5 Age and Growth

J. Jeffery Isely and Timothy B. Grabowski

5.1 INTRODUCTION

The ability to determine ages of fishes without bias is critical to effective management and research. Accurate age information can provide valuable insights into critical life history events. Often, migrations related to spawning or ontogenetic changes in environmental requirements are also age dependent. Age data can be coupled with numbers of individuals to produce an age-frequency distribution, from which patterns in mortality can be determined. Similarly, deviations in expected numbers at age can provide insights into year-class strength variability and the effects of environment on survival.

When age and size information are combined, we can evaluate growth. Growth provides us with some indication of resource utilization and the effectiveness of our management strategies. Our ability to model growth and to understand variables that affect growth both within and among populations is critical to our ability to manage fisheries effectively. When we evaluate age, growth, and mortality (see Chapter 6) in combination, we begin to understand the complex relationship between population size and biomass (see Chapter 8). This understanding is the basis of modern fisheries resource allocation and management.

5.2 AGE DETERMINATION AND VALIDATION

Primary methods employed by fisheries scientists to estimate ages of fishes are recovery of known-age fish, evaluation of length-frequency distributions, and interpretation of calcified structures. Under unique circumstances, additional methods employed by researchers include evaluations of isotope decay rates and chemical microanalysis.

5.2.1 Use of Known-Age Fish

The most direct method of determining age is by the recovery of known-age fish. Although costly and time consuming, the method is most useful to validate ages determined by other methods. In this method, fish of known age are reared under natural conditions or marked and released into the wild to be recaptured at a later time. Dyes and stains that are incorporated in hard parts, such as oxytetracycline or alizarin complexone, have been used to validate annual and daily growth-increment formation (Brothers 1990). Individuals are either immersed into a bath containing a dye or injected with a chemical that is incorporated into the aging structure. After a minimum of one annual growth cycle (or several daily growth cycles), the fish is recaptured and the structure is examined. Although the relationship between the number of annuli between the mark and the margin of the structure is used to validate the annual deposition of increments, the technique validates annual increment formation during only the time period of the study. It is then inferred that all rings are similarly formed. It is important to examine a variety of sizes and ages when employing this technique (Campana 2001).

5.2.2 Length-Frequency Method

Because fishes in temperate climates generally spawn over a relatively short period each year, but grow over a relatively long period each year, there are natural discontinuities in the length-frequency distribution between age-classes within a population (Macdonald and Pitcher 1979; Macdonald 1987). At any given time, the length-frequency distribution of a population is composed of a variety of age-classes. In theory, each year-class forms a unique length distribution resulting in a separate mode in the cumulative distribution. The method of estimating age by separating overlapping length distributions has been used since the late 1800s.

Although this method works well to separate early age-classes, the decrease in annual growth in length as individuals age, combined with natural variability in growth among individuals, results in increasing overlap in age-specific length distributions with older cohorts (Figure 5.1). In most species, only the youngest two or three cohorts are readily distinguished using this method. The method also has several other disadvantages. Environmental conditions often result in disjunct spawning or survival within a single spawning season, resulting in multi-modal length-frequency distributions within year-classes. Geographic differences in environmental quality, density dependency, or other factors may also result in differential growth between groups spawned within the same time period. Differences in year-class strength may result in an underrepresentation of one or more year-classes that are masked by a more dominant cohort. Schooling species often associate by size, resulting in little within-school variability in size across age-classes. Most sampling and fishing gear are size selective and collect samples that are biased by size or growth rates of individuals. As a result, most samples represent a subset of the population length distribution that contains only the fastest-growing younger fish and slowest-growing older fish along with normally growing fish of intermediate age. The success of the length-frequency method of age estimation requires a large sample drawn at random from the population. Although it is useful in fast-growing, short-lived species, the technique is most useful to corroborate age distributions derived from some other method. Separating the overlap in length-frequency distributions requires an iterative statistical procedure. Fournier

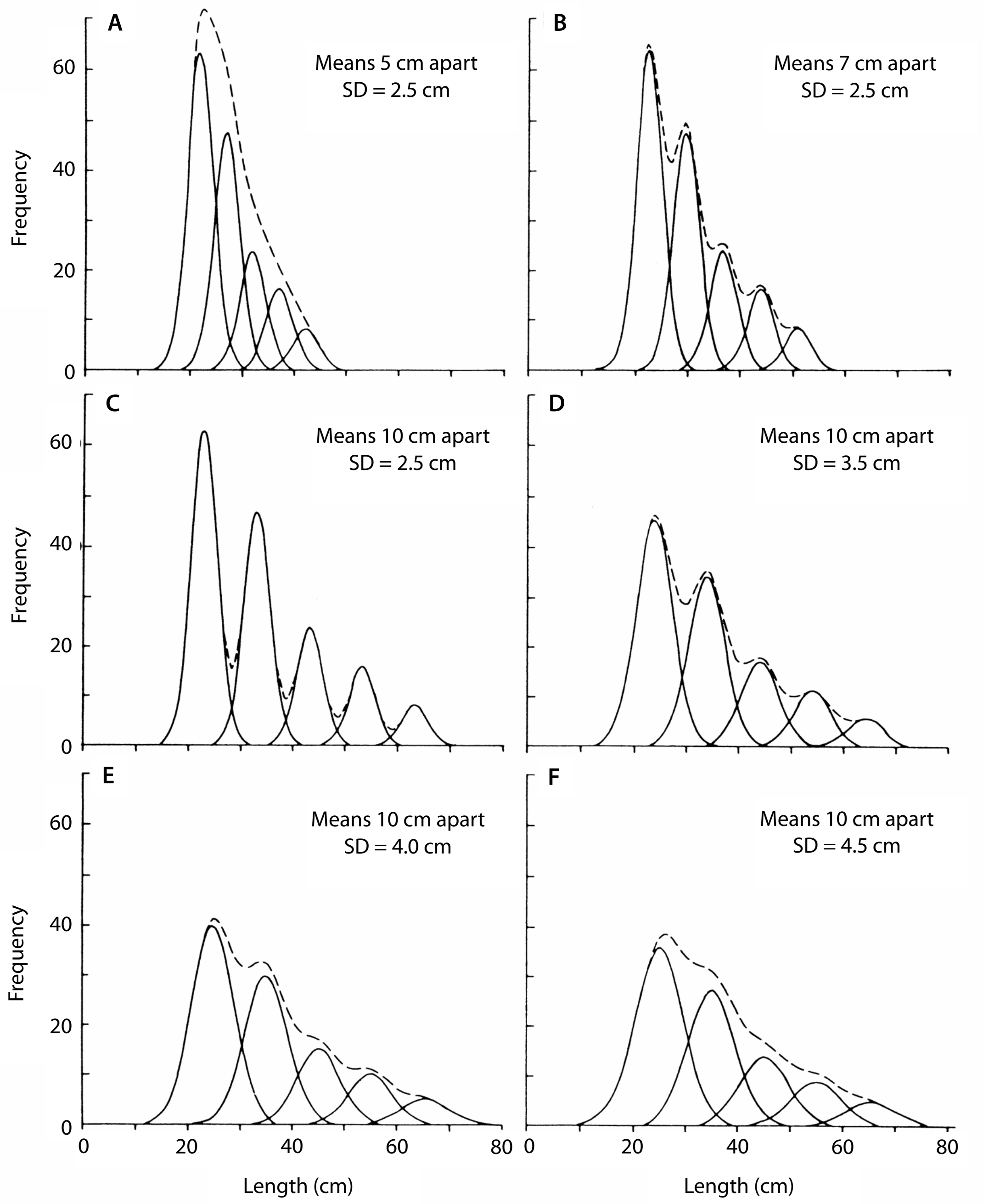

Figure 5.1 Illustration of the effect of changes in the mean, standard deviation, and relative sizes of cohorts upon a length-frequency distribution. The dashed lines represent the frequency distribution of a hypothetical population and solid lines indicate cohorts. The contribution to the population by each cohort is constant. Reprinted from Macdonald and Pitcher (1979) with permission.

et al. (1998) developed a length-based, age-structured model, MULTIFAN–CL, which provides an integrated method of estimating age composition and other parameters from length-frequency data. The method incorporates Bayesian parameter estimation and procedures for hypothesis testing to assist model development. The reader is referred to Macdonald and Pitcher (1979) and Macdonald (1987) for further information on the use of length-frequency distributions to assign individuals to age-groups.

5.2.3 Interpretation of Calcified Structures

Intra-annual variability in environmental variables such as temperature, salinity, dissolved oxygen, and productivity often produce a seasonal cycle in fish growth. This seasonal cycle is recorded as discernible increments in calcified structures in fishes because of the differential deposition of calcium and protein in relation to growth. Structures commonly used to age fish include scales, otoliths, spines, fin rays, vertebrae, and other bony structures (DeVries and Frie 1996). The successful interpretation of calcified structures to age individuals relies on the ability to recognize patterns in the layered deposition of material. As annual growth increments decrease with age, the spacing and distinctness of growth increments in calcified structures also decreases, often resulting in a negative bias in age estimates of older fishes.

5.2.3.1 Scales

Historically, scales were the most popular structure used to estimate age. Despite their limitations, they remain an important and commonly employed tool for assessing age and growth in many species. Scales were first recognized to contain age information as early as 1890. The technique was commonly used in assessments of European marine fisheries at the turn of the century but was not applied widely in North America until the 1920s (Carlander 1987). A review by Van Oosten (1929) described the methods and established guidelines for scale interpretation that led to widespread employment of the method beginning in the 1930s. With a few modifications, the techniques described by Van Oosten (1929) are still used today. Although it is relatively easy and inexpensive to collect and prepare scales, the identification of annuli requires skill and experience. The identification of false annuli can be a critical component of age and growth studies utilizing scales. Additionally, scales do not develop at hatching and may not appear until the fish is at a relatively advanced stage of development (Ward and Leonard 1954; Sire and Arnulf 1990; Sire et al. 1997).

