Chapter 15

Age and Growth

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15.1 INTRODUCTION

The phrase "age and growth" is common in fisheries science and captures two related, but different, concepts. Age refers to a quantitative description of how long an organism has been alive. Growth represents a change in size (e.g., length or weight), typically as a function of time. Age and growth can be measured across a variety of temporal scales, from hours and days to months and years. Although age and growth data are often presented and discussed together, each component provides unique and valuable information on individuals and populations.

Growth, recruitment, and mortality are the primary functions that regulate fish population dynamics and thereby influence the ecology and management of fishes (Ricker 1975). Age and growth data can provide direct and indirect information on each of these functions. Consequently, collecting accurate information should be a high priority for all fisheries scientists because age and growth information is critical to almost every aspect of fisheries science.

Estimation of age provides valuable insight regarding the characteristics of individual fish (e.g., age at maturity) as well as information on the age structure of the entire population. Age structure data have a number of important uses, such as estimating mortality rates and providing information on recruitment dynamics (Hsieh et al. 2006; Cassoff et al. 2007). Growth information is important because it provides an integrated evaluation of environmental conditions (e.g., prey availability, thermal conditions, and habitat availability) and genetic factors. Growth also has direct and indirect effects on recruitment dynamics, trophic interactions, and mortality through its effects on age at maturity, size structure of both predator and prey populations, and the susceptibility of fish to environmental alterations and harvest (Birkeland and Dayton 2005; Winemiller 2005; Rowell et al. 2008).

Although age data and growth data each individually provide important information on individuals and populations, their greatest value is obtained when they are combined. When combined, age and growth information may identify potential problems (e.g., recruitment limitations or overfishing; Beamish et al. 2006) or provide feedback on the effectiveness of management practices (e.g., harvest regulations or habitat or prey manipulations). In addition to providing a unique assessment of fish populations, age and growth information can supplement other studies, such as those focusing on movement patterns and habitat use, population densities, or food habits (Buktenica et al. 2007). As such, determining the age and growth of fishes has been and will continue to be one of the most important activities conducted by fisheries professionals (Hilborn and Walters 1992; Jackson 2007).

The purpose of this chapter is to provide an overview of the most common and widely accepted techniques used to obtain information on age and growth of fish. We first describe approaches and techniques used to quantify fish age, followed by a discussion of summarizing and analyzing age data. We then discuss methods for measuring and analyzing growth. Last, we present additional considerations and resources (e.g., software packages) associated with age and growth analyses. Age and growth are easy to measure relative to many other types of fisheries data, but many idiosyncrasies and complexities exist in their estimation. Because this topic is diverse and complex, a comprehensive discussion of all facets of age and growth is not possible here, but where appropriate, we identify additional resources that should be consulted prior to beginning an age and growth analysis.

15.2 APPROACHES TO AGING FISH

Several techniques can be used to determine the age of individual fish. However, the commonly used techniques typically fall into one of three categories: (1) direct observation; (2) statistical evaluation of length-frequency distributions; and (3) interpretation of patterns observed in calcified body parts (commonly referred to as hard structures). Each approach has benefits and limitations that vary from the accuracy and precision of age estimates to the logistic and economic factors associated with collecting the data. Because a number of technical terms are used to describe the process of preparing and assigning ages to individual fish, standard terminology (Glossary, this volume, and Box 15.1) is necessary to reduce confusion and improve communication among fisheries scientists.

15.2.1 Observation of Individuals

The most accurate method to determine individual fish ages is through direct observation. Direct observation data can be collected by holding fish in a contained area (e.g., laboratory, mesocosm, or net pen) and determining age over a known time period (e.g., days or years). Releasing physically or chemically marked individuals of known ages to uncontained habitats (e.g., lakes, oceans, or rivers) and then capturing these individuals at a later date can also be used to determine ages (Oliveira 1996; Neilson et al. 2003). Whereas direct observation is the most accurate aging technique, it is time consuming and labor intensive because confined fish must be cared for or, more commonly, large numbers of released fish must be marked and recaptured to get a reliable sample. Long-lived fishes may also require many years of study to answer specific age-related questions, resulting in substantial expense over long time periods. Despite these caveats, a need still exists to determine individual ages by means of direct observation because it can be used to validate other aging techniques and can provide hard structures (see section 15.2.3) of known age for training, practice, and confirmation of laboratory technique.

15.2.2 Length-Frequency Analysis

The distribution and frequency of fish lengths can sometimes be used to estimate age. Generally, the frequency (or relative frequency) of fish collected by a method that minimizes length bias is plotted as a function of fish length (Figure 15.1; Isaac 1990). The resulting peaks are assigned ages, beginning with the youngest age present for the mode of the smallest fish. For example, the peak representing the smallest fish in the distribution from a sample collected during autumn would be considered age-0 fish, assuming that age-0 fish are susceptible to the collection gear; often they are not (see Chapters 6, 7, and 8). In the following spring and before spawning (i.e., for spring-spawning fishes), the peak of smallest fish in the distribution would represent age-1 individuals. After spawning, the smallest peak would represent age-0 fish (again assuming age-0

Box 15.1 Conventions for Age Designations

A great deal of confusion often centers on the nomenclature used to designate fish ages. Although both Roman and Arabic numerals are commonly used to designate fish age, we adhere to the recommendations of the American Fisheries Society *Guide for Authors* by using Arabic numerals exclusively to designate the current year of life of a fish. Because the time at which fish produce an annual mark differs among species and regions, we consider fish to have completed their current year of life on 1 January in the northern hemisphere and 1 July in the southern hemisphere (see figure below). We do not use a plus sign to designate growth between the last annulus and the edge of the hard structure (for fish aged with hard structures), as has sometimes been done previously. For example, a northern hemisphere fish spawned and hatched in the spring (say of 2008) is considered to be age 0 (or young of year) from time of hatch until 31 December 2008. On 1 January 2009, the fish is considered age 1 until 31 December 2009. On 1 January 2010, the fish is considered age 2 until 31 December 2010, and so forth. Therefore, an age-0 fish is in its first year of growth, an age-1 fish has completed a year of growth (hatching to 31 December) and is in its second year of growth (1 January to 31 December), an age-2 fish has completed two full years of growth and is in its third year of growth, and so forth.

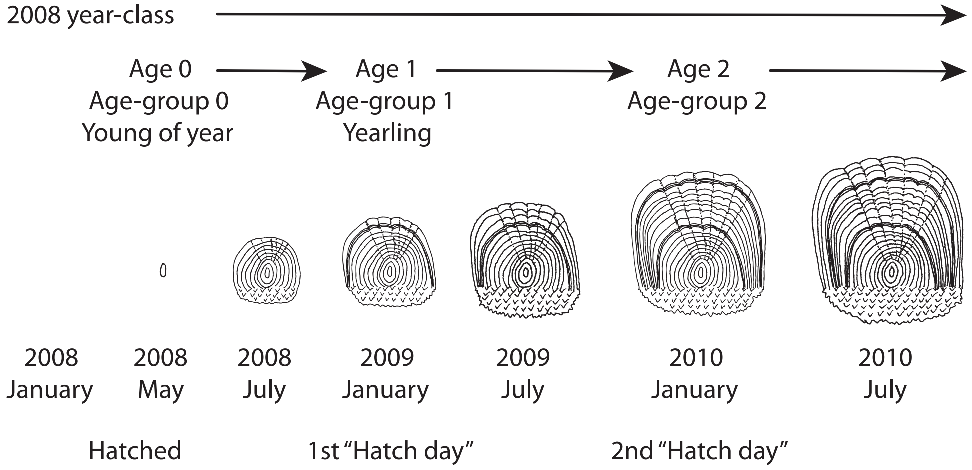

Figure Illustration of fish age terminology adopted herein.

fish are susceptible to the sampling gear). The underlying assumption of this technique is that fish lengths within each age-class are normally (or at least unimodally) distributed.

The ability to age fish by use of length-frequency distributions is enhanced by using a sample that provides an accurate representation of the lengths of fish present in the population, focusing on species that have relatively short spawning seasons, and concentrating on species or populations that exhibit rapid growth that is uniform among individuals within age-groups (Leigh and Hearn 2000). Small sample sizes, or samples that are truncated to a limited size distribution of fish, may result in a lack of discrete peaks or separation of age-groups. Slow growth among age-

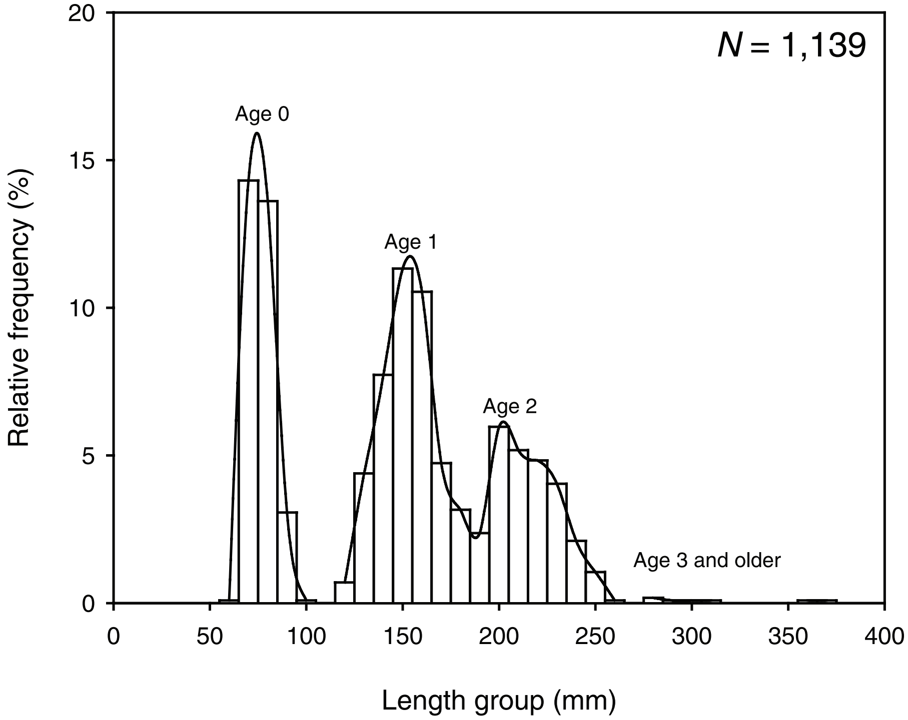

Figure 15.1 Length-frequency distribution of white crappies sampled from Kirwin Reservoir, Kansas. The distribution illustrates the relative frequency of fish among length-groups and how ages were assigned. Note how assigning an age to fish between 170 mm and 190 mm would be difficult; also note the problems associated with assigning ages to fish that are age 3 and older.

groups or highly variable growth within age-groups can also result in significant overlap among age-groups (MacDonald 1987). If any or all of these problems occur, age assignments by means of length-frequency analysis can be difficult or impossible. Even when samples are large and representative, slow growth of older fish may make discrete peaks indiscernible. However, length-frequency distributions can be useful for aging young fish, fast-growing, short-lived species, and, sometimes, species that cannot be reliably aged using other techniques (e.g., hard structures from fishes in tropical regions).

