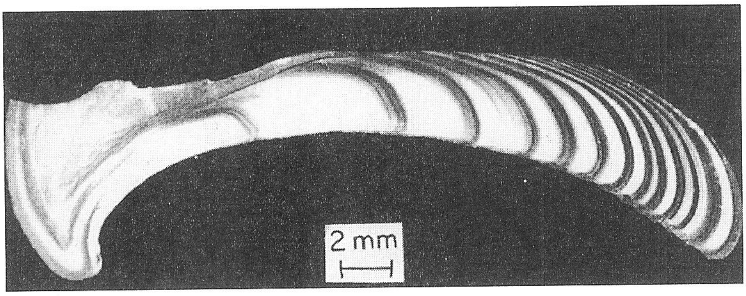

Fig. 9.17 Growth rings on a sectioned shell of the surf clam *Spisula solidissima* (Mactricidae) (Ropes & Shepherd, 1988). Photograph copyright US National Marine Fisheries Service.

Growth estimates for these species are usually obtained by tagging or length frequency analysis (section 9.3.3). Bivalves and gastropod molluscs may be aged from seasonal growth patterns in the shell matrix. Shells of bivalves are usually cleaned, bleached and sectioned from the base of shell across the valve to the margin (Ropes & O'Brien, 1979; Ropes & Shepherd, 1988). The section is mounted in resin for examination (Fig. 9.17).

9.3.3 Growth

For species that can be aged, growth is determined directly from size at age data, or back-calculated from scale readings. If the species cannot be aged, then growth may be estimated from length frequency distributions by treating length as a non-linear measure of biological time.

Back-calculation of growth using scales

Back-calculation is a technique that uses fish length and fish scale measurements at the time of capture to infer length at times in the past (Francis, 1990). Back-calculation requires that a relationship between fish length (L) and scale radius (S) can be established. If fish length at capture is denoted by L_c, and scale radius at capture by S_c, then L_i and S_i can be taken as the corresponding measurements at the time when the ith annulus was formed. Back-calculation formulae allow the calculation of L_i from L_c, S_c and S_i and are reviewed by Francis (1990).

As an example, we will consider the formula of Whitney and Carlander (1956) that assumes a constant proportional deviation of the length or scale measurements of an individual from the mean length or scale measurement of the population.

$$f(L_i) = (S_i/S_c)f(L_c) \tag{9.13}$$

where f is the function describing the relationship between body length and scale radius, such that $f(L)$ is the mean scale radius for fish of length L. If the body length to scale radius relationship is linear, then:

$$L_i = -(a/b) + (L_c + a/b)(S_i/S_c) \tag{9.14}$$

where a and b are the parameters from a linear regression of the form $y = a + bx$.

There are many potential errors associated with back-calculation, and the methods used should be validated. Francis (1990) recommends any validation must show:

1 that the radius of a scale mark is the same as the radius of the scale at the time the mark was formed;

2 that the supposed time of formation of the mark is correct;

3 that the formula used accurately relates scale radius and body size for each fish.

Back calculation of fish length from annuli is easily automated using digitizing tablets and simple software, so that scale measurements are immediately converted to fish lengths (Pickett & Pawson, 1994).

Growth models

The fitting of growth models to age and size data is almost a field in its own right, but choice of model is generally less important than obtaining representative samples. For many stock assessments it is acceptable to calculate mean body size at age in a tabular form and enter this into analyses directly. Those tables should be updated annually to allow for growth changes. Such an approach is used with yield per recruit analysis (section 7.7).

The only growth model we describe here is the **von Bertalanffy growth equation (VBGE)** because it provides a good description of growth in most species and because the parameters have been widely compiled and have considerable utility in life-history studies (section 3.4.2). It is given as:

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \qquad (9.15)$$

Where L_t is the length at age, L_∞ is the asymptotic length (the length at which growth rate is theoretically zero), K is the Brody growth coefficient (rate of growth towards asymptote) and t_0 is the time when length would have been zero on the modelled growth trajectory. t_0 can be seen as a parameter that shifts a growth trajectory defined by K and L_∞ along the x-axis.