The major advantage of the use of scales for aging is that the fish need not be sacrificed for data collection. This is of particular importance in studies focusing on endangered or threatened species as well as in situations where the removal of fish from the study area would bias study results. However, the potential bias toward underestimation of age is a major disadvantage.

5.2.3.2 *Otoliths*

Otoliths, or ear stones, are acellular structures formed by the crystallization of calcium carbonate in a protein matrix. This process is growth dependent and occurs throughout the life of the fish (Popper and Lu 2000). Material is permanently deposited and is not resorbed as in scales. Consequently, otoliths constitute a permanent record of growth for a fish to the extent that fossil otoliths can be used to reconstruct the life histories of ancient fishes (Woydack and Morales-Nin 2001). Otoliths were first used to determine fish age in the late 1800s (see review by Van Oosten 1929). However, the discovery in the 1970s that otoliths form daily increments has become an important advancement in fisheries science (Pannella 1971). Daily ages determined from age-0 fish have led to the incorporation of early life history information, such as cohort-specific growth and mortality, into stock assessments and the evaluation of the effects of environmental conditions on growth and mortality over short temporal scales. The analysis of daily otolith increments in fisheries research has been reviewed by Campana and Neilson (1985). Although otolith increments are usually easier to interpret than are scale increments, the recognition of otolith annuli and daily growth increments still requires skill and experience. There are two disadvantages to the use of otoliths in age determination: sacrifice of the fish is necessary for otolith removal and a large investment of time is required to prepare them for reading. These factors should be considered when designing an age and growth study.

5.2.3.3 *Spines and Fin Rays*

In cases in which sacrifice is impractical and scales are inadequate or nonexistent, spines or fin rays may be used to determine age. This method is most commonly employed to age catfishes and sturgeons but can be applied to a wide range of species (Beamish 1981). The reader is referred to Boyko (1946) and Sneed (1951) for details regarding preparation and reading. A major disadvantage of this technique is that spines contain a central lumen, which expands as the fish grows. The expanding lumen erodes early annuli and can cause age and growth estimates to be biased (Nash and Irwin 1999; Buckmeier et al. 2002). Annuli can be somewhat more irregular than those in scales and otoliths, potentially rendering them useless for back-calculating growth. However, the use of spines or rays in conjunction with other structures or in cases where other structures fail to produce reliable results warrants consideration (Beamish 1981).

5.2.3.4 *Vertebrae and Other Bony Structures*

Historically, other structures such as opercular bones (Bardach 1955) and cleithra have been used to determine the ages of fishes. Studies utilizing these structures are not common, despite yielding age estimates that are comparable to those from scales and otoliths (Baker and Timmons 1991; Baker and McComish 1998). The usual methods of age determination for bony fish do not work for cartilaginous fish. However, some structures such as vertebrae contain mineralized calcium phosphate, which is deposited in proportion to size and has proven useful in determining age (Stevens 1975; Clement 1992; Natanson et al. 2001). Other structures such as the thorns of skates and rays (Gallagher and Nolan 1999) and the spines of dogfishes (McFarlane and Beamish 1987a) also have been employed for determining age and growth in elasmobranchs.

5.2.4 Validation of Age Estimates from Calcified Structures

Common assumptions of estimating age from hard parts is that increments are formed annually or daily and that all marks are readily identifiable. Although generally correct, these assumptions are not always valid (Beamish and McFarlane 1983; Campana 2001). Variability in growth resulting from environmental extremes, spawning, disease, or injury may result in marks that appear similar in structure to annual increments (Mugiya and Uchimura 1989; Morales-Nin 2000). Allometric growth and the slowing of growth with increasing age may render annual or daily marks difficult to distinguish. In recent years, the potentially large effects of underestimates in age on management decisions related to harvest and growth have re-emphasized the importance of validating age estimation procedures (Beamish and McFarlane 1983; Campana 2001).

5.2.4.1 Natural Marks

In some cases natural marks have been used as a method of age validation. Occasionally a natural or anthropogenic event will create a reference mark on calcified structures. For example, the eruption of Mount Pinatubo in 1992 resulted in reduced productivity in lakes throughout the northeastern United States and Canada. This reduced productivity has manifested in slow growth of fishes during that year, which can be seen across age-classes (King et al. 1999a; 1999b). This natural mark has been used to validate the ages of fishes that were living in 1992. Another widespread mark that has been used to validate ages in long-lived fishes is the incorporation of radioactive carbon (^{14}C) from nuclear bomb tests in the 1950s into tissues (Kalish 1993; Kalish et al. 1997; Campana et al. 2002). Typically, the nucleus of the otolith is used to determine the year of birth of the individual. The technique can be used broadly to separate fish into individuals born prior to and after nuclear weapons testing or to validate specific ages when used in conjunction with a reference chronology of atmospheric ^{14}C levels. Other events such as El Niño–La Niña events (Woodbury 1999) and oil spills (Gallego et al. 1995) that are associated with a specific date have the potential to be used as marks for independent validation of age estimates. However, to date, this method has not been widely investigated.

5.2.4.2 Radiochemical Dating

The ages of fishes determined from otoliths can also be validated using radiochemical dating. This process takes advantage of the decay of radioactive trace elements deposited in the otoliths during their formation. The ratio of parent to daughter isotopes in the nucleus of the otolith can be used to estimate the time of its formation. This technique is dependent upon removal of the nucleus and can be extremely sensitive to the removal of excess material. Additionally, the resolving power of the technique renders it suitable only for long-lived species (Francis 2003). The reader is referred to Bennett et al. (1982) and Andrews et al. (1999) for detailed descriptions of this technique.

5.2.4.3 *Marginal Increment Analysis*

Marginal increment analysis (MIA) is a commonly used method for evaluating both annulus and daily increment formation to validate age estimates. It tests the assumption that a growth increment formed on an annual or daily cycle will fit a saw-toothed pattern when the average state of completion of that increment in the population is plotted against time (Figure 5.2). Marginal increment analysis is popular because it is easy and cost effective relative to other validation techniques. It uses repeated sampling at regular intervals through time to determine when an annulus or increment is deposited. The application of the technique has come under question, as reviewed by Beckman and Wilson (1995) and Campana (2001). There are severe technological limitations in measuring a growth increment along the increasingly thin and curved edge of an otolith. These limitations often lead

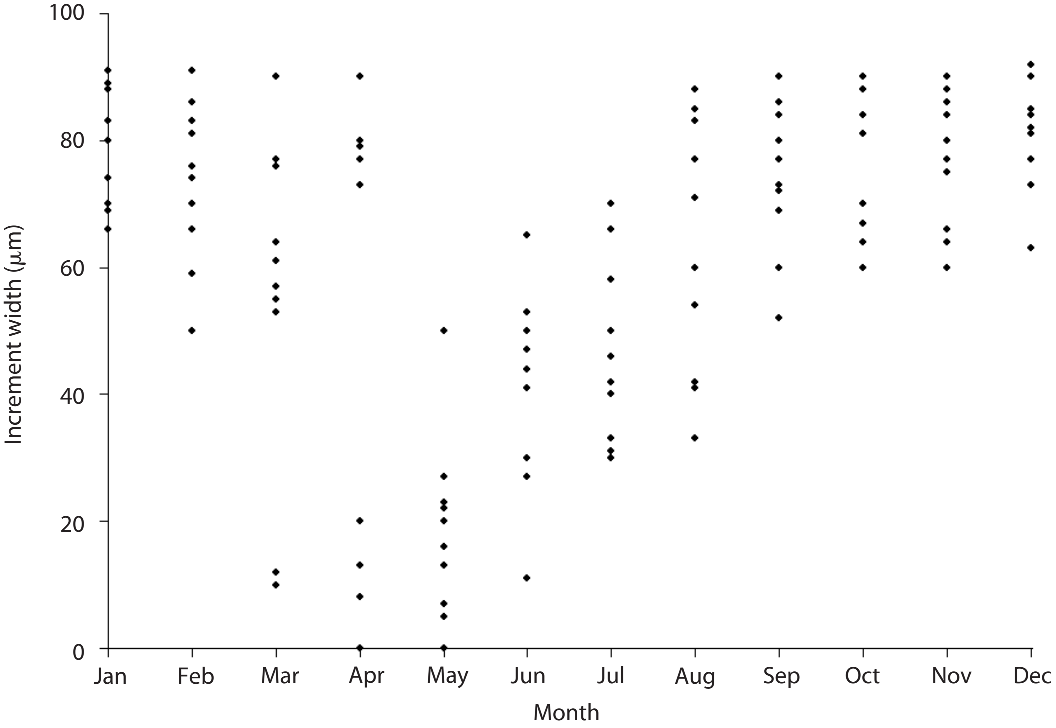

Figure 5.2 Plot of marginal increment, the amount of translucent material between the last increment and the otolith margin, for largemouth bass sampled monthly in a southeastern reservoir. Increment width increases until another annulus is deposited, in this case, between March and May.

to subjective interpretation of results. There are also problems with applying the results of MIA from a younger, faster-growing age-class to older cohorts within the same population (Campana 2001). This tends to result in bias toward underestimating age in older individuals. There also have been unexplained instances where inconsistencies in the timing of increment formation among years and locations have been observed (Beckman and Wilson 1995).

Campana (2001) outlined several aspects of a well-designed validation study using MIA. The most important point is to interpret the results objectively by means of an appropriate statistical analysis. It is essential that only a limited number of age-classes are used in a MIA and that samples from these age-classes be randomized before reading to avoid subjectivity. Finally, at least two complete annual or daily growth cycles should be examined during the course of MIA.

5.2.4.4 *Date-Specific Marking*

Validation of both annual and in some cases daily growth increments can be accomplished through the recapture of physically or chemically marked fish. The use of chemical marks is perhaps the most powerful of the validation tools, but it also carries the same drawbacks as any mark–recapture study (see DeVries and Frie 1996 for details). Otoliths and other hard parts will incorporate chemicals such as oxytetracycline, alizarin complexone, calcein, and strontium. These chemicals bind to calcium, resulting in a mark on the growth increment forming at the time that will fluoresce under ultraviolet light (Weber and Ridgway 1962, 1967; Rahn and Perrin 1970; Hettler 1984; Wilson et al. 1987). For a review of the use of these chemicals the reader is referred to McFarlane and Beamish (1987b) and Brothers (1990). The marks have a high retention rate on internal structures (Reinert et al. 1998) but may degrade on external structures, such as scales and fin rays, which are exposed to sunlight.