15.2.3 Hard Structures

Whereas direct observation and length-frequency analyses have value for aging fish, collecting age data by use of calcified or hard body structures is the most frequently used method to estimate fish ages. The most commonly used structures include scales, otoliths, spines, fin rays, vertebrae, opercular bones, dentary bones, and cleithra (Maceina et al. 2007). However, other structures, such as scutes, statoliths, branchiostegal rays, and coracoid, urohyal, and supraoccipital bones, have also been used to age fish (see Suzuki and Kimura 1990). Use of these structures is based on the assumption that changes in structural zonation reflect annual or daily growth cycles and that certain zones or "marks" can be counted to estimate age. Marks on these body parts have a variety of names including annual marks, annual rings, or annuli (annulus is the singular form) for marks deposited annually and daily rings or marks for marks deposited daily.

The formation of annual marks is typically caused by changes in growth related to environmental or physiological changes during the year. Spawning activity, low food availability, reduced habitat, and many other factors could explain the formation of marks. Growth marks largely correspond to relatively fast growth during the warmer months and slower growth during the colder months in temperate climates. Age estimates for tropical fishes by means of hard structures are considerably more difficult because less-pronounced variation in the growing season results in less-clear marks (Tesch 1971; Morales-Nin 1992).

Daily age data are used for determining ages of fish in their first year of life, first-year growth rates, and hatch date, among other things. Daily increments are formed by differential deposition of calcium carbonate and protein over a 24-h period (Jones 1992). The exact cause of daily ring deposition is unknown but has been attributed to circadian rhythms, feeding activity, feeding periodicity, and diurnal temperature fluctuations (Campana and Nielson 1985; Radtke 1989).

15.2.3.1 Choice of Hard Structure

Choice of a hard structure depends on many factors. Often a biologist must weigh the quality of age estimates (i.e., accuracy and precision) against lethality because the accuracy and precision of nonlethal techniques have not been evaluated for many species. Collection of some structures requires killing the fish, which may be unacceptable for endangered species or populations whose viability could be negatively affected by sacrificing several individuals. Other factors that influence the choice of structure include processing time, readability of the structure, degree of bias of the age data from the structure, and validity of the marks on the structure as annuli or daily rings (see section 15.5 for further information on validation; also see Maceina et al. 2007). Benefits and limitations of each structure are provided in later sections.

Regardless of the specific structure used to estimate age, fish collection should be as unbiased as possible. Gear biases can influence the sizes, sex, and maturity of collected fish, thereby biasing age and growth estimates. Sampling biases are addressed in other portions of this volume (e.g., Chapters 2, 6, and 7). The following sections provide information that can be used to help guide decisions on which structure may or may not be suitable for evaluating age.

15.2.3.2 Techniques for Processing Hard Structures

Collection, storage, and preparation of hard structures depend on the study species, hard structure, and capabilities of the laboratory. Similarly, a myriad of approaches are used for reading structures and assigning ages. We present only the most common methods of collecting and processing hard structures for aging. Keep in mind that for most species estimates of age made using hard structures are simply estimates and not absolute determinations of age. Even when structures have been validated (i.e., accuracy has been confirmed; section 15.5), errors can and do occur when estimating age. To help eliminate errors and promote consistency in age estimates, readers should be trained by experienced personnel and with the aid of known-age structures (if available); additionally, fish should be aged without knowledge of the fish's length (see section 15.5). Structures should be read by multiple readers whenever possible to provide an estimate of precision (section 15.5).

Scales. Scales have historically been the most commonly used calcified structure. Compared with other structures, their advantages are that collection is nonlethal and requires little time in the field. However, scales may not always form distinguishable annuli (Lentsch and Griffith 1987). Scales, including annuli, can be resorbed during severe stress, a process known as the

Crichton Effect (Simkiss 1974), which can result in aging errors. Growth-ring deposits and annuli can also crowd the edge of the scale in slow-growing individuals, which makes aging difficult or impossible (Scoppettone 1988; Hoxmeier et al. 2001). This phenomenon worsens as age increases because relative growth typically slows, thus crowding the annuli. Another drawback to using scales is that they can be damaged or lost; regenerated new scales lack preexisting growth rings and are therefore unsuitable for aging. Because of these concerns, annulus validation is important to ensure accurate data from scales (Hoxmeier et al. 2001; McBride et al. 2005).

The most commonly used scale types for aging are cycloid scales, which are typically found on soft-rayed fishes, and ctenoid scales, which are typically found on spiny-rayed fishes (Figure 15.2). Both have similar scale characteristics in that they have a focus that forms first followed by radii that linearly extend from the focus to the anterior margin of the scale. Circuli (circulus is the singular) form regularly around the scale until growth slows or stops. As growth slows, the circuli become crowded, and if this occurs on an annual basis (e.g., during winter), an annulus is formed. When growth resumes, the circuli often grow around or over the incomplete circuli from the previous growth deposition period. The resulting pattern in the circuli is termed "cutting-over" and creates an annulus if it forms on an annual basis (Figure 15.3; Everhart and Youngs 1981). The exact location used to identify the annulus on a scale is not important when aging fish (i.e., at the beginning or end of the slow-growing period) but is vital for making growth measurements (section 15.4.3). Therefore, the standard practice is to identify annulus formation at the outer border of the closely spaced circuli or at the point of cutting-over for growth estimates (see Figure 15.3).

Scales have traditionally been taken from different body locations for different taxa (Figure 15.4; Bagenal and Tesch 1978; Jearld 1983; DeVries and Frie 1996). The aim is to select an area that produces consistently large, symmetrical scales. Locations that are susceptible to scale loss, have irregularly shaped scales, or have extremely small scales should be avoided (e.g., Quist et al.

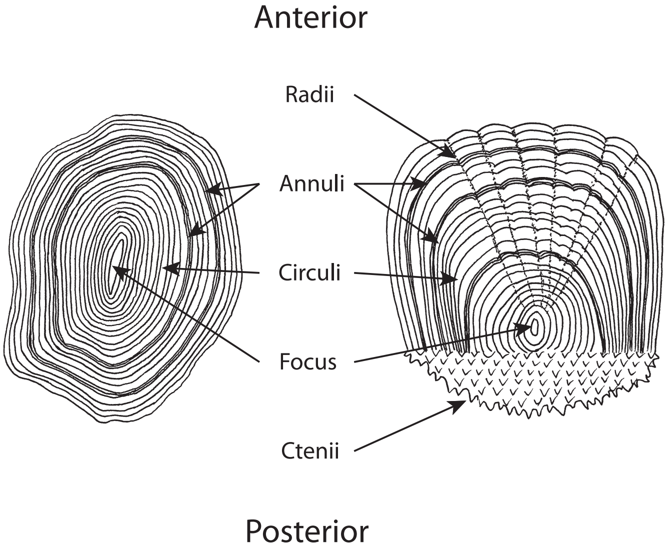

Figure 15.2 Cycloid (left) and ctenoid (right) scales and morphological characteristics important for estimating age and growth of fishes.

