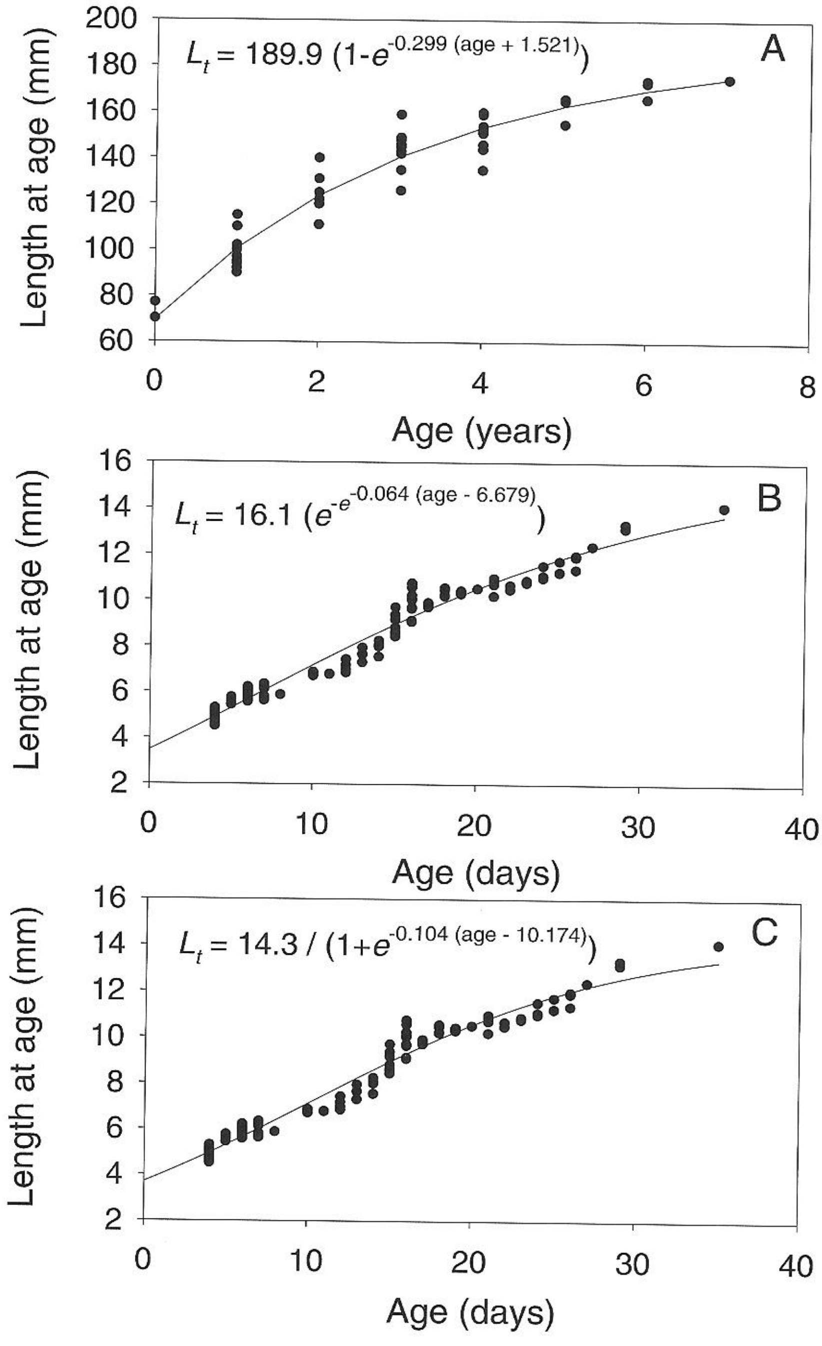

Figure 15.19 Examples of von Bertalanffy (**A**; creek chub), Gompertz (**B**; larval white bass), and logistic (**C**; larval white bass) growth models.

fish, which may oscillate over time (Haddon 2001). Modifications incorporating sine functions or additional coefficients can be incorporated to help account for these patterns (e.g., Campana and Jones 1992; Haddon 2001).

The Gompertz and logistic growth models. The Gompertz, or Laird–Gompertz, growth function is used extensively for describing growth of larval and juvenile fishes (Campana and Jones 1992). The Gompertz growth model is sigmoid shaped (i.e., S-shaped) and is well suited to fish or life history stages that exhibit low initial growth rates (Figure 15.19). A common form of the equation is

$$L_t = L_\infty \cdot e^{-e^{[-G(t-t_0)]}}, \qquad (15.6)$$

where L_t is the length at time t, L_∞ is the asymptotic length, G is the instantaneous rate of growth at age t_0, and t_0 is the inflection point of the curve and the age at which absolute growth rate begins to decline. A number of alternative and equivalent forms of the equation can be found in Ricker (1975) and Campana and Jones (1992). A similar model is the logistic growth model, one form of which is

$$L_t = L_\infty / [1 + e^{-G(t-t_0)}], \qquad (15.7)$$

where L_t, L_∞, and t_0 are as above, and G is the instantaneous growth rate at the origin of the curve. The logistic growth function often results in a growth curve that is similar to the Gompertz model. However, the logistic model differs in that regions above and below the inflection are symmetrical, whereas those of the Gompertz are not. The logistic curve is often used to describe population growth rates, but it has also been used to describe growth of individual fish (Campana and Hurley 1989).

Other growth models. Other common growth models include simple linear regression models (ordinary least-squares means and geometric mean regressions; Ricker 1975), exponential models, and polynomial models. Choosing an appropriate growth model is largely dependent on the data and how the resulting model and parameter estimates will be used. Readers are referred to excellent reviews and discussions by Ricker (1975, 1979), Brett (1979), Kaufmann (1981), Campana and Jones (1992), Quinn and Deriso (1999), and Haddon (2001) for detailed explanations of the models presented here and other growth functions.

15.4.3.4 Size-Specific Growth Analysis

All of the techniques presented in the previous discussion can be categorized as age-specific growth analyses because they focus on growth of fish within the context of age. Age-specific analytical techniques are by far the most common growth analyses conducted by fisheries scientists. Although age-specific analyses are widely accepted and meet most management and research needs, some scientists have suggested that growth should also be considered within the context of size (i.e., size-specific growth analysis; Larkin et al. 1956; Pauly 1987; Osenberg et al. 1988).

Size-specific growth analysis is based on the premise that fish experience ontogenetic (developmental) changes that modify their ecological roles. Examples of common ontogenetic changes include changes in food habits (e.g., switch to piscivory), sexual maturation, and habitat use. Because growth is largely a reflection of environmental conditions, such as the availability of prey, the growth response of an individual to limited resources or habitat conditions is a function of its size rather than its age (Larkin et al. 1956; Parker and Larkin 1959; Gerking and Raush 1979;