Traditional marks such as externally visible marks or electronic tags such as passive integrated transponder (PIT) tags have been used. With this technique, known-age fish are released and recaptured some time later. By comparing a reference sample collected at the time of release with samples collected from recaptured marked fish, annual deposition can be validated.

5.2.4.5 *Captive Rearing*

Individuals held and reared in captivity can be used to validate daily growth increment formation. This technique generally is not considered suitable to validate annulus formation because laboratory conditions cannot fully recreate the natural environment. Even daily increments differ in appearance in captive-reared individuals. However, their frequency of formation is rarely influenced because of the endogenous control of the process (Geffen 1987; Morales-Nin 2000).

5.2.5 **Applications of Age Data**

In addition to its use in estimating growth (see section 5.3), age data can be used in several other applications. Data collected from otoliths and other hard parts are utilized to construct age- or cohort-specific models of mortality and survivorship. Otoliths are increasingly being used as biological data recorders of temperature and salinity regimes (Campana 2005). However despite these advances, age–length keys and hatch date analysis remain important tools frequently used to evaluate population structure and events that are not easily observed, such as spawning and migration.

5.2.5.1 *Age–Length Keys*

The relationship between age and length is relatively stable within a population. Consequently, age can account for a large amount of the variability in length. Given a sample of fish that has been aged, we can produce a probability matrix of the proportion of individuals within a certain length-class having a certain age (Fridriksson 1934; Ketchen 1949; Isermann and Knight 2005). This table is often referred to as an age–length key (Box 5.1). The age–length key can then be used to estimate the age of fish of a given length so that length frequency from a much larger sample can be converted to age frequency (Isermann and Knight 2005). The use of ages estimated from age–length keys can significantly reduce the time or cost associated with aging large numbers of fish. The method is particularly valuable when applied to rare or endangered species, for which the collection of tissues used in aging may be problematic. When applied to early life stages, age-frequency information can provide insight into spawning and migration not available from length information alone. It is important to note that the usefulness of age–length keys is generally restricted in time and space. Variability in growth among years and geographic locations (Westrheim and Ricker 1978; Terceiro and Ross 1993; Bettoli and Miranda 2001) may bias the results obtained from using age–length keys developed from other times or places.

5.2.5.2 *Hatch Date Analysis*

By using information obtained from otolith daily growth increments, it is possible to determine the hatch date of larval and juvenile fishes. In early life stages, hatch date distributions can be used to glean information on the importance of density dependent and independent factors on spawning, growth, and survival. This technique has numerous applications including identifying the periodicity of spawning events, locating spawning habitats, and examining cohort-specific patterns of mortality. Although similar to age-frequency analysis, hatch date analysis uses age to back-calculate hatch date; then adjustments are made for the effects of cumulative mortality on the numbers produced at each date. By incorporating mortality information, scientists are better able to estimate egg production and other variables important in assessing stocks.

5.3 GROWTH

Growth is the addition of biomass to either a population or an individual. In fisheries management, we attempt to optimize the efficiency of harvest by balancing individual growth, population biomass, and mortality. If we harvest young fish, we

Box 5.1 Creating an Age–Length Key

Fisheries scientists often collect length data on large samples, but age data, because of the large amount of effort involved, are generally collected on smaller samples (i.e., subsamples). In some cases, we wish to convert our length data to age data. We do this through the use of an age–length key. We start with a data set containing individual length and age data. By dividing length data into a series of discrete intervals, we can determine the frequency of ages within each interval. These frequencies are transformed into probabilities, which are later used to convert numbers at length to numbers at age. In this example, we have age and length (tl) data for adult spotted sucker. We create a series of length intervals and create a new variable (tlint) that is a discrete representation of the length data. In this case, we develop 2 cm (20 mm) length-groups and name each group by the low end of the interval. We then determine cell frequencies and calculate cell probabilities using Proc Freq in SAS (SAS 2004). By adding some options to the tables statement, we can suppress the printing of the frequencies and percentages we don't need.

Program

```
data spotted;
input tl age;

if 90<= tl < 100 then tlint = 90;
else if 100<= tl < 120 then tlint = 100;
else if 120<= tl < 140 then tlint = 120;
else if 140<= tl < 160 then tlint = 140;
else if 160<= tl < 180 then tlint = 160;
else if 180<= tl < 200 then tlint = 180;
else if 200<= tl < 220 then tlint = 200;
else if 220<= tl < 240 then tlint = 220;
else if 240<= tl < 260 then tlint = 240;
else if 260<= tl < 280 then tlint = 260;
else if 280<= tl < 300 then tlint = 280;
else if 300<= tl < 320 then tlint = 300;
else if 320<= tl < 340 then tlint = 320;
else if 340<= tl < 360 then tlint = 340;
else if 360<= tl < 380 then tlint = 360;
else if 380<= tl < 400 then tlint = 380;
else if 400<= tl < 420 then tlint = 400;
else if 420<= tl < 440 then tlint = 420;
else if 440<= tl < 460 then tlint = 440;
else if 460<= tl < 480 then tlint = 460;
else if 480<= tl < 500 then tlint = 480;
else if 500<= tl < 520 then tlint = 500;
else if 520<= tl < 540 then tlint = 520;

datalines;
100                 1
111                 1
114                 1
384                 4
(input remaining data)
;

proc freq;
tables tlint*age / nocol nofreq nocum nopercent;
run;
```

Program Output

The output consists of a table containing the row percent, which is equal to the probability that a fish within a certain size interval is a certain age.

Table Output from the frequency procedure. Given is the probability that a fish within a given length interval (tlint) is a certain age.

tlint and total number fish	Age										Total number
	1	2	3	4	5	6	7	8	9	10	
90	16.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
100	66.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
120	16.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
240	0.00	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
300	0.00	0.00	9.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
320	0.00	0.00	18.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
340	0.00	0.00	27.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
360	0.00	0.00	27.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
380	0.00	0.00	18.18	30.77	0.00	0.00	0.00	0.00	0.00	0.00	
400	0.00	0.00	0.00	46.15	0.00	0.00	0.00	0.00	0.00	0.00	
420	0.00	0.00	0.00	23.08	60.00	0.00	0.00	0.00	0.00	0.00	
440	0.00	0.00	0.00	0.00	40.00	100.00	0.00	100.00	40.00	0.00	
460	0.00	0.00	0.00	0.00	0.00	0.00	100.00	0.00	40.00	0.00	
480	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	20.00	100.00	
Total number	6	4	11	13	10	5	2	3	5	2	61

Program

Once an age–length key is generated, the length-frequency distribution from the larger sample is put into the same interval format as the aged sample. The cell frequencies are then multiplied by the frequencies from the age–length key to estimate the age distribution of the sample.

```
data spotall;
input tl;

if 90<= tl < 100 then tlint = 90;
else if 100<= tl < 120 then tlint = 100;
else if 120<= tl < 140 then tlint = 120;
else if 140<= tl < 160 then tlint = 140;
else if 160<= tl < 180 then tlint = 160;
else if 180<= tl < 200 then tlint = 180;
else if 200<= tl < 220 then tlint = 200;
else if 220<= tl < 240 then tlint = 220;
else if 240<= tl < 260 then tlint = 240;
else if 260<= tl < 280 then tlint = 260;
else if 280<= tl < 300 then tlint = 280;
else if 300<= tl < 320 then tlint = 300;
else if 320<= tl < 340 then tlint = 320;
else if 340<= tl < 360 then tlint = 340;
```

(Box continues)

Box 5.1 *(continued)*

```
else if 360<= tl < 380 then tlint = 360;
else if 380<= tl < 400 then tlint = 380;
else if 400<= tl < 420 then tlint = 400;
else if 420<= tl < 440 then tlint = 420;
else if 440<= tl < 460 then tlint = 440;
else if 460<= tl < 480 then tlint = 460;
else if 480<= tl < 500 then tlint = 480;
else if 500<= tl < 520 then tlint = 500;
else if 520<= tl < 540 then tlint = 520;

datalines;
336
336
336
395
395
395
395
386
386
386
386
416
416
416
416
452
452
(input remaining data)
;

proc means mean;
class tlint;
run;
```

Program Output

The above program will produce a summary table of the number of fish per length interval.

Table Output from the means procedure. Summary statistics for the variable length (tl) for each length intervals (tlint).

tlint	*N*	Mean	SD	Minimum	Maximum
300	3	318.0000000	0	318.0000000	318.0000000
320	6	335.5000000	0.5477226	335.0000000	336.0000000
340	12	350.7500000	6.3263518	344.0000000	359.0000000
360	12	372.2500000	7.8985039	360.0000000	379.0000000
380	30	392.3333333	6.1941760	382.0000000	399.0000000
400	28	413.0000000	4.4886689	405.0000000	418.0000000
420	48	432.5625000	5.5039879	420.0000000	438.0000000
440	51	449.7450980	4.5380310	443.0000000	459.0000000
460	61	466.9836066	4.1412229	462.0000000	474.0000000
480	83	492.4216867	6.2627830	480.0000000	499.0000000
500	29	512.2068966	2.0244807	510.0000000	514.0000000
520	36	528.4444444	1.6978044	526.0000000	530.0000000