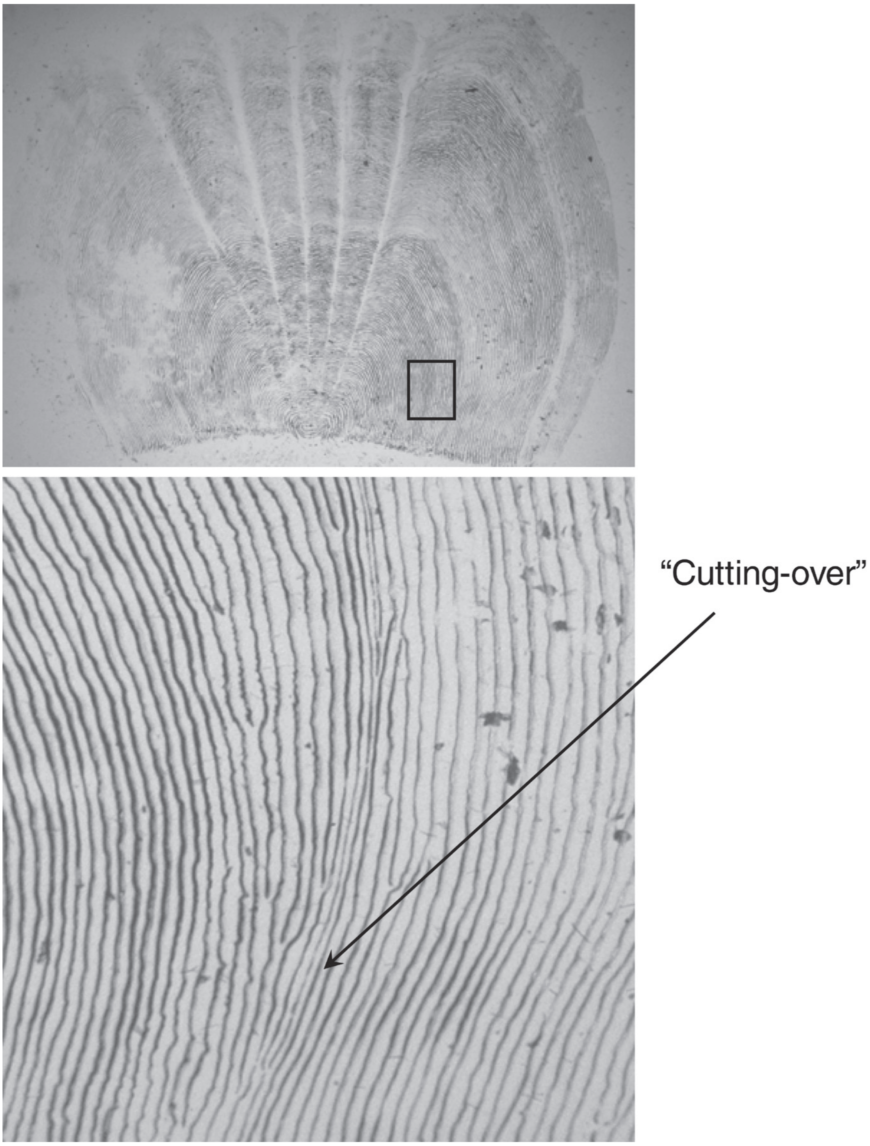

Figure 15.3 Scale projection from a palmetto bass collected from Lake Manawa, Iowa. The lower image is a magnification of the inset in the upper image. The magnified image shows how fast growth results in "cutting-over." Also note the close spacing of circuli near the point of cutting-over and the wider spacing beyond it.

2007). Some experimentation may be required on species that have not been well studied to determine which area is best suited for scale collection. Scales should be consistently removed from the same location on a given species.

The designated body location should be wiped clean prior to collecting scales because mucus and other material (e.g., inorganic debris) often reduce scale clarity. Cleaning the area makes the scales easier to process in the laboratory. Several scales should be collected from each individual

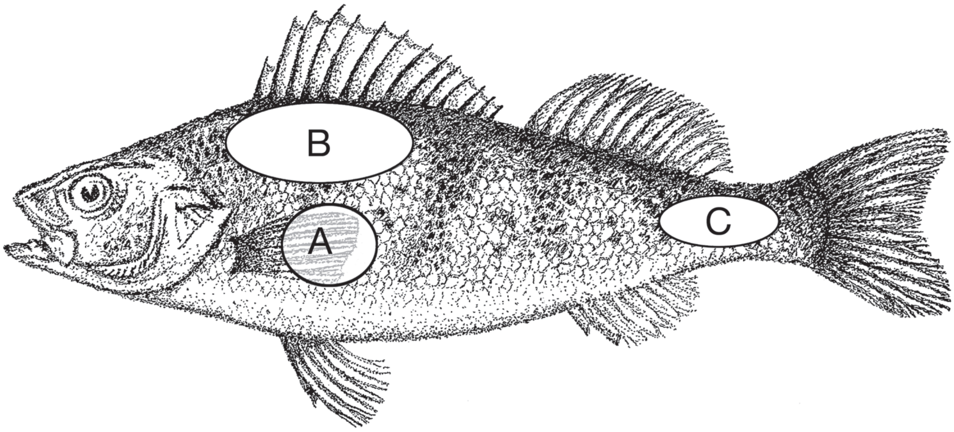

Figure 15.4 Common locations for removing scales include areas just posterior to the pectoral fin (A), just dorsal to the lateral line and ventral to the dorsal fin (B), and on the caudal peduncle (C).

because identification of regenerated scales is typically not feasible in the field. No set guidelines exist, but a sample of 10 scales is usually sufficient for most species to ensure that there are several useable scales per individual. Scales can be removed individually by pulling them with forceps or by scraping, typically in an anterior to posterior direction, the designated area on the fish's body with the blade of a knife or similar object to remove several scales simultaneously. The scales are then placed into a scale envelope (usually a coin envelope) labeled with pertinent information including species, sample site location, fish length, fish weight, date, individual fish identification code, and any other information that may be useful for future sample identification or analyses. The scraping technique quickly yields many scales and expedites processing time in the field because the scales from an individual can be deposited en masse into an envelope. The forceps or knife should be cleaned of all scales after each fish to prevent contamination among samples.

Scales placed in envelopes may be stored dry for future processing. Dried scales often curl, making them difficult to view and measure. Storing the envelopes so that the scales dry flat will help with this problem, but scales can often be "reconstituted" by soaking them in water for a few minutes prior to processing. When care is taken in the field to clean scales prior to removal, additional cleaning is usually not necessary. However, any large debris particles can be individually removed, and scales can be further cleaned using soapy water or a 2–3% solution of KOH without damaging their integrity (Mackay et al. 1990; Marwitz and Hubert 1995). Typically, the scales are soaked in the cleaning solution and then individually pulled across a paper towel saturated with solution. At least for larger scales, this is also the point at which regenerated scales can be identified and discarded to preclude their future use. Scales can be further processed for aging after cleaning.

Use of scales to age fish is conducted with either the actual scale (i.e., raw scales) or with scale impressions pressed into acetate slides (Smith 1954). Raw scales can be viewed without any additional processing, but standard practice is to place scales between two glass slides that are then taped together. Scale impressions on acetate slides are usually made with a scale press. Commercially available scale presses imprint scale characteristics onto the acetate slide by means of pressure alone or a combination of pressure and heat (Figure 15.5). A good technique when using

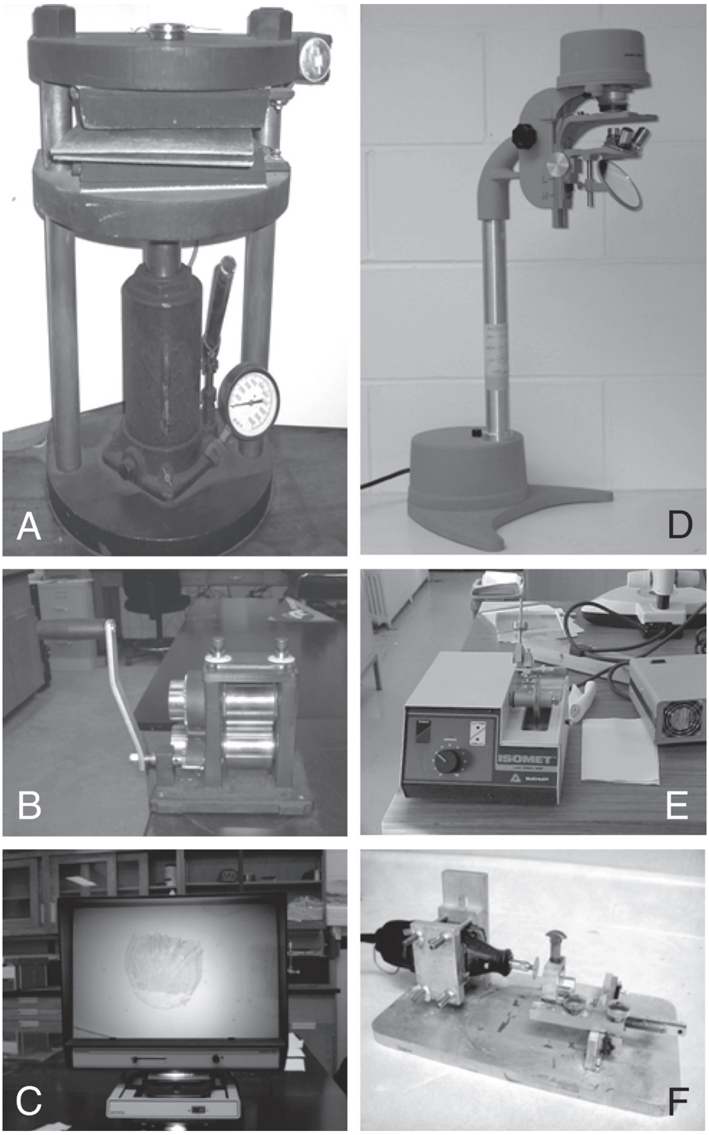

Figure 15.5 Equipment commonly used in age and growth studies. Scales are typically pressed using a combination of heat and pressure (**A**; image courtesy of Donald Klein, Iowa Department of Natural Resources [IDNR]) or pressure **(B)**. Scale impressions or raw scales are commonly viewed using a microfiche reader **(C)** or a microprojector **(D)**. Some structures, such as fin rays or spines, are commonly sectioned using a low-speed saw **(E)** or a laboratory-made sectioning jig equipped with a rotary tool (**F**; image courtesy of Ed Thelen, IDNR).

a roller press is to use three separate acetate slides. The middle slide receives the scale impressions and will exit the press uncurled, whereas the outer two slides will be curved from pressing (but can be reused). Developing the skills to make high-quality scale impressions takes practice because too little pressure (or temperature) will not fully capture the detail of the scale surface and too much pressure (or temperature) will distort the impression. Information used to identify specific individuals (e.g., fish number or identification code from the field sample) should be recorded on slides to ensure data integrity.

Choice of raw scales or acetate impressions is often dependent on the size and type of scale. For example, samples from small-scaled fishes may be difficult to handle when making scale impressions and are often viewed as raw scales. Impressions of large scales on acetate slides may remove scale characteristics that obscure annulus detection, such as pigmentation or poor light transparency caused by scale thickness. Processing time is also a factor in deciding which technique to use because making acetate impressions is often more time consuming than is placing scales between glass slides.

Several options are available for viewing scales and assigning ages. Traditionally, scales have been viewed directly under a dissecting microscope or by means of a microprojector or microfiche projector to enlarge the scale image (Figure 15.5). Identification of scale characteristics (e.g., annuli) is typically easier using the microprojector or microfiche approach because scale image quality is often better than is direct observation with a dissecting scope. The large size of projected images also helps reduce error when taking growth measurements in association with aging fish (section 15.4.3). Both of these issues can be important if annuli are close together. More recently, computerized image analysis systems have moved to the forefront for aging fish. An image analysis system typically comprises a microcomputer equipped with a digital camera that is attached to a dissecting microscope. An image of the scale or acetate slide is projected onto a computer screen where the annuli can then be identified. Image analysis systems have the added advantage of reducing processing time when making measurements for growth determination because the data can be automatically transferred to a spreadsheet or other data storage system.