If this equation is combined with the length–weight relationship $W = aL^b$ (equation 9.10) and the asymptotic weight is defined as W_∞, it can be rearranged to give the von Bertalanffy growth curve for weight:

$$W_t = W_\infty(1 - e^{-K(t-t_0)})^b \qquad (9.16)$$

Where W_t is weight at age and b is the parameter from the length–weight relationship (equation 9.10).

Methods used to fit the von Bertalanffy growth equation should account for the error structure in the data and indicate the precision of parameter estimates. Many computer programs allow von Bertalanffy growth parameters to be fitted using models with additive or multiplicative error structure and these are described in Quinn and Deriso (1999).

Growth parameters can also be derived from tagging data if size is measured at release and recapture and if the interval between release and recapture is known (Francis, 1988; Quinn & Deriso, 1999). The following approach is taken from Quinn and Deriso (1999). Suppose that fish i was of length $L_{1i} = L_{(t_{1i})}$ at age t_{1i} when tagged and of length $L_{2i} = L_{(t_{2i})}$ at age t_{2i} when recaptured. The elapsed time between tagging and recapture can be denoted as $\Delta t_i = t_{2i} - t_{1i}$ and growth as $\Delta L_i = L_{2i} - L_{1i}$. If we assume that the VBGE describes growth (equation 9.15) and that an additive error structure applies to growth then:

$$\Delta L_i = (L_\infty - L_{1i})(1 - e^{-K\Delta t_i}) + \varepsilon_i \qquad (9.17)$$

Where ε_i is a random error term with mean 0 and variance σ^2. Parameters L_∞ and K can be estimated by non-linear least squares. The value of t_0 is obtained by solving the VBGE when length at age is known.

With seasonal samples taken from fluctuating environments, growth can vary with season. Various modifications of the VBGE have been produced to allow for this. One seasonally modified growth model is:

$$L_t = L_\infty(1 - e^{-K(t-t_0)-(CK/2\pi)\sin(2\pi(t-t_s))}) \qquad (9.18)$$

This is simply a VBGE with the added term $(CK/2\pi)\sin(2\pi(t - t_s))$ to give a seasonal oscillation (Pauly, 1982). The constant C describes the amplitude of seasonal oscillations and t_s the phase shift of these oscillations. An example of the seasonal growth curve is given in Fig. 9.18.

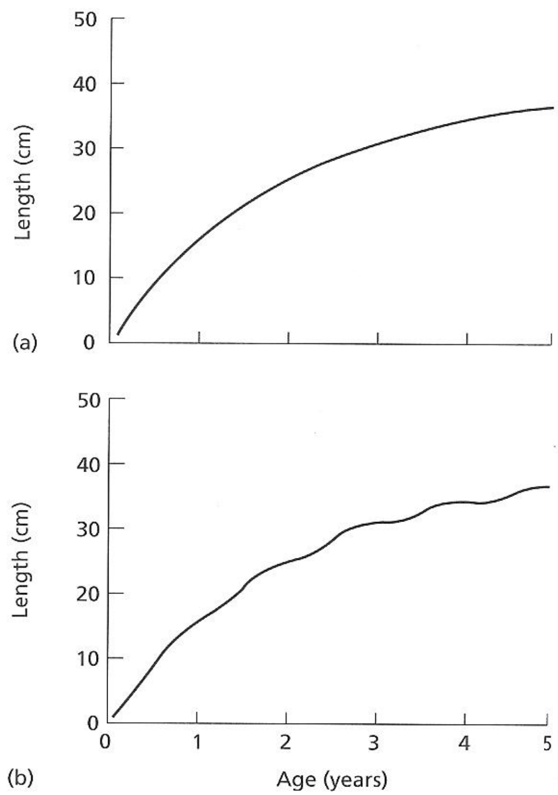

Fig. 9.18 (a) A von Bertalannfy growth curve (C = 0), and (b) its seasonally adjusted equivalent when C = 0.2.

Growth parameters from length-frequency data

The problems with ageing some fished species have encouraged some biologists to use length as a non-linear measure of biological time (Rosenberg & Beddington, 1988; Sparre & Venema, 1998). The aim of estimating growth from length frequencies is to separate a complex length-frequency distribution for the whole population into cohorts and to assign ages to them (Fig. 9.19). We used this approach for length-