Program

By using the information from this table as a summary data set, we create a data set for each age-group and then merge the data sets to create an aged sample.

```
data spotfreq;
input tlint num;
datalines;
300              3
350              6
340             12
360             12
380             30
400             28
420             48
440             51
460             61
480             83
500             29
520            36;
run;

data spotage1;
set spotfreq;
if tlint = 90 then age = 1;
else if tlint = 100 then age = 1;
else if tlint = 120 then age = 1;
if tlint = 90 then nage = (num* 100)/100;
else if tlint = 100 then nage = (num* 100)/100;
else if tlint = 120 then nage = (num* 100)/100;
if nage = . then delete;
run;

data spotage2;
set spotfreq;
if 240 then age = 2;
if 240 then nage = (num* 100)/100;
if nage = . then delete;
run;

data spotage3;
set spotfreq;
if tlint = 300 then age = 3;
else if tlint = 320 then age = 3;
else if tlint = 340 then age = 3;
else if tlint = 360 then age = 3;
else if tlint = 380 then age = 1;
if tlint = 300 then nage = (num* 100)/100;
else if tlint = 320 then nage = (num* 100)/100;
else if tlint = 340 then nage = (num* 100)/100;
else if tlint = 360 then nage = (num* 100)/100;
else if tlint = 380 then nage = (num* 33.33)/100;
if nage = . then delete;
run;
```

(Box continues)

Box 5.1 *(continued)*

```
   data spotage4;
   set spotfreq;
   if tlint = 380 then age = 4;
   else if tlint = 400 then age = 4;
   else if tlint = 420 then age = 4;
   if tlint = 380 then nage = (num* 66.67)/100;
   else if tlint = 400 then nage = (num* 100)/100;
   else if tlint = 420 then nage = (num* 33.33)/100;
   if nage = . then delete;
   run;

   data spotage5;
   set spotfreq;
   if tlint = 420 then age = 5;
   else if tlint = 440 then age = 5;
   if tlint = 420 then nage = (num* 66.67)/100;
   else if tlint = 440 then nage = (num* 28.57)/100;
   if nage = . then delete;
   run;

   data spotage6;
   set spotfreq;
   if tlint = 440 then age = 6;
   if tlint = 440 then nage = (num* 35.71)/100;
   if nage = . then delete;
   run;

   data spotage7;
   set spotfreq;
   if tlint = 460 then age = 7;
   if tlint = 460 then nage = (num* 50.00)/100;
   if nage = . then delete;
   run;

   data spotage8;
   set spotfreq;
   if tlint = 440 then age = 8;
   else if tlint = 480 then age = 8;
   if tlint = 440 then nage = (num* 21.43)/100;
   else if tlint = 480 then nage = (num* 33.33)/100;
   if nage = . then delete;
   run;

   data spotage9;
   set spotfreq;
   if tlint = 440 then age = 9;
   else if tlint = 460 then age = 9;
   else if tlint = 480 then age = 9;
   if tlint = 440 then nage = (num* 14.29)/100;
   else if tlint = 460 then nage = (num* 50.00)/100;
   else if tlint = 480 then nage = (num* 66.67)/100;
   if nage = . then delete;
   run;

   data spotage;
   set spotage1 spotage2 spotage3 spotage4 spotage5 spotage6 spotage7 spotage8
spotage9;
   run;

   proc print;
   run;
```

Program Output

The resulting data set contains the number of fish in each age-group (nage) by length category.

Table Number of fish in each age-group (nage) by length category (tlint) for the larger sample.

tlint	Number	Age	nage
300	3	2	3.0000
350	6	2	6.0000
340	12	2	12.0000
360	12	2	12.0000
380	30	2	30.0000
400	28	2	28.0000
420	48	2	48.0000
440	51	2	51.0000
460	61	2	61.0000
480	83	2	83.0000
500	29	2	29.0000
520	36	2	36.0000
300	3	3	3.0000
340	12	3	12.0000
360	12	3	12.0000
380	30	1	9.9990
380	30	4	20.0010
400	28	4	28.0000
420	48	4	15.9984
420	48	5	32.0016
440	51	5	14.5707
440	51	6	18.2121
460	61	7	30.5000
440	51	8	10.9293
480	83	8	27.6639
440	51	9	7.2879
460	61	9	30.5000
480	83	9	55.3361

may optimize numbers but lose biomass because we have not allowed individuals to reproduce. Alternatively, if we harvest older fish, individual biomass may be maximized, but a large portion of the population will be lost to natural mortality. The interplay between growth and mortality is, therefore, critical in determining management strategies. Growth is also an important component in understanding the ecology of a species at both the individual and population level, as it is a convenient method for assessing the quality of a habitat and tracing life histories.

On an individual basis, change in length is proportional to change in weight. We can relate length and weight using the equation

$$W = aL^b, \tag{5.1}$$

where W is weight, L is length, and a and b are constants. This relationship can be expressed in linear form with the equation

$$\log_e W = a + b \log_e L . \tag{5.2}$$

When change in all three dimensions is similar across all sizes, we consider growth to be isometric. This results in the special case in which the exponent $b = 3$. In most species, body shape does not change with age; therefore, most species grow isometrically. In species for which individuals change shape with age either through metamorphosis, development of secondary sex characteristics, or senescence, growth is said to be allometric, and $b \neq 3$.

For a variety of reasons including ease, we often measure length rather than weight. One representation of growth can be obtained by simply comparing the change in modal lengths through time within a population when the modes are considered to represent distinct age-classes. Similarly, the progression of modes through time can be used to estimate growth (Figure 5.3). This method of growth determination assumes that the sample is drawn at random with respect to size and that growth across age-classes is similar through time. Variation in growth within and among years may result in biased estimates when different year-classes are compared.

There are several different methods to express growth numerically (Ricker 1975; Busacker et al. 1990). If growth is reported as the change in length or weight over a given time interval, then it is termed absolute growth and expressed as

$$\Delta L_{\text{absolute}} = L_2 - L_1 , \tag{5.3}$$

where $\Delta L_{\text{absolute}}$ is absolute growth, L_1 is initial length, and L_2 is final length. However, growth can also be expressed as a percent increase in length or weight relative to an initial value. This is referred to as relative growth and is generally expressed as

$$\Delta L_{\text{relative}} = \frac{L_2 - L_1}{L_1} 100 , \tag{5.4}$$

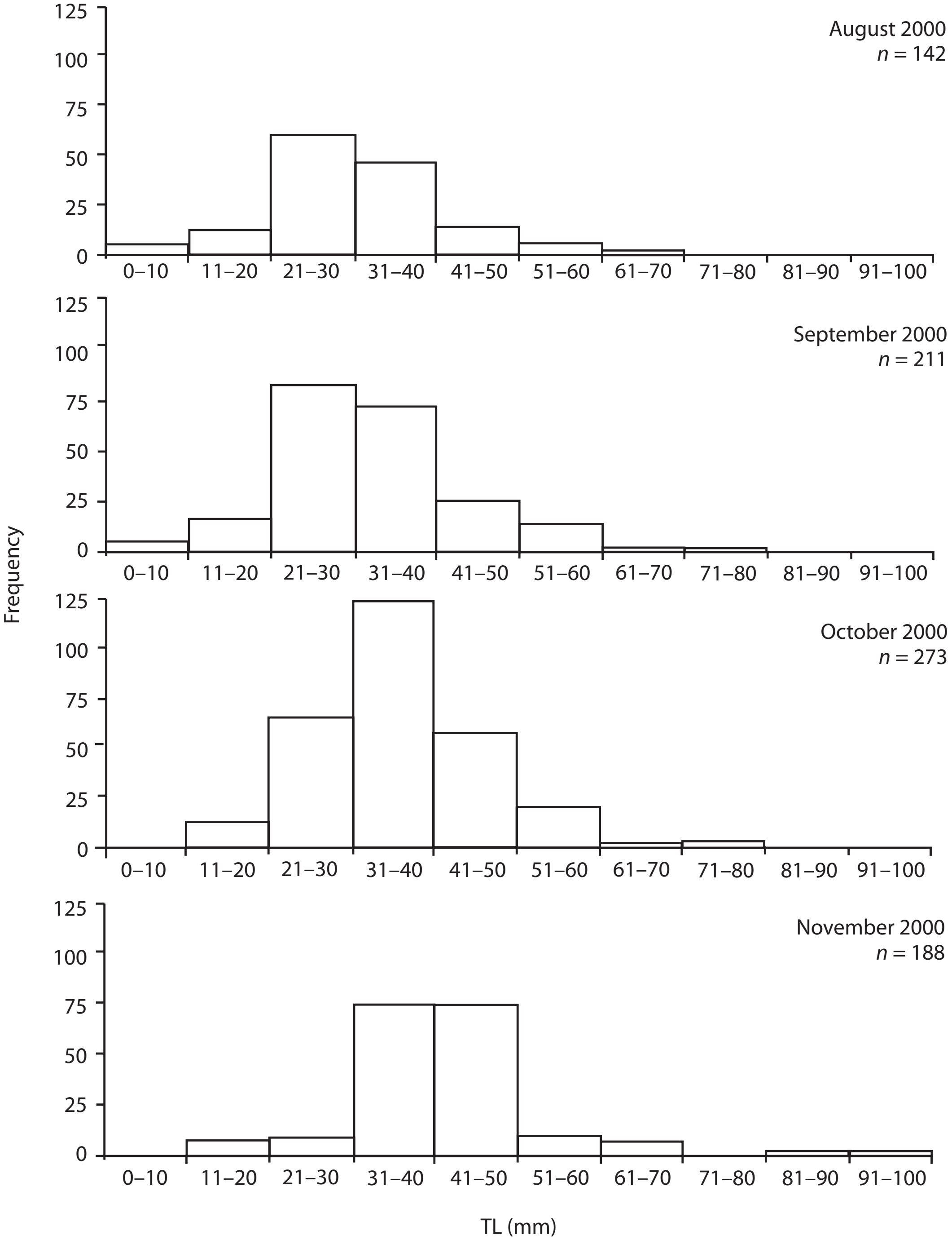

Figure 5.3 Length-frequency distributions of molly miller from August through November 2000 showing an increase in total length (TL) through time of age-0 fish represented in the samples.

where $\Delta L_{\text{relative}}$ is relative growth. Both absolute and relative growth also can be expressed as a rate in terms of growth per unit time:

$$G_{\text{absolute}} = \frac{L_2 - L_1}{t_2 - t_1}, \text{ and} \tag{5.5}$$

$$G_{\text{relative}} = \frac{L_2 - L_1}{L_1(t_2 - t_1)}, \tag{5.6}$$

where G is growth rate either absolute or relative, t_1 is initial time, t_2 is final time, and L_1 and L_2 are the corresponding lengths for those times. In the case that growth is exponential over a short period of time (<1 year) it is best reported as an instantaneous rate:

$$G = \frac{\log_e L_2 - \log_e L_1}{t_2 - t_1}. \tag{5.7}$$

These calculations of growth rates yield an estimate of growth that is appropriate over short time scales (days to months). Growth over longer time periods tends to deviate from these simple, linear, or exponential estimates and requires more complex models that will be discussed later.