Otoliths. Otoliths are paired calcified structures that are located in the heads of fish and function in hearing and balance. There are three pairs, named the sagittae, lapilli, and asterisci. Although sagittal otoliths are generally the largest and preferred otolith for aging, other otoliths have been used, such as the asteriscus for ostariophysan fishes (Brown et al. 2004; Quist et al. 2007) and the lapillus for larval fish (Secor et al. 1992; MacInnis and Corkum 2000; Fey et al. 2005). Otolith removal is time consuming and requires sacrificing the fish, but otoliths are generally considered to be more reliable than are scales for many species because they form at the embryonic stage, are better at recording the age of older fish because they continue to form annuli or increments when growth slows or stops, and do not appear to be reabsorbed during periods of food deprivation or stress (Popper et al. 2005; but see Krueger and Hubert 1997). Otoliths can also provide morphological information useful for describing the systematics and evolution of fishes (Begg et al. 2005). Compared with other structures, aging is often easier using otoliths because growth rings are usually clearer. Otoliths are also the only structures used for examining daily growth of age-0 fish (Stevenson and Campana 1992).

The exact techniques used to extract otoliths vary by species but all require either cutting through the top of the skull and across the head (Tesch 1971; Secor et al. 1991, 1992; Buckmeier et al. 2002) or cutting the isthmus, removing the gill arches, and accessing the otoliths through the base of the skull (Schneidervin and Hubert 1986). After exposure, otoliths can be removed using forceps. As with scales, otoliths can be stored dry in envelopes; however, otoliths are easily damaged, leading many scientists to place otoliths into plastic microcentrifuge tubes that are then placed into coin envelopes. Otoliths may also be stored in vials with water, glycerin, ethanol, or a 2:3 mixture of glycerin to ethanol (Jearld 1983). Caution should be used when storing otoliths in water because a chalky film may form on the surface of the otolith. Glycerin will clear the otolith, and whereas some clearing may be desirable to help make the otolith more readable, prolonged exposure can result in unusable samples. Therefore, it is important to check otoliths stored in water or glycerin periodically. Otoliths should never be stored in formalin because it can decalcify structures, rendering them useless. Removal and storage of otoliths from larval fish often require different techniques than those described above. Secor et al. (1992) provide a comprehensive review of techniques associated with processing otoliths from early life history stages of fishes.

The time required to prepare and age an otolith varies greatly among species and sizes of individuals. Preparation times can vary from just a few minutes if whole otoliths are used to several days if additional processing is employed. As with other structures, no single method is consistently better than others for all species and sizes; testing the various approaches on a case-by-case basis is necessary to get the best results when working with new species or sizes of fish.

Otoliths exhibit alternating bands of growth representing fast- and slow-growth periods that correspond to annual growing-season cycles. Daily growth rings are interpreted in the same manner. These growth periods are manifest on otoliths as translucent and opaque bands. Unfortunately, a great deal of confusion remains regarding the interpretation of these bands (see discussions in Panella 1974; Casselman 1983; Beckman and Wilson 1995; Campana 2001; Schill et al. 2010). For instance, Panella (1980) stated that "it is obvious that the opaque zone is the zone of active growth." A number of other authors have also interpreted the opaque zone as the period of fast growth (e.g., Casselman 1987; Admassu and Casselman 2000; Schill et al. 2010). In contrast, other authors have argued that the translucent zone is associated with rapid growth (e.g., Buxton and Clarke 1989; Schramm 1989; Hales and Belk 1992). As noted by Schill (2009), this confusion has been partly complicated by previous versions of *Fisheries Techniques*. In the first edition, Jearld (1983) stated that the opaque zone is the period of fast growth and the translucent zone represents the period of slow growth. In the second edition, DeVries and Frie (1996) stated the exact opposite. Discrepancies may be due to species-specific differences in otolith growth (Schramm 1989) or differences in sample preparation, illumination (i.e., reflected versus transmitted light), or reader interpretation (Beckman and Wilson 1995; Campana 2001; VanderKooy and Guindon-Tisdel 2003). Additional research is clearly needed to understand and better clarify the interpretation of otolith growth zones among species and ecosystems.

Numerous options are available for reading otoliths, but the techniques generally fall into two major categories: (1) using the whole otolith or (2) using a sectioned otolith (Figure 15.6). Whereas one technique or the other is typically used in a single study, a combination of whole and sectioned otoliths is sometimes useful (Nitschke et al. 2001), such as the use of whole otoliths for young fish and sectioned otoliths for older fish. Whole otoliths generally require less time to prepare and process than do sectioned otoliths, but they have several potential problems. For instance, annuli can be difficult to detect because of opacity of whole otoliths. Curvature of the otolith can also prevent accurate detection of annuli in some species.

Sectioned otoliths are popular for estimating ages and making growth measurements (section 15.4.3) because they typically provide clear images of annular or daily growth marks (e.g., Figure 15.6). Sectioning can involve simply breaking or "cracking" the otolith through the nucleus to get a sectional view or cutting a thin cross section of the otolith. Cracking requires less processing time because the otolith is typically broken along the transverse plane that encompasses the nucleus (Figure 15.7). Some polishing may be required to ensure the nucleus is visible (see below and Secor et al. 1991 for more information). The cracked otolith is typically placed in a small

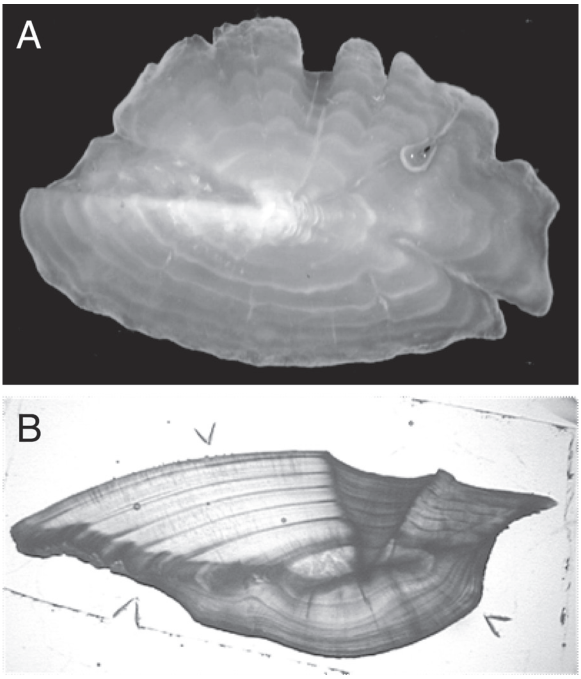

Figure 15.6 Image of a whole otolith from an age-7 yellow perch (**A**; seventh annulus is near the edge; image courtesy of Daniel Isermann, University of Wisconsin-Stevens Point) and a cross-sectioned otolith from an age-6 red drum (**B**; image courtesy of James Cowan, Louisiana State University).

petri dish filled with modeling clay, plumber's putty, or a similar substance to hold the otolith in place for reading. A small amount of glycerin, clove oil, or microscope immersion oil placed on the otolith enhances annulus detection. Side illumination by means of a flexible fiber-optic light usually works best to highlight annuli under these conditions. The cracked otolith can be returned to the envelope or vial after examination.

Making cross sections of otoliths (typically along a transverse plane) requires the most effort because of the added steps associated with mounting and cutting. Otoliths, particularly small ones, are usually mounted on a glass slide with thermoplastic cement, epoxy, or cyanoacrylate glue. Larger otoliths are often first cut using a saw equipped with a diamond blade or a jeweler's handsaw; alternatively, they are mounted on a glass slide and sanded to achieve a thin cross section. Sections may also be obtained by cutting otoliths with a saw equipped with two or more diamond blades that are separated by spacers. Regardless of the specific technique, the objective is to leave a thin section of the otolith that incorporates the nucleus, as shown in Figures 15.6 and 15.8. The cross section may require additional refinement if the nucleus is not clearly visible. Refinement usually requires sanding first with relatively fine sandpaper (e.g., 600–1,000 grit) and progressing to very fine wet–dry sandpaper (e.g., 1,200 grit or smaller) to the point where the nucleus is visible. Otoliths may be further polished using silicon carbide powder and a felt cloth to improve clarity. *Extreme care must be taken to ensure that the sanding process does not remove too much material.* Sanding through the nucleus may inadvertently remove some annuli or daily

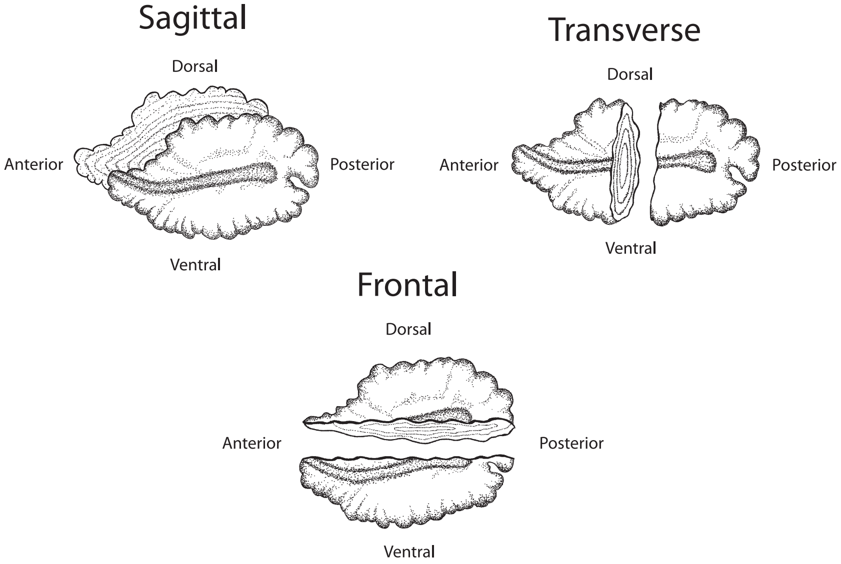

Figure 15.7 Examples of sectioned otoliths showing three sectioning planes (from Secor et al. 1991).

growth rings and bias resulting estimates. After processing, the slide can be stored in the envelope or a slide case. If sections are not mounted to slides, they can be stored in microcentrifuge tubes or placed into envelopes.