5.3.1 Back-Calculation of Length from Calcified Structures

If we assume that the growth of calcified structures is proportional to overall fish growth, a simple ratio or direct proportion method can be used to back-calculate size at annulus formation (Box 5.2). If we know the length of the fish, the radius of the calcified structure, and the radius to each annulus, we can use the equation

$$\frac{L_i}{L_c} = \frac{S_i}{S_c}, \text{ or } L_i = \frac{S_i L_c}{S_c}, \tag{5.8}$$

where S_i is the radius at annulus formation, S_c is the overall radius, L_i is the length at annulus formation, and L_c is the fish length at capture (Box 5.2). Although this relationship generally holds true, fisheries scientists have noticed that it often results in an underestimation of length when scales are used. A tacit assumption of proportionality is that scales are formed early in development. For many species, this is not true. Scales may not form in some species until the individual reaches lengths of 5 cm or greater. Work done by Fraser (1916) and Lee (1920) suggested that a correction factor (a) be added to the equation to account for the delay in scale formation. The resulting equation,

Box 5.2 Determining Mean Back-Calculated Length at Age

In addition to providing estimates of age, hard parts are often used to back-calculate length at younger ages. To demonstrate how this is accomplished, we will be using a data set determined from scales and describing the age and growth of spotted sucker from the Savannah River. For each fish, our data set contains an identification number (ID), sex, total length at capture (L_c), year of capture (date), age, radius of ageing structure (scale) at capture (S_c), annulus *i* (inc), and scale radius at each annulus *i* (S_i) for each individual annulus.

Dahl–Lea Method

We start with the simple case in which the growth of the structure used for ageing is directly proportional to the growth of the fish. This method is generally referred to as the Dahl–Lea method (Dahl 1907; Lea 1910) and allows one to back-calculate length at age for individual fish. The formula is

$$L_i = L_c(S_i / S_c),$$

where L_i is back-calculated length at annulus *i*, L_c is length at capture, S_i is ageing-structure radius at annulus *i*, and S_c is ageing-structure radius at capture. Using the SAS code below, we can generate back-calculated total lengths (L_i) and calculate mean length at age for the spotted sucker population.

Program

```
data sucker;
input ID$ sex$ Lc date age Sc inc Si;
Li = LC * (Si/Sc);
cards;
07447              M    336    2004      3    16.3      1       5
07447              M    336    2004      3    16.3      2    12.9
07447              M    336    2004      3    16.3      3    16.3
35334              F    395    2004      4    18.4      1     4.8
35334              F    395    2004      4    18.4      2     9.9
35334              F    395    2004      4    18.4      3    16.5
35334              F    395    2004      4    18.4      4    18.4
44736              F    386    2004      4    18.6      1     4.9
44736              F    386    2004      4    18.6      2     8.5
44736              F    386    2004      4    18.6      3    13.6
44736              F    386    2004      4    18.6      4    18.6
(input remaining data)
;
run; quit;

proc means data=sucker mean stderr std;
title 'Mean back-calculated TL at age for spotted sucker';
class inc;
var Li;
run; quit;
```

(Box continues)

Box 5.2 *(continued)*

Program Output

The above SAS program will yield the following output for our spotted sucker data set.

Table Mean back-calculated total length (L_i) at age for spotted sucker generated the means procedure.

Annulus *i*	Number of observations	Back-calculated total length Mean	SE	SD
1	65	93.2168665	2.3905126	19.2729288
2	65	217.2709364	5.0262681	40.5230692
3	65	328.9349467	5.6120787	45.2460251
4	52	373.7611035	6.1277514	44.1878437
5	35	388.8813533	7.3027812	43.2038363
6	27	404.2197909	7.3382603	38.1307192
7	21	413.5260280	6.5852539	30.1774246
8	18	430.0907986	6.5060450	27.6028112
9	18	452.1169315	6.6510322	28.2179397
10	14	464.0779850	7.4847926	28.0055297
11	11	478.1245135	9.1952021	30.4970351
12	9	488.7881206	8.7617199	26.2851596
13	6	498.4247331	10.1487390	24.8592322
14	4	501.2899579	10.1750810	20.3501620
15	3	516.9213162	17.0469489	29.5261816
16	2	540.9583333	26.9583333	38.1248406
17	1	580.0000000		

Fraser–Lee Model

In some cases, structures such as scales may take some time to form after hatch or metamorphosis. Consequently, early length estimates are biased. The Fraser–Lee model (Fraser 1916; Lee 1920) accounts for this bias by including a biological intercept in the model. The model is

$$L_i = a + (L_c - a)(S_i / S_c).$$

The variable *a* is the intercept determined from the ageing-structure radius and fish length relationship and the other variables are previously defined.

Because we are using scales to back-calculate length at age, we will likely require a correction factor. Because we did not collect empirical data or find information in the literature regarding the length of scale formation in spotted sucker, then we must estimate this parameter by modeling the known relationship between ageing-structure radius and fish-length at capture from our spotted sucker data set. Even had we found this information in the literature, performing the below calculations is another good way to check one's data.

Program

```
proc glm data=sucker;
title ‘Estimate of biological intercept’;
model Li = Si;
run; quit;
```

We use regression analysis to determine the relationship between scale radius at age and back-calculated total length at age. In a larger data set, it may be possible to use L_c and S_c directly to estimate the Fraser–Lee correction factor. However, our spotted sucker data set does not have any individuals younger than age 3. Using L_c and S_c provides us with unrealistically large estimates.

Another important consideration is that units of measurement for L_i and S_i are the same for this calculation. Whereas this is not a concern during calculations of length at age because the units cancel, it will yield inaccurate estimates for the correction factor. In our spotted sucker data set, scales were magnified 24× and measured in centimeters. A conversion will be necessary as total length was measured in millimeters. Therefore, we will create a new variable containing the converted scale radii with the following statement.

```
data sucker_Si2;
set sucker;
Li = Lc * (Si/Sc);
Si2 = (Si*10)/24;
run; quit;

proc glm data=sucker_Si2;
title ‘Estimate of biological intercept’;
model Li = Si2;
run; quit;
```

This will convert scale radius from centimeters to millimeters and account for making the measurements under magnification. The program will now yield the following output.

Program Output

Table Estimate of biological intercept for the dependent variable mean back-calculated total length (L_i) based on the general linear model (GLM) procedure. The number of observations used and read was 416. Abbreviations are given for coefficient of variation (CV), mean square error (MSE), and sum of squares (SS).

General linear model

Source	*df*	Sum of squares	Mean square	*F*-value	*P* > *F*
Model	1	6486640.962	6486640.962	3672.42	<0.0001
Error	414	731253.767	1766.313		
Corrected total	415	7217894.729			
R^2	0.898689	Root MSE	42.02753		
CV	13.00363	Li mean	323.1985		

(Box continues)

Box 5.2 *(continued)*

Source	*df*	Type I SS	Mean square	*F*-value	$P > F$
Si2	1	6486640.962	6486640.962	3672.42	<0.0001

Source	*df*	Type III SS	Mean square	*F*-value	$P > F$
Si2	1	6486640.962	6486640.962	3672.42	<0.0001

Variable	Estimate	SE	*t*-value	$P > \|t\|$
Intercept	35.49138299	5.17548973	6.86	<0.0001
Si2	50.88336354	0.83965286	60.60	<0.0001

The intercept of this linear model will be an estimate of the Fraser–Lee correction factor. Therefore, we must be able to reject the null hypothesis that the intercept is not different from 0. If we cannot reject this null hypothesis, then a correction factor is not likely to be necessary. In the case of our spotted sucker data, a correction factor is necessary. Now, the correction factor a can be used to calculate mean back-calculated total length (L_i) at age with the Fraser–Lee correction.

Program

```
data sucker_a;
set sucker;
Li = Lc * (Si/Sc);
Si2 = (Si*10)/24;
a = 35.5;
Li_corrected = a + (Lc - a) * (Si/Sc);
run; quit;

proc means data=sucker_a mean stderr std;
title 'Corrected mean back-calculated TL at age for spotted sucker';
class inc;
var Li_corrected;
run; quit;
```

$$L_i = \frac{L_c - a}{S_c} S_i + a \,, \tag{5.9}$$

where a is the size of the individual at the time of scale formation, provides an unbiased estimate in length when scales are used and is referred to as the Fraser–Lee or intercept-corrected direct proportion model. While this formula is widely used, it may not be the most precise estimate of length at age. There can also be differences in the precision of back-calculation depending upon the structure,

Program Output

The above program produces the following output.

Table Corrected mean back-calculated total length (L_i) at age for spotted sucker generated by the means procedure.

Annulus i	Number of observations	Back-calculated total length		
		Mean	SE	SD
1	65	120.8801223	2.1454817	17.2974263
2	65	234.5165149	4.4996539	36.2773695
3	65	336.8015953	4.9458073	39.8743735
4	52	379.4639509	5.3958210	38.9098182
5	35	394.8724181	6.4986305	38.4464168
6	27	409.7792454	6.5739649	34.1593235
7	21	419.0105377	5.9427822	27.2332491
8	18	434.8327817	5.9630989	25.2992861
9	18	455.2899399	6.1182144	25.9573855
10	14	466.9561266	7.0110838	26.2330736
11	11	480.5614840	8.7472611	29.0113831
12	9	490.6474731	8.3865848	25.1597543
13	6	499.9279199	9.9833260	24.4540545
14	4	502.6128845	10.6974006	21.3948012
15	3	517.8177039	17.4957374	30.3035062
16	2	541.3281250	27.3281250	38.6478050
17	1	580.0000000		

This method is very useful when sample sizes are small and additional growth information is needed. It can also be used to develop data to test for size-selective mortality (or Lee's phenomenon), a common occurrence in commercial fisheries. Growth histories from specific year-classes can be compared or data can be converted to year-specific growth to compare inter-annual variations.

necessitating careful selection of the model used (Campana 1990; Klumb et al. 2001). The reader is referred to Francis (1990) for a review of alternative methods. Once calculated, size-at-age information between sexes and populations can be compared (Box 5.3).