Many options are available for improving the clarity of otoliths during both the preparation and reading processes, including the use of protein-affinity dyes (Albrechtsen 1968; Bariche 2005), burning (crack-and-burn technique described by Christensen [1964]), different polishing techniques, acid etching (Haake et al. 1982; Campana and Neilson 1985), and even chamomile essence (Bariche 2005). Viewing otoliths and their cross sections through the microscope with different light sources (e.g., transmitted or reflected), light or dark backgrounds, different microscope types (e.g., dissecting, compound, or scanning electron), and variable amounts of magnification to increase detection of annuli or daily rings are all valid options to increase otolith readability and should be used in combination with the other approaches we have discussed to produce the best possible image.

Complete descriptions of procedures useful for accurate annulus identification can be found in Beamish (1979) or Morales-Nin (1992); for daily ages consult Campana (1992) or Itoh et al. (2000). Reader skill and experience, growth ring formation, and growth ring clarity are issues that should be considered when using otoliths. Finally, although the use of otoliths for aging fish dominates much of the current literature, ages (annular or daily) must still be validated (section 15.5) as with any other structure.

Spines and fin rays. Fin rays or spines are popular structures for age estimation, particularly for fish lacking scales or when other structures (including otoliths; Walsh et al. 2008) are not reliable. These structures have the added benefit of not requiring sacrifice of fish. Collection of fin rays and spines is usually conducted in the field and requires little time. The first or second dorsal or anal spine is typically collected from spiny-rayed fishes for aging, whereas the leading pectoral

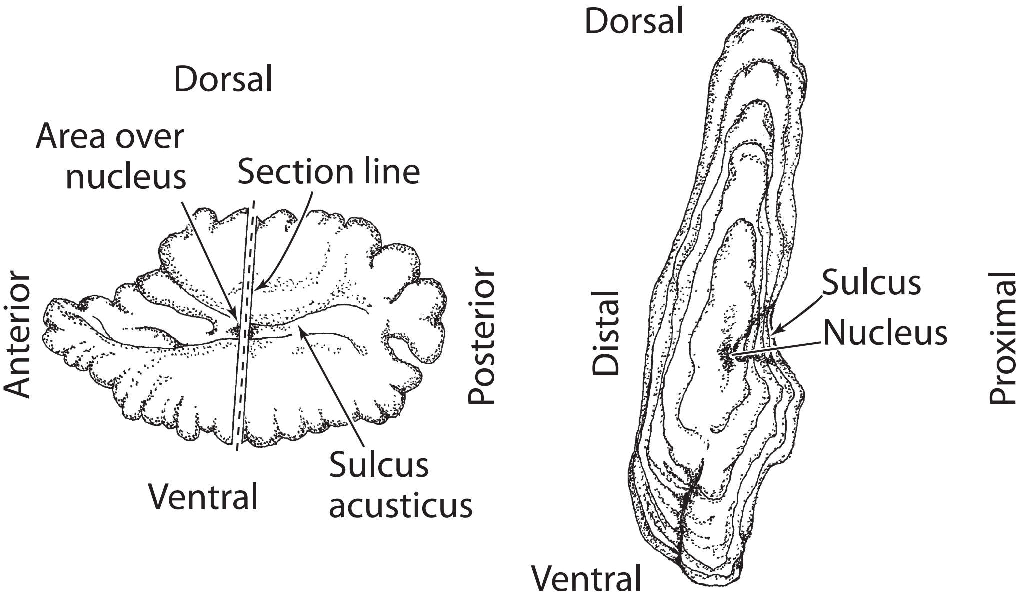

Figure 15.8 Location of the sulcus acusticus and nucleus of an otolith. Illustration on the left shows where to make a transverse section of the otolith, and the illustration on the right depicts a sectioned otolith.

or pelvic fin ray is typically used for aging soft-rayed fishes. The dorsal spine (typically from the second dorsal fin) is often used to estimate age of squalid sharks (McFarlane and Beamish 1987; Irvine et al. 2006). Spiny and soft fin rays are collected by cutting near the base of the spine or ray with side-cutter pliers, scissors, a knife, or a scalpel (Hughes et al. 2005). Cutting as close to the body as possible is important because the first annulus may be present in only the basal section of the structure (Mackay et al. 1990; Koch et al. 2008). Pectoral spines, such as those found in ictalurids, are also used for aging. Disarticulating pectoral spines is accomplished by pressing the spine flat against the body and then, with pliers, rotating the spine in a counterclockwise direction (i.e., for the right spine) (Mayhew 1969). Removing spines and rays does not appear to cause significant deleterious effects to fish (Stevenson and Day 1987; Collins and Smith 1996; Michaletz 2005). Excess flesh attached to the spine or fin ray should be removed, taking care not to damage the structure. The structure can then be placed in a coin envelope and allowed to air dry.

Although spines of some species may be read whole (Logsdon 2007), including spines from squalid sharks (Figure 15.9), fin rays and spines are typically cut in cross section by means of a low-speed saw or jeweler's handsaw. Small spines and rays may be difficult to section because of their small size and fragility and are commonly mounted in epoxy. Rubber molds are commercially available for this purpose. Alternatively, molds can be fashioned by removing the tapered end from a microcentrifuge tube (Figure 15.10; Koch and Quist 2007). A small piece of modeling clay is then placed in the cap to hold the fin ray or spine in place while epoxy that has been added to the tube cures. The first cut on fin rays and spines is typically made perpendicular to the long axis of the structure to facilitate rapid processing as only one additional cut is needed to make a useful cross section. Cross sections from disarticulated ictalurid spines can be cut at the distal end

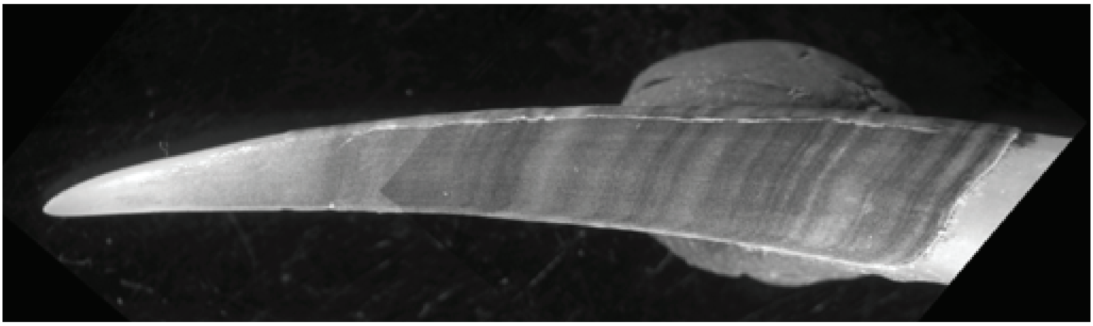

Figure 15.9 Dorsal spine from a spiny dogfish (image courtesy of Steven Campana, Bedford Institute of Oceanography [BIO]).

of the basal groove (Figure 15.11). Because the central lumen often erodes as fish age (Mayhew 1969), sectioning ictalurid spines along the articulating process is also common (Buckmeier et al. 2002). Typical cross-sectional thickness of spines and rays is 0.3–1.0 mm.

Processing cross sections of fin rays and spines is similar to processing otolith cross sections (Figure 15.12). The sections can be placed directly under a dissecting or compound microscope or attached to a glass slide with thermoplastic cement, epoxy, or cyanoacrylate glue. Fin rays and

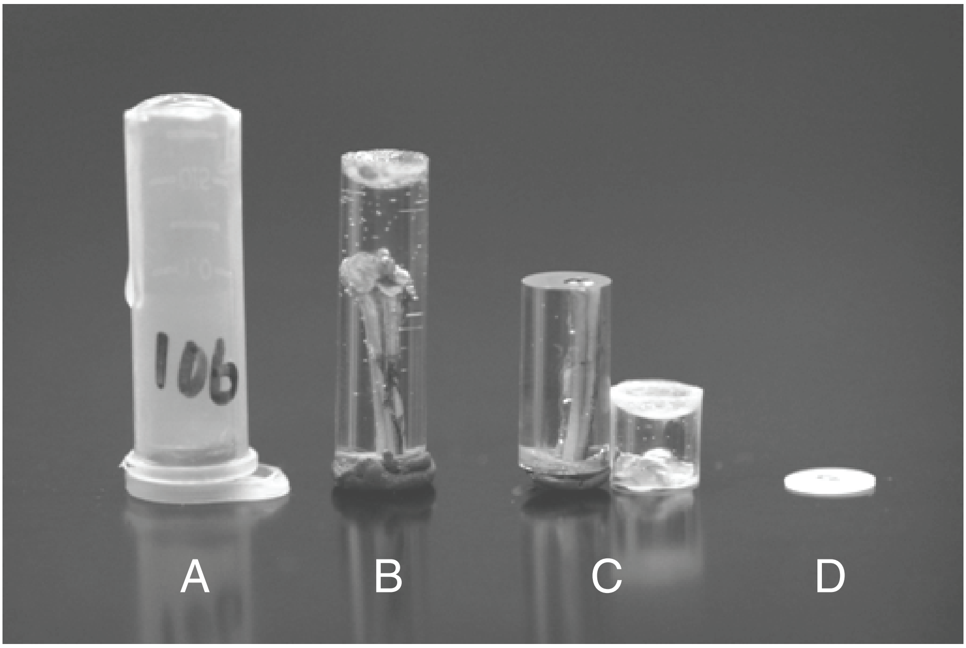

Figure 15.10 A method for mounting spines or fin rays in epoxy for sectioning. The tip of a microcentrifuge tube is removed and a small piece of clay is placed in the cap **(A)**. The clay holds the structure while the epoxy in the tube cures. After the epoxy cures **(B)**, the end of the fin ray is removed using a low-speed sectioning saw **(C)**. The last step is to cut a thin section of the fin ray for age and growth analysis **(D)**.

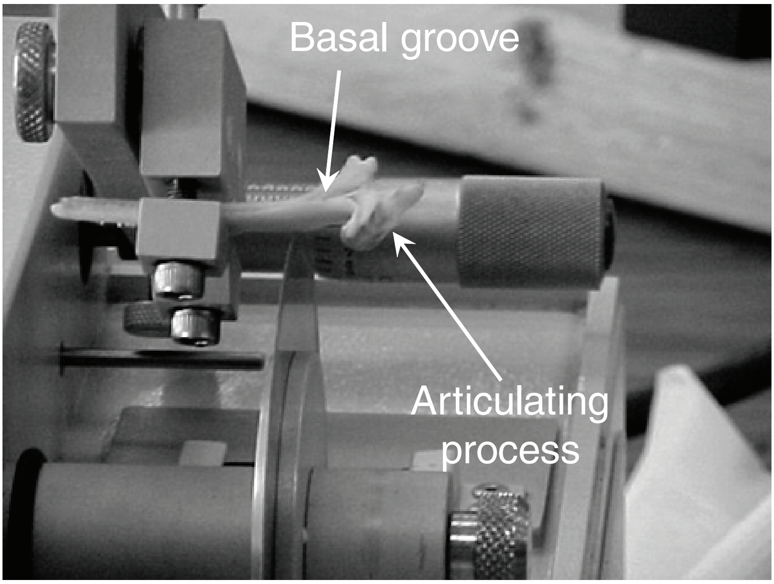

Figure 15.11 A blue catfish spine being sectioned distal to the basal groove.

spine cross sections generally need little additional clarification if read under a drop or two of immersion oil or glycerin but can be sanded or polished to increase clarity as described for otolith sections. After processing, slides can be placed back into an envelope or into a slide case for storage. If sections are not mounted to slides, they can be stored in microcentrifuge tubes and placed into an envelope.

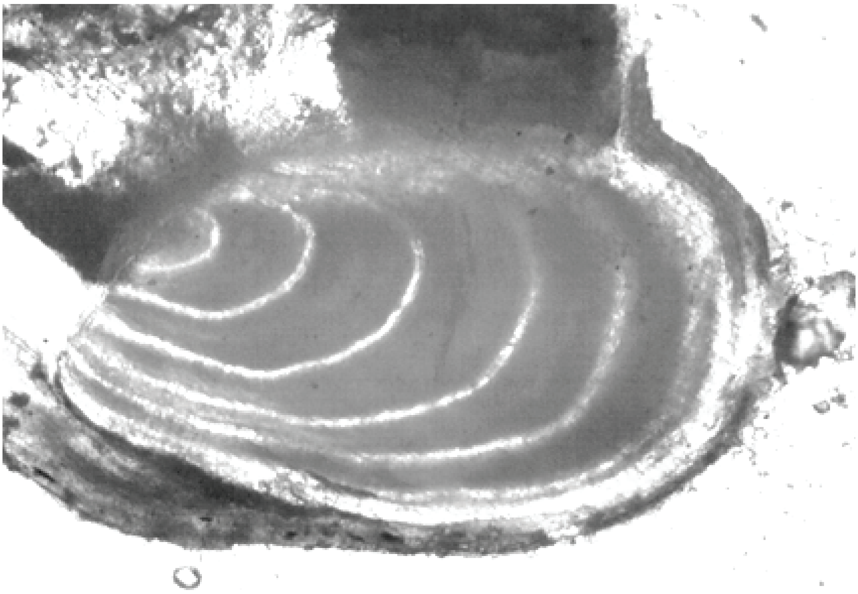

Figure 15.12 Cross section of a pectoral fin ray from an age-7 flannelmouth sucker.

Other structures. Other structures used to age fish include dentary bones, cleithra, vertebrae, statoliths, opercles, scutes, branchiostegal rays, and the urohyal bone (Suzuki and Kimura 1990; Figure 15.13). Use of these structures typically requires sacrificing the fish but can provide reliable age information. For example, cleithra are the preferred structure for esocids (Harrison and Hadley 1979; Owens and Pronin 2000); cross sections taken from the mesial bend of dentary bones are the primary method for aging paddlefish (Lein and DeVries 1998; Scholten and Bettoli 2005); branchiostegal rays are the preferred structure for aging gars (Johnson and Noltie 1997); and vertebrae are frequently used to age elasmobranchs (Neer and Cailliet 2001; Natanson et al. 2002; Cailliet and Goldman 2004). Many species have been aged using opercular bones (Scoppettone 1988; Sharp and Bernard 1988), white sturgeon have been aged using scutes (Brennan and Cailliet 1989), and lampreys have been aged using statoliths (Meeuwig and Bayer 2005). In addition to these structures, a wide array of additional structures has been used to age fishes (Suzuki and Kimura 1990; McFarlane et al. 2002).

As with fin rays and spines, processing these other structures requires some additional work in the preparation stages, primarily given the flesh and connective tissue that must be removed from around the structure. Structures can be immersed for 5–15 s in boiling water and then cleaned with a small plastic brush. However, care should be taken because a longer boiling time may completely clear the structure of annuli. Soaking the structure in a mild laundry detergent solution heated to 40–50°C to loosen the flesh may also be useful (see Johnson and Noltie 1997 and Scholten and Bettoli 2005 for example cleaning processes). Because some structures can

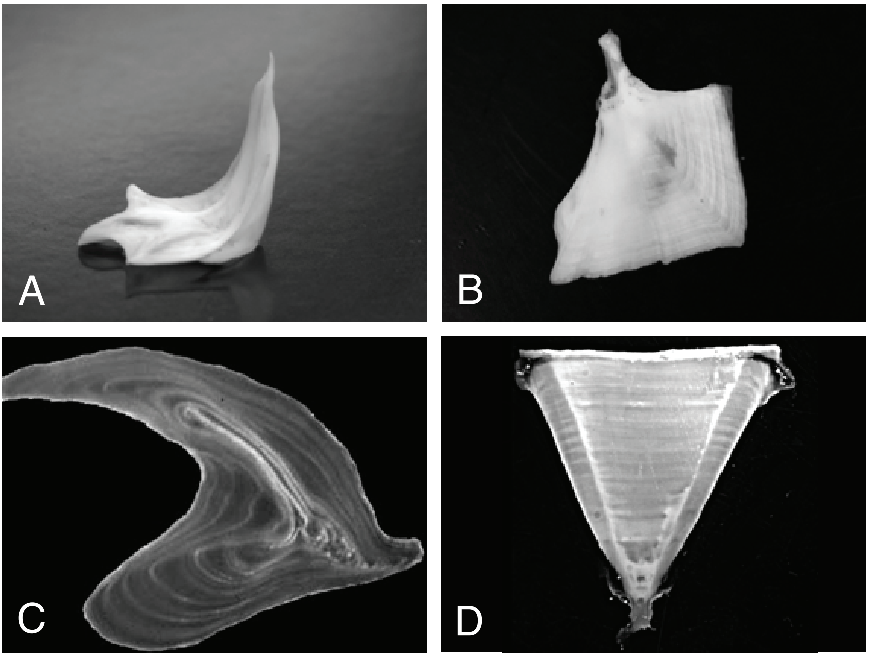

Figure 15.13 Examples of other hard structures used to age fish, including the cleithrum (**A**; bluehead sucker), opercle bone (**B**; flannelmouth sucker), sectioned dentary bone (**C**; paddlefish; image courtesy of Phillip Bettoli, Tennessee Technological University), and sectioned vertebra (**D**; porbeagle; image courtesy of Steven Campana, BIO).

become more opaque when stored dry for long periods, structures are often frozen until aging (Mackay et al. 1990). Structures can be read whole or cross-sectioned similar to otoliths, fin rays, or spines. Growth marks can be enhanced somewhat by soaking the specimens in a clearing agent (ammonia, acetic acid, bleach, mineral oil, or other compounds listed above). However, caution and careful testing of these clearing agents are necessary because they can quickly remove calcified marks on structures.

15.2.3.3 False or Missing Annuli

Gathering reliable age information is dependent on one major assumption—*annual or daily ring counts accurately reflect the true age of the individual.* The assumption for fishes found in temperate regions is that these annuli form in response to the end of cold water conditions during winter. However, many other biotic and abiotic factors can result in slow or no growth, including lack of food resources, spawning, rapid fluctuations in water temperature not associated with seasonal changes, and injury (Morales-Nin 2001). All of these factors could result in the fish forming (or failing to form) annulus-like growth rings, termed checks (note that some scientists refer to any mark on a structure as a check, including annuli). Similar issues, particularly the presence of extra rings, are also important in the daily aging of fish because subdaily rings are often present. The presence of subdaily rings and the identification of true daily rings has been the topic of considerable discussion in the literature (e.g., DiCenzo and Bettoli 1995).

False and missing annuli may result in inaccurate age estimates and lead to erroneous conclusions or propagate errors in subsequent analyses (e.g., age structure or growth estimates). Therefore, it is critical to consider all of these potential influences on structures and to take them into account in any study of fish ages. In contrast to these cautions associated with false annuli, accessory checks are often used to provide important insight on the ecology and management of fishes, such as information on spawning frequencies (Taubert 1980) and contributions of hatchery-reared and naturally produced fish to a population (Daugherty et al. 2003).

15.3 AGE ANALYSIS

Given the time and expense associated with aging fish, fisheries professionals should extract as much information as possible from age data. Although age data are commonly combined with growth information, they can be used in and of themselves to address a number of important research and management questions. For instance, age data may provide insight into the age at which fish recruit to a sampling gear or fishery, or the ages and proportion of fish in a population that are sexually mature. Estimation of population age structure is a common and insightful use of age data. Age structure data can be used to estimate mortality rates (e.g., Ricker 1975; Miranda and Bettoli 2007) or evaluate changes in population demographics caused by harvest or habitat alteration (Scholten and Bettoli 2005). If multiple years of age structure data are available, changes in year-class abundances can be used to assess the effects of management actions or environmental change on recruitment dynamics. Techniques even exist to characterize recruitment variability (Guy and Willis 1995; Isermann et al. 2002) and estimate relative year-class strength (Maceina 1997) from a single sample of age data.