Often times, back-calculated lengths fall below the mean of observed lengths from the same population. This apparent change in growth over time was first described by Lee in 1920 and is discussed by Ricker (1975) and others to a greater extent. Interestingly, Lee's phenomenon can be related to (1) failure to use the

Box 5.3 Assessing Differences in Length at Age between Groups

Now that we have corrected back-calculated length at age, we can test for differences between groups. For example, we commonly want to test for a sex effect on length at age. We can use our previous example to evaluate differences between sexes by means of an analysis of covariance (ANCOVA) approach. We start with our spotted sucker data set containing fish identification number (ID), sex, total length at capture (L_c), year of capture (date), age, radius of aging structure (scale) at capture (S_c), annulus increment number (inc), and radius of aging structure at inc (S_i). We calculate the length at each increment using a direct proportion method and incorporate the Fraser–Lee correction factor calculated in Box 5.2. Given that growth has a curvilinear component, we create a dummy variable (incsq) to be incorporated into the model.

Program

```
data sucker;
input ID$ sex$ Lc date age Sc inc Si;
a = 35.5;
Li_corrected = a + (Lc - a) * (Si/Sc);
incsq = inc*inc;
cards;
07447           M    336   2004     3   16.3     1      5
07447           M    336   2004     3   16.3     2   12.9
07447           M    336   2004     3   16.3     3   16.3
35334           F    395   2004     4   18.4     1    4.8
35334           F    395   2004     4   18.4     2    9.9
35334           F    395   2004     4   18.4     3   16.5
35334           F    395   2004     4   18.4     4   18.4
44736           F    386   2004     4   18.6     1    4.9
44736           F    386   2004     4   18.6     2    8.5
44736           F    386   2004     4   18.6     3   13.6
44736           F    386   2004     4   18.6     4   18.6
(input remaining data)
;
run; quit;
```

Once the data are entered we can run the GLM procedure to test the null hypothesis that there is no difference between males and females in the slope of the length at age regressions.

```
proc glm data=sucker;
title ‘Testing for equal slopes between males and females’;
class sex;
model Li_corrected= sex inc incsq sex*inc sex*incsq;
run; quit;
```

This program will yield the following output.

Program Output

Table Test of the assumption of equal slopes for male and female spotted suckers (ANCOVA) by means of the GLM procedure with Li-corrected (back-calculated total length, L_i, with the Fraser–Lee correction factor) as the dependent variable.

General linear model

Source	*df*	Sum of squares	Mean square	*F*-value	*P* > *F*
Model	5	5486250.292	1097250.058	589.40	<0.0001
Error	410	763266.344	1861.625		
Corrected total	415	6249516.636			
R^2	0.877868	Root MSE	43.14656		
CV	12.92255	Li-corrected mean	333.8859		

Source	*df*	Type I SS	Mean square	*F*-value	*P* > *F*
Sex	1	116871.182	116871.182	62.78	<0.0001
Inc	1	4286871.155	4286871.155	2302.76	<0.0001
Incsq	1	937786.528	937786.528	503.75	<0.0001
Inc*sex	1	9742.781	9742.781	5.23	0.0227
Incsq*sex	1	134978.646	134978.646	72.51	<0.0001

Source	*df*	Type III SS	Mean square	*F*-value	*P* > *F*
Sex	1	49896.978	49896.978	26.80	<0.0001
Inc	1	1974734.921	1974734.921	1060.76	<0.0001
Incsq	1	688068.591	688068.591	369.61	<0.0001
Inc*sex	1	143885.275	143885.275	77.29	<0.0001
Incsq*sex	1	134978.646	134978.646	72.51	<0.0001

The value of interest here is the *P*-value for the interaction terms inc*sex and incsq*sex. This tests the null hypothesis that the slopes are equal between males and females. In this case, it appears that males and females have different slopes and thus grow at different rates. We would use this information to justify modeling the growth of the two sexes separately.

Similarly, differences in growth rates between populations or other treatment variables can be evaluated by placing a population or treatment identifier in the data set and substituting it for sex in the analysis.

corrected body–scale relationship, (2) a bias resulting from size-selective sampling or harvest, or (3) variation in mortality rates as a function of growth. Size selectivity may be the most common bias, as fish tend to be sampled or harvested by size-selective gear rather than by age-selective gear, so the fastest-growing individuals are sampled or harvested first. Consequently, individuals that live the longest tend to be the slowest-growing individuals in the population, resulting in smaller back-calculated sizes at younger ages.

5.3.2 Growth in Weight

Theoretically, in an unlimited environment growth is exponential and can be modeled using the equation

$$w_t = w_0 e^{gt}, \tag{5.10}$$

where w_t is weight at time t, w_0 is initial weight, e is the base of the natural logarithm, and g is a growth coefficient. Although this equation could be used to estimate population growth as well as individual growth, it is seldom applicable for either over long periods. This model assumes no limitations on growth, and this is rarely the case. The model is useful, however, to estimate production of growth within a single growing season or early in development. As previously mentioned, growth in weight is not used as commonly as growth in length. However, weight can be substituted for length in the growth models presented below and will maintain the same form. Coefficients estimated for the resulting equations, obviously, will be different.

5.3.3 Growth in Length

The weight model presented above is not useful to represent growth in length. Early in life, length and weight both increase very rapidly. However, as fish age, small changes in length can result in large changes in weight (equation [5.1]). Although fish are thought to exhibit indeterminate growth, length often approaches an asymptote. A number of models have been used to model length, but the model developed by von Bertalanffy (1938) generally fits fish length data well. It has become a standard among fisheries scientists. The model is represented as

$$l_t = L_\infty (1 - e^{-K(t - t_0)}), \tag{5.11}$$

where l_t is length at time t, L_∞ is the asymptotic length, K is a growth coefficient, and t_0 is a time coefficient at which length would theoretically be 0.

Unlike the simple exponential model, obtaining estimates of L_∞, t_0, and K requires an iterative solution. Most statistical and graphics software packages now contain programs that calculate maximum likelihood estimates (see Chapter 8 for explanation of maximum likelihood) of nonlinear regression parameters such as those in the von Bertalanffy growth equation. Historically, these parameters were estimated using a graphical solution. Walford (1946) observed that when length at age $t + 1$ was plotted against length at age t, the slope of the line was equal to e^{-K}, where K is the same growth coefficient as in the von Bertalanffy model (Figure 5.4). If a line with a slope of 1 (i.e., a 45° line) is drawn through the

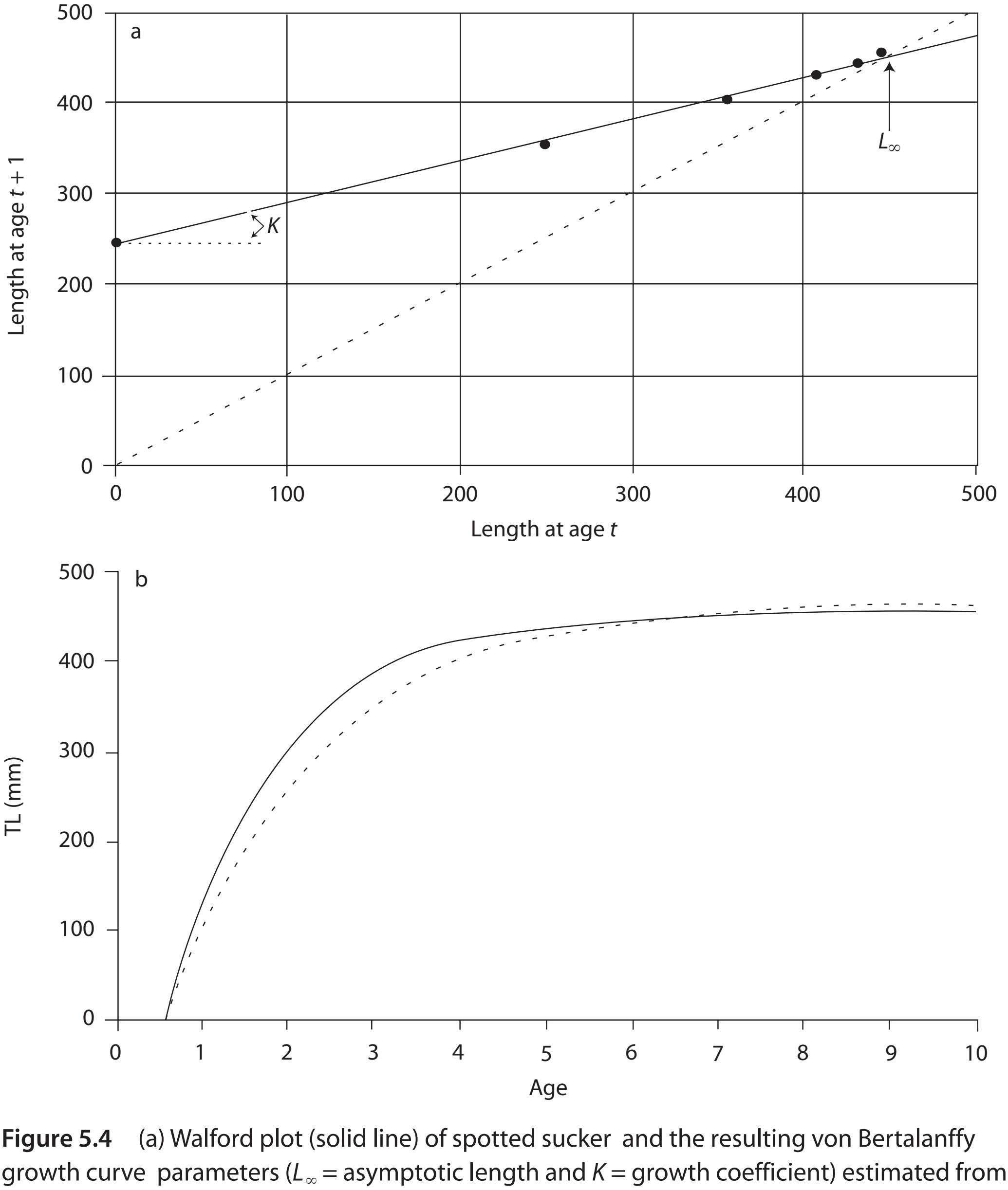

Figure 5.4 (a) Walford plot (solid line) of spotted sucker and the resulting von Bertalanffy growth curve parameters (L_∞ = asymptotic length and K = growth coefficient) estimated from the Walford plot. Dashed line with a slope of 1 is drawn through the origin to provide an estimate of L_∞ at its intersection with the Walford plot. (b) The von Bertalanffy growth curve generated from a Walford plot (solid line) is compared with one generated using iterative procedures illustrated in Box 5.4 (dotted line).

origin, the intersection of the two lines indicates the size at which change in length is theoretically 0 and provides an estimate of L_∞. The parameter t_0 may be estimated by substituting known values for length and age, and the estimates of K and L_∞ derived from the Walford plot may be placed into the von Bertalanffy equation. Although this method produces reasonable estimates, mathematical solutions are more precise (Box 5.4).

The von Bertalanffy model often works well across the entire life history of a fish, meaning it can be applied to a single sample integrated across year-classes or can be developed for individual year-classes. Data also may be stratified by sex or geographic area, modeled independently, and compared using analysis of covariance (ANCOVA) (Box 5.5).

In some mark–recapture studies, we may know size at capture and recapture and time at large, but we may not know age. Fabens (1965) proposed a modification of the von Bertalanffy equation to model growth under this unique circumstance. This model is useful for work on relatively rare or endangered species for which collection of materials on which to base age is impractical or on marine reptiles and other organisms for which a method to determine age has not been identified. The Fabens model is

$$R_{\hat{i}} = M_i + (L_\infty - M_i)(1 - e^{-K\Delta t_i}) \tag{5.12}$$

where $R_{\hat{i}}$ is the length at recapture of the ith individual, M_i is the length at marking (or first capture) of the ith individual, L_∞ and K are parameters of the von Bertalanffy growth equation, and Δt_i is the time at large. Model parameters can be estimated using a maximum likelihood estimator, or nonlinear fit program, as with the von Bertalanffy model (Box 5.6). Note that this method does not provide and estimate for the time at zero length, t_0, which must be estimated through some other method, by using empirical early growth data, or by substituting known age and length values and parameter estimates into the equation as above.

Although the von Bertalanffy model has become the method of choice for modeling growth in length, other growth models may be more appropriate depending upon the species of interest and the specific circumstances (Ricker 1975). Other commonly applied growth models are included below.

Richards (1959):

$$l_t = D + (L_\infty - D)(1 + He^{-k(t-t_0)})^{-1/H}; \tag{5.13}$$

Gompertz (1825):

$$l_t = L_\infty e^{-ke^{-gt}} \tag{5.14}$$

and the logistic (Verhulst 1838, 1845):

$$l_t = \frac{L_\infty A}{A + (L_\infty - A)e^{-kt}}\,. \tag{5.15}$$

Box 5.4 Fitting a von Bertalanffy Growth Curve

The length-at-age data on spotted sucker illustrated in Figure 5.4 and Box 5.2 will be used here. For each individual in the data set, we have entered total length (tl) and age. Therefore, each fish represents a single degree of freedom in the analysis. To minimize bias, similar numbers of fish from each year-class should be included in the model. If older or younger age-classes are not well represented in the analysis, confidence limits at the extremes of the curve may expand dramatically or the model will fail to converge. Parameters for the growth curve can now be estimated iteratively using a nonlinear regression approach with the following SAS program.

Program

```
data spotage;
input tl age;
cards;
388              4
418              4
438              4
428              5
539             10
432              4
444              7
421              4
438              4
(input remaining data)
;
run;

proc nlin data = spotage;
model tl = linf*(1-EXP(-k*(age-t0)));
parameters linf = 1000 k = 0.1 t0 = 0.1;
output out = explen p = extl;
run;
```

The model statement expresses the von Bertalanffy model in SAS format. Other models may be substituted. Here are some examples of common growth models expressed in SAS format.

Richards:

model Lt = D+(Lmax–D)*(1+ He**(–k*(t–t0)))**(–1/H) ;

Gompertz:

model Lt = Lmax*exp(–k*exp(–g*t)) ; and

logistic:

model Lt = (Lmax*A)/(A+(Lmax –A)*exp(–k*t) .

The parameters statement provides initial parameter estimates. These values can be estimated from traditional methods such as the Walford plot or by using reasonable values obtained from the literature or from similar species. For example, the asymptotic length, L_∞ (linf), can be estimated as the average length of the oldest age-group. The output statement creates a data set with expected (predicted) values for length at each age, which can then be plotted or analyzed further.

(Box continues)

Box 5.4 *(continued)*

Program Output

The output consists of the results of the iterations, the associated sums of squares, a regression analysis containing the statistical significance of the model, the parameter estimates and associated confidence limits, and a correlation matrix for the parameter estimates.

Table Nonlinear regression analysis (NLIN procedure) of the total length (tl) of spotted sucker and estimates of the von Bertalanffy growth model parameters: asymptotic length (linf), growth coefficient (k), and time coefficient (t0) where length would theoretically be 0. Iterations based on the based on the Gauss-Newton method; convergence criterion was met. The acronyms PPC (prospective parameter change measure) and RPC (retrospective parameter change measure) refer to how well the model met its convergence criteria; the reader is advised to see SAS for details of definitions and procedures.

		Iterative phase		
Iteration	linf	k	t0	SS
0	1000.0	0.1000	0.1000	469817
1	776.8	0.1027	–1.5355	326499
2	579.8	0.1096	–4.5622	302753
3	549.8	0.1226	–6.6931	44520.3
4	542.7	0.1382	–6.3290	30574.0
5	535.5	0.1505	–5.8205	30269.8
6	530.3	0.1599	–5.4872	30190.3
7	526.6	0.1670	–5.2450	30171.2
8	523.9	0.1725	–5.0682	30165.6
9	522.0	0.1766	–4.9377	30163.7
10	520.5	0.1798	–4.8406	30163.0
11	519.5	0.1822	–4.7680	30162.6
12	518.7	0.1841	–4.7134	30162.5
13	518.1	0.1855	–4.6723	30162.4
14	517.6	0.1865	–4.6412	30162.3
15	517.3	0.1874	–4.6177	30162.3
16	517.1	0.1880	–4.5999	30162.3
17	516.9	0.1885	–4.5864	30162.3
18	516.7	0.1888	–4.5761	30162.3
19	516.6	0.1891	–4.5683	30162.3
20	516.5	0.1893	–4.5624	30162.3
21	516.5	0.1894	–4.5579	30162.3
22	516.4	0.1896	–4.5544	30162.3
23	516.4	0.1897	–4.5518	30162.3
24	516.3	0.1897	–4.5498	30162.3
25	516.3	0.1898	–4.5483	30162.3
26	516.3	0.1898	–4.5472	30162.3
27	516.3	0.1899	–4.5463	30162.3
28	516.3	0.1899	–4.5457	30162.3
29	516.3	0.1899	–4.5451	30162.3
30	516.3	0.1899	–4.5448	30162.3

Estimation summary	
Method	Gauss-Newton
Iterations	30
Subiterations	1
Average subiterations	0.033333
R	9.028×10^{-6}
PPC(t0)	0.000065
RPC(t0)	0.000085
Object	2.48×10^{-10}
Objective	30162.26
Observations read	95
Observations used	95
Observations missing	0

Regression analysis

Source	*df*	SS	Mean square	Approximate *F*-value	*P* > *F*
Model	2	38328.9	19164.4	58.45	<0.0001
Error	92	30162.3	327.9		
Corrected total	94	68491.2			

Parameter estimates

Parameter	Estimate	Approximate SE	Approximate 95% confidence limits	
linf	516.3	48.8409	419.3	613.3
k	0.1899	0.1194	–0.0473	0.4271
t0	–4.5448	3.4102	–11.3178	2.2283

Approximate correlation matrix

	linf	k	t0
linf	1.0000000	–0.9872305	–0.9616729
k	–0.9872305	1.0000000	0.9927332
t0	–0.9616729	0.9927332	1.0000000

The model indicates that growth of spotted sucker can be estimated using the equation

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

where

$$l_t = 516.3[1 - e^{-0.1899(t + 4.5448)}].$$

Box 5.5 Identifying Environmental Effects on Growth

Often, fisheries scientists are interested in evaluating the effects of some management strategy on growth. Length limits, fertilization, and water level manipulations, for example, may all produce time-specific effects. We cannot simply compare pre-treatment length with post-treatment length. Weisburg and Frie (1987) demonstrated a method of isolating annular growth effects by calculating growth increment and assigning this not only to a specific age but to a specific year. We will use data collected from a population of spotted sucker to test the effects of an extended drought on growth. The drought occurred from 2000 through 2003. Rather than test for the effect of a specific individual year, we group years together by rainfall. Although it would have improved the statistical performance of the model, note that it is not necessary to sample pre-treatment fish length as long as the post-treatment sample contains a representative sample of fish that were alive during the pre-treatment period. In this case, year-classes from normal and drought (dry) years were present in the sample.