If all fish in a sample are aged, an estimate of the population age structure is reflected by the distribution of ages encountered in the sample. A limitation to collecting age information from direct observation or hard structures is that the data are time consuming and expensive to obtain. This limitation often precludes gathering age information for all sampled individuals. More commonly, length measurements are obtained from all individual fish in a sample, but only a subsample of those individuals is aged (Ricker 1975). Common subsampling protocols call for aging a fixed number of fish from specified length-groups, typically 5 or 10 fish per 1-cm length-group. Age structure of the entire population is then estimated by combining the subsampled age data with the length structure data from the entire sample using an age–length key. When using age–length keys, care should be taken to avoid combining data across gears or seasons or age data obtained from different structures (Westrheim and Ricker 1978; Hoenig and Heisey 1987). The general approach is to assign fish of a specific length to a specific age-class. Conceptually, plotting length-frequency information can provide initial insights into the age structure of a fish population (Figure 15.1). However, a more quantitative approach is to assign ages according to the probability that a fish of given length is of a given age. This process (Box 15.2) estimates the frequency of ages among different length categories. Whereas this approach provides age estimates for only individual fish that were actually aged, biologists often require estimates of ages of individual fish that were not aged to estimate parameters such as catch per unit effort of an age-class. Because un-aged fish should not be subjectively assigned an age for such analyses, an assignment procedure that incorporates randomization within age- and length-groups should be used. For example, Isermann and Knight (2005) assigned ages to un-aged fish by randomly sampling from an array that reflected the distribution of observed ages for a specific length-group.

Age–length keys have also been used to provide estimates of age structures of populations from larger systems (e.g., oceans and the Great Lakes) when only length data are collected. However, such estimates may be biased because age–length keys are often developed from samples or groups of samples taken from large geographic areas. Such "composite approach" samples may be flawed if sampling intensity is not constant through space and time within the given region. If the age information or sample selection does not accurately reflect the entire population(s), an inaccurate assessment of population age structure may result (Westrheim and Ricker 1978; Cotter et al. 2004). Statistical problems can also emerge from using age–length keys in this manner, including correlations among fish in different size and age-groups, spurious correlations associated with habitat use and availability, and gear biases that can influence the outcome of age-frequency calculations. Some of these problems can largely be alleviated by using dynamic age–length keys that account for ontogenetic and other temporal shifts influencing the age–length relationship (Salthaug 2003). However, it is important to ensure that the age–length key is accurately parsing length-frequency data into age-frequency data through a validation process.

15.4 APPROACHES TO ESTIMATING GROWTH OF FISHES

Growth is defined as the change in weight or length of an individual, and growth rate is growth expressed as a function of time. Although these are somewhat different concepts, the techniques for estimating growth and growth rate are similar. Growth is one of the most important factors influencing individuals, populations, and assemblages of fishes and provides an indicator of fish health, population dynamics, and habitat quality. As such, reliable estimates of growth are necessary for effective management and conservation of fishes. Growth estimation is a broad and often challenging topic that has been the focus of entire books (e.g., Bagenal 1974; Summerfelt and Hall 1987) and thousands of manuscripts. We will restrict our coverage to the most common and applicable techniques of estimating growth as they relate to the process and techniques associated with aging fish discussed in section 15.2. The focus of this section will be primarily on annual growth of fish, but daily growth estimation of larval fish will also be discussed because the

Box 15.2 Computation of an Age-Frequency Distribution from an Age–Length Key

Below is an example of use of an age–length key to estimate the age distribution of fish (creek chubs in this example) based on the relation between age and length observed in an aged subsample of fish. The length distribution of fish in the entire sample is shown in the first two columns. Scales were taken and aged (column 3) from a 10-fish subsample from each 1-cm length-group (or from all fish if less than 10 were present in a length-group). The number at each age i in the jth length-group (N_{ij}) is estimated as $N_{ij} = N_j\,(n_{ij}/n_j)$, where N_j is the total number of fish in the sample in the jth length-group, n_{ij} is the number of fish of the ith age-group in the jth length-group, and n_j is the number of fish in the jth length-group that were subsampled and aged. For instance, the total number of fish sampled in the 10-cm length-group (N_{10}) was 32, the number of fish subsampled and aged from the 10-cm length-group (n_{10}) was 10, and the number of age-1 fish in the subsample from the 10-cm length-group ($n_{1,\,10}$) was 5. Therefore, 16 fish from the 10-cm length-group in the sample were age 1 (5/10 or 50% of 32). The age structure of the population was estimated by summing the numbers within each age-group column.

Table Example of using an age–length key to estimate the age distribution of a sample of creek chubs. Symbols and calculations are described in above text.

Length-group (cm)	Number in sample (N_j)	Number (age) in subsample (n_{ij})	Sample allocation among ages (N_{ij}) Age 0	Age 1	Age 2	Age 3	Age 4
4	11	10 (0)	11				
5	33	3 (0), 7 (1)	10	23			
6	42	10 (1)		42			
7	32	10 (1)		32			
8	8	8 (1)		8			
9	25	8 (1), 2 (2)		20	5		
10	32	5 (1), 5 (2)		16	16		
11	10	10 (2)			10		
12	6	6 (2)			6		
13	3	3 (2)			3		
14	6	1 (2), 5 (3)			1	5	
15	2	1 (2), 1 (3)			1	1	
16	3	1 (2), 1 (3), 1 (4)			1	1	1
17	3	1 (3), 2 (4)				1	2
18	0	–					
19	1	1 (4)					1
20	1	1 (4)					1
Total	218		21	141	43	8	5

techniques are similar to those used to estimate annual growth from hard structures. Although growth can be described in terms of length or weight, we will generally limit our discussion to growth in length. Length and weight are closely related (Chapter 14), and the techniques used to estimate growth in length can be easily applied to growth in weight.

A number of methods exist to estimate growth of fish, including direct observation, changes in length-frequency distributions through time, and back-calculation of length from hard structures. We will briefly review techniques associated with direct observation and length-frequency analysis followed by a more detailed discussion of estimating growth from hard structures by means of an age–length key or back-calculation. Growth models, size-specific growth analyses, and growth standards will also be presented to introduce more advanced analytical techniques.

15.4.1 Observation of Individuals

Direct observation of individual fish is the least variable and most accurate technique for quantifying growth because the only source of variation is measurement error. Based on this technique, growth is the change in fish length between recapture events (Neilson et al. 2003). Whereas fish are marked in some field studies for the sole purpose of obtaining growth data (Chapter 11), direct observation of growth in natural systems is often supplementary information obtained from mark–recapture studies, for which the primary focus is on movement or population estimation. Direct observation provides accurate information on growth, but capturing, marking, and recapturing fish in natural systems is labor intensive, time-consuming, and costly and often yields low sample sizes given the difficulty of recapturing individual fish.

15.4.2 Length-Frequency Analysis

Length-frequency distributions can be used to estimate growth of fish by following changes in the modal length for an age-group through time (Taylor and Miller 1990; Roa-Ureta 2009; Figure 15.14). Identification of age-groups can be difficult, particularly for older fish, and is therefore usually limited to estimating growth of young fish (e.g., age-0 or age-1 fish). Similar to aging fish, estimating growth of fish from length-frequency distributions is commonly conducted for short-lived species (e.g., some cyprinids) or in situations in which growth cannot be estimated from hard structures (e.g., fish from tropical regions).

15.4.3 Growth Estimates from Hard Structures

One of the most common techniques used by fisheries scientists to estimate growth is from hard structures. Section 15.2.3 provides guidance on how to age fish by measurement of different structures, but this section outlines how growth data can be obtained from the same structures. The methods for determining growth are nearly as diverse as the methods for determining ages in fish and vary from relatively straightforward techniques to more complex mathematical approaches.

15.4.3.1 Length at Age from an Age–Length Key

If all fish in a sample are aged, then mean length at age (i.e., at capture) is simply the average length of fish in each age-group. However, when a subsample of fish is collected, alternative methods must be used. Section 15.3 addressed assigning ages to fish by use of an age–length key, but age–length keys can also be used to estimate lengths at specific ages. These data can then be used to evaluate annual growth by comparing changes in length across age-classes. The general approach is to determine the mean length of individuals of a certain age using the knowledge gained from a subset of aged fish. However, care must be taken when fish are subsampled. Sup-

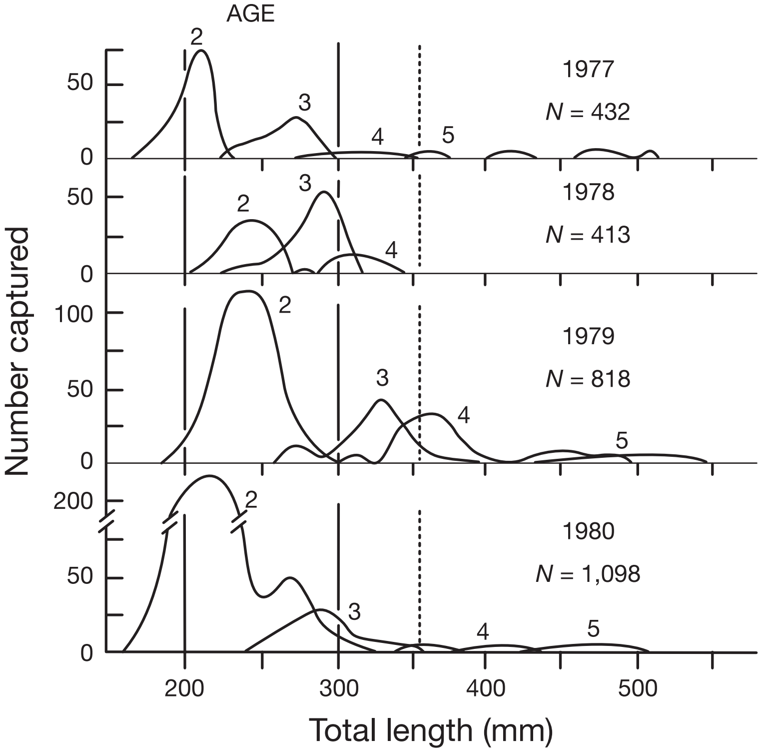

Figure 15.14 Example of following age-groups and growth through time. Figure contains length-frequency distributions of age-2 and older largemouth bass collected in Ross Lake, Ohio, in spring 1977–1980. Solid vertical lines denote minimum stock and quality lengths (Chapter 14) and dotted vertical lines indicate the 356-mm-minimum-length limit (adapted from Carline et al. 1984).