Program

```
data spotted_weather;
input id $ sex $ tl w year age bcyear bcage bctl growth;
if bcyear < 2000 then group = “normal”;
else if bcyear >1999 then group = “dry”;
cards;
04111       F        486     710    2004       9    1995       1      76      76
04111       F        486     710    2004       9    1996       2     181     104
04111       F        486     710    2004       9    1997       3     275      94
(input remaining data)
;
run;

proc glm;
class bcage group;
model growth = bcage group bcage*group;
run;
```

The model statement evaluates annual length increment (growth) as a function of weather conditions (group), age (bcage), and the interaction between age and weather (bcage*group). In cases in which the interaction is significant, results can be interpreted that the treatment affected age-classes differently. For example, we could conclude that during a drought, younger fish might grow slower because of poor habitat but that older fish would grow faster due to a concentration of prey caused by decreased water levels.

Program Output

The output consists of a standard *F* table including model degrees of freedom, the associated model and partial sums of squares, model and partial *F*-values, and significance levels.

Table Evaluation of annual length increment (growth) as a function of weather conditions (group) and age (bcage).

General linear model					
Source	*df*	SS	Mean square	*F*-value	$P > F$
Model	13	341678.9817	26282.9986	60.18	<0.0001
Error	230	100453.0305	436.7523		
Corrected total	243	442132.0123			
R^2	0.772799	Root MSE	20.89862		
CV	23.71861	Growth mean	88.11066		

Source	*df*	Type I SS	Mean square	*F*-value	*P* > *F*
bcage	8	333756.1313	41719.5164	95.52	<0.0001
group	1	6500.5460	6500.5460	14.88	0.0001
bcage*group	4	1422.3044	355.5761	0.81	0.5173

Source	*df*	Type III SS	Mean square	*F*-value	*P* > *F*
bcage	8	210629.6102	26328.7013	60.28	<0.0001
group	1	3025.6062	3025.6062	6.93	0.0091
bcage*group	4	1422.3044	355.5761	0.81	0.5173

The model indicates that both age (bcage) and weather (group) accounted for significant proportions of variation in growth, but that no significant interaction between age and weather was detected. Therefore, we can reduce the model and further evaluate the effects of age and year on growth. Using the same data, we now run the following model.

Program

```
proc glm;
class bcage group;
model growth = bcage group;
means group;
lsmeans group / adjust=dunnett pdiff=control(‘dry’);
run;
```

The reduced model drops the interaction term. We then calculate mean growth for each category of rainfall. The lsmeans statement calculates least-squares means for normal and drought levels and then compares mean values using a *t*-test. The following output is produced.

Program Output

Table Comparison of growth of spotted suckers in dry and normal years. The number of observations read and used was 244. The least-squares means (lsmeans) comparisons are made with the Dunnett–Hsu adjustment for multiple comparisons. The null hypothesis being tested LSMean1 = LSMean2 compares mean growth in dry and normal conditions.

Class level information

Class	Levels	Values
bcage	9	1 2 3 4 5 6 7 8 9
group	2	dry normal

(Box continues)

Box 5.5 *(continued)*

The GLM procedures

Source	*df*	SS	Mean square	*F*-value	$P > F$
Model	9	340256.6774	37806.2975	86.84	<0.0001
Error	234	101875.3349	435.3647		
Corrected total	243	442132.0123			
R^2	0.769582	Root MSE	20.86539		
CV	23.68090	Growth mean	88.11066		

Source	*df*	Type I SS	Mean square	*F*-value	$P > F$
bcage	8	333756.1313	41719.5164	95.83	<0.0001
group	1	6500.5460	6500.5460	14.93	0.0001

Source	*df*	Type III SS	Mean square	*F*-value	$P > F$
bcage	8	340056.3180	42507.0398	97.64	<0.0001
group	1	6500.5460	6500.5460	14.93	0.0001

Group statistics

Level of group	*N*	Growth mean	Growth SD
Dry	195	87.6564103	45.5918683
Normal	49	89.9183673	28.3870839

Least-squares means

Growth	Group lsmean	$P > \|t\|$
Dry	60.7771191	0.0001
Normal	47.1788748	

The model indicates that growth of spotted suckers was higher during drought conditions than during normal conditions. In this case, there were only two groups and the results of the pairwise *t*-test are the same as for the general model. However, the same procedure could be used when more than two groups are present.

Box 5.6 Estimating Growth from Mark and Recapture Data

In this example, data on the carapace length of loggerhead turtles at mark and at recapture will be used to fit a von Bertalanffy growth curve by means of the Fabens (1965) method. For each individual in the data set, time at large (days) has been calculated from the mark and recapture dates. Carapace length at mark (clmark) and at recapture (clrecap) and time at large (timeoutd) has been entered for each individual. To calculate the von Bertalanffy growth parameters in a standard form, time at large has been converted from days to years (timeouty). Each individual, therefore, represents a single degree of freedom in the analysis. If older and younger age-classes are not well represented in the analysis, or if time at large is long with respect to the expected age of the animal, convergence criteria for parameter estimation may not be met. Parameters for the growth curve can now be estimated iteratively using a nonlinear regression approach with the following SAS program.

Program

```
data turlen;
input markd $ clmark recapd $ clrecap timeoutd;
timeouty = timeoutd/365;

cards;
6/28/00          70.3 6/24/03   76.0    1091
7/20/00          60.5 7/15/03   64.7    1090
8/3/00           65.6 7/18/02   67.9     714
8/3/00           61.2 6/25/03   65.2    1056
7/9/01           76.9 6/24/03   79.1     715
7/12/01          64.4  6/9/03   67.5     697
7/18/01          97.4 6/17/02   97.9     335
3/30/98          60.9 6/21/02   67.7    1544
6/27/00          62.5 6/19/03   69.1    1087
5/12/99          67.0 7/12/00   69.5     427
6/18/89          41.0 9/21/91   52.0    1187
8/28/91          60.412/24/94   70.5    1945
7/14/86          19.3 8/28/91   42.0    1869
6/29/90          40.5  2/6/93   49.8     890
5/10/92          28.0 6/23/96   48.0    1503
6/30/92          26.011/15/95   42.0    1230
8/8/96           64.0 6/19/98   69.6     680
;
run;

proc nlin data = turlen;
model clrecap = clmark + (linf - clmark)*(1 - exp(-K*timeouty));
parms linf = 100 k = 0.1;
output out = pturlen p = pclrecap;
run;
```

The model statement expresses the von Bertalanffy model in SAS format without the usual t_0 parameter. The parameter t_0 can be estimated independently or by using a known-age individual to “anchor” the growth curve once L_∞ (linf) and K (k) have been estimated. As with our initial nonlinear fit exercise, the Fabens (1965) approach can be used to estimate parameters of other growth models.

(Box continues)

Box 5.6 *(continued)*

Again, the parameters statement provides initial parameter estimates, and the output statement creates a data set with expected (predicted) values for carapace length at recapture, which can then be plotted or analyzed further.

Program Output

The output consists of the results of the iterations and the associated sums of squares, a regression analysis containing the statistical significance of the model, parameter estimates and associated confidence limits, and a correlation matrix for the parameter estimates.

Table Nonlinear regression analysis (NLIN) of loggerhead turtle carapace length at recapture (clrecap). Estimates of growth model parameters L_∞ (linf) and K (k) are produced; convergence criterion was met. An intercept was not specified for the regression model.

Iterative phase			
Iteration	linf	k	SS
0	100.0	0.1000	375.4
1	89.5614	0.0839	30.3416
2	87.4962	0.0857	28.9656
3	88.0507	0.0847	28.9197
4	88.0477	0.0845	28.9169
5	88.0490	0.0845	28.9169
6	88.0481	0.0845	28.9169

Estimation summary	
Method	DUD
Iterations	6
Object	4.114×10^{-9}
Objective	28.91686
Observations read	17
Observations used	17
Observations missing	0

In these models, l_t is the size at time t, L_∞ is the asymptotic length, t_0 is the time at size 0, k and g are generalized growth parameters that vary slightly in definition between models, and A, D, and H are position parameters used to constrain the inflection point. The logistic model differs from the von Bertalanffy, Richards, and Gompertz models in that it is symmetrical in relation to the inflection point. These models are not commonly employed in fisheries but are frequently used for other organisms.

Regression model

Source	*df*	SS	Mean square	Approximate *F*-value	*P* > *F*
Regression	2	74210.9	37105.4	19247.7	<0.0001
Residual	15	28.9169	1.9278		
Uncorrected total	17	74239.8			
Corrected total	16	3257.3			

Parameter estimates

Parameter	Estimate	Approximate SE	Approximate 95% confidence limits	
linf	88.0481	3.5192	80.5471	95.5491
k	0.0845	0.00820	0.0671	0.1020

Approximate correlation matrix

	linf	k
linf	1.0000000	–0.9079249
k	–0.9079249	1.0000000

The model indicates that growth (as carapace length, *Cl*) of loggerhead turtle can be estimated using the equation

$$Cl_t = L_\infty(1 - e^{Kt}),$$

where

$$Cl_t = 88.0481(1 - e^{-0.0845t}).$$

The model assumes $t_0 = 0$. If t_0 can be estimated independently, then the model can be adjusted accordingly.

5.4 SUMMARY

In this chapter, we learned about the unique properties of fish calcified structures to record growth history and the importance of validating the interpretation of these structures. We learned that unbiased age determination is the backbone of modern stock assessment. Because of the close relationship between age and length, ages determined from a subsample can be used to estimate the age distribution of the population. If we know age and size, we can determine growth and compare growth attributes between populations. If our age data are frequent relative to the age of the fish, we can model the change in size through time using nonlinear models such as the model proposed by von Bertalanffy (1938). We can also compare current growth with historic or back-calculated growth to evaluate size-selective processes in fisheries. Age and growth data are a critical component in the effective management of fisheries resources. While age and growth analyses are generally straightforward, collection and interpretation requires skill and experience. The application of age and growth data to recruitment, mortality, and other population models can be expensive and time consuming but are critical to the conclusions drawn from these studies. All attempts should be made to incorporate them whenever possible. One of the most important recent advances in the field of age and growth has been the detection of daily increments in otoliths. This discovery has allowed fisheries scientists to apply analytical techniques to age-0 fish that were previously reserved for adult fish. Consequently, we now have a better ability to evaluate factors affecting recruitment and year-class strength formation.

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