pose one collects hard structures from a fixed number of fish in a sample (e.g., 10 fish per 1-cm length-group). A seemingly logical, but incorrect, method of estimating mean length at age is to estimate the mean length of each age-group from individuals in the aged subsample (Bettoli and Miranda 2001). Unfortunately, this practice provides biased estimates of mean length at age because the data do not represent a simple random sample of the population (Kimura 1977; Bettoli and Miranda 2001). The correct method for estimating mean length at age of fish collected using a fixed number of fish per length-group is to use information from the age–length key (section 15.3). Bettoli and Miranda (2001) provide the following method:

$$L_i = (\sum N_{ij} \cdot l_{ij}) / N_i, \text{ and} \tag{15.1}$$

$$S_i^2 = [\sum N_{ij}(l_{ij} - L_i)^2] / (N_i - 1), \tag{15.2}$$

where L_i is the mean length of the ith age-group, S_i^2 is the variance in mean length of the ith age-group, N_{ij} equals $N_j(n_{ij}/n_j)$, N_j is the total number of fish in the jth length-group, n_{ij} is the number of fish of the ith age-group subsampled from the jth length-group, n_j is the number of fish subsampled in the *j*th length-group, l_{ij} is the mean length of fish of the *i*th age-group subsampled from the *j*th length-group, and N_i equals $\sum N_{ij}$ over all *j* length-groups. For an example of these calculations, see Box 15.3. An alternative method is to substitute the midpoint of each length-group for l_{ij} in the equations (e.g., DeVries and Frie 1996). If the midpoint is equal to l_{ij}, then the results are equivalent. Another technique is to assign ages to individual un-aged fish, allowing mean length of fish in the entire sample to be estimated by age-group (Isermann and Knight 2005). This method will produce results similar to those of the method described by Bettoli and Miranda (2001), but the extent of similarity depends on the specific length-group interval used for subsampling.

Box 15.3 Computation of Mean Length at Age and Its Variance from an Age–Length Key

When fish are subsampled for aging, mean length at age can be estimated using information contained in the age–length key and equations (15.1) and (15.2) in the text. In the example below, the length at age 1 of fish presented in Box 15.2 is estimated. Six length-groups encompassed age-1 fish. The number at each age (N_{ij}) was estimated in Box 15.2. Mean lengths of fish in each age-group and length-group (i.e., l_{ij}) are presented below and represent the mean length of age-1 fish that were aged in the subsample.

Table Example of estimating mean length at age from an age–length key. Length data are of fish presented in Box 15.2. Symbols defined in section 15.4.3.1.

Length-group (cm) (*j*)	Number of age-1 fish in sample (N_{ij})	Mean length of age-1 fish from subsample (l_{ij})	$N_{ij} \times l_{ij}$	Mean length of age-1 fish (L_i)	$(l_{ij} - L_i)^2$	$N_{ij} \times (l_{ij} - L_i)^2$
5	23	53	1,219	74	441	10,143
6	42	62	2,604	74	144	6,048
7	32	74	2,368	74	0	0
8	8	81	648	74	49	392
9	20	98	1,960	74	576	11,520
10	16	103	1,648	74	841	13,456
Sum	141		10,447			41,559

Using these data and the total number of age-1 fish across length-groups (i.e., $N_i = \sum N_{ij}$ for age-1 fish), mean length at age 1 is estimated as

$$L_i = \sum \left(N_{ij} \cdot l_{ij} \right) / N_i = 10{,}447 / 141 = 74 \text{ mm.}$$

Variance is estimated as

$$S_i^2 = \sum \left[N_{ij} \left(l_{ij} - L_i \right)^2 \right] / (N_i - 1) = 41{,}559 / 140 = 297.$$

Sampling bias can bias growth estimated by length-at-age analyses. If sampling tends to be biased toward young or old fish, or slow- or fast-growing fish, mean length at capture will reflect these biases among ages. In addition, mean length at capture must be presented within the context of when fish were captured. Mean length at age 1 in May is much different than mean length at age 1 in November. Mean length at age may also have little value unless data are collected in several years. For instance, suppose the mean length of several age-2 yellowfin tuna is 1,000 mm. This information has limited value unless one knows whether the fish from that year-class averaged 400 mm or 900 mm at age 1. In addition, caution is warranted when interpreting growth increments (e.g., growth between ages 1 and 2) by use of mean length at age unless there is strong evidence that growth is consistent through time among ages or if the time interval is extremely short (e.g., daily growth of larval fish). Common uses of length-at-age data include simple summarizations or incorporation into growth models (section 15.4.3.3).

15.4.3.2 Back-Calculation of Fish Growth

The preceding techniques (e.g., length-frequency analysis and mean length at age) may require multiple samples through time to provide interpretable and insightful estimates of fish growth. However, information on the growth histories of individual fish and age-groups from a single sample can be obtained by back-calculation of growth. Back-calculation of growth is based on a repeatable relation between the size of a hard structure and fish length (Box 15.4). If such a relationship exists and one is able to identify annular or daily marks on hard structures accurately, then fish lengths at all previous marks (e.g., annuli) can be back-calculated by translating the distance between marks on the hard part into fish length. The only data that are required are the measured length at capture, the radius of the hard structure at capture, and the radius of the hard structure to the outer edge of each growth increment. These measurements can be obtained using a variety of techniques; the most common are described below.

Measurement of growth from hard structures. Scales are one of the most common structures used for back-calculation. Measurements are typically recorded along an axis that originates at the focus and extends to the anterior edge of the scale. However, annuli on the anterior edges of scales of some species with cycloid scales may be difficult to identify because of crowding. When scale morphologies prevent identification of annuli along the anterior axis, the accepted practice is to select an alternative measurement axis, such as a lateral axis (i.e., focus to dorsal or ventral edge of scale). Regardless of the specific measurement axis, maintaining a standardized axis is critical. In other words, if an anterior axis works well for cutthroat trout in a sample, but a lateral axis is most appropriate for longnose suckers, then all measurements of cutthroat trout scales should be on the anterior axis and all measurements of longnose sucker scales should be taken along the lateral axis. Though not common, identification of the focus may be difficult or impossible for some species and may require measurement of diameters of annuli and subsequent conversion to radius estimates (Przybylski and Garcia-Berthou 2004). Although estimating annual growth is by far the most common use of scales, some studies have used measurements of circuli increments to provide information on the ecology of fishes (e.g., Moss et al. 2005).

Fin rays and spines are commonly used for estimating back-calculated lengths at age. Sections of fin rays and spines are often V-shaped, with one side of the V being longer than the other (Figure 15.15). In these instances, measurements are usually recorded on the longer side because of increased clarity of annuli. However, fin ray or spine morphologies vary among species, making standardization problematic. For some species, finding an adequate starting point or measurement axis

Box 15.4 Back-Calculation of Past Length at Age

Back-calculation is a technique that allows fisheries biologists to obtain information on the past size of a fish based on the relation between the radius of a hard structure and fish length. If the relationship is directly proportional, then it can be graphically demonstrated as follows.

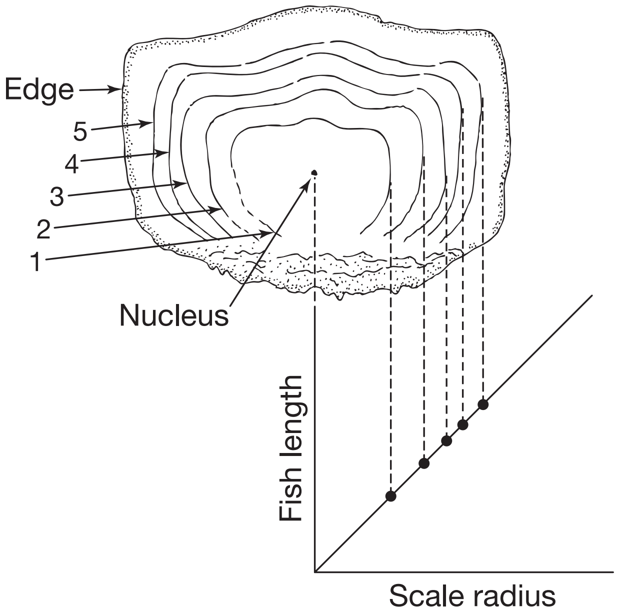

Figure Graphical representation of the basis of back-calculation of past length at age.

The Dahl–Lea equation (equation 15.3) is commonly used to estimate the length of a fish at various ages. For example, given the length of a walleye at capture (L_c) is 610 mm and its scale radius at capture (S_c) is 4.91 mm, if scale radii (S_i) at previous annuli are as presented in table below, then the back-calculated lengths at these annuli (L_i) are as shown in table below. The annual growth increment is the difference between the initial length of a fish at the start of a particular growing season and its length at the end of the year. For instance, the fish described below had an initial length of 221.1 mm at the beginning of its second growing season (first season = hatching to age 1; second season = age 1 to age 2) and was 387.6 mm at the end of that season. Thus, the fish grew 166.5 mm during its second growing season.

(Box continues)

may be difficult because of erosion of the central lumen, the presence of vascularized regions in the spine (e.g., some scombrids), or simply the morphology of the spine or ray. In such cases, measurement of the diameters of the structure and growth rings along a standardized axis may be a suitable alternative (see Cayre and Diouf 1983 for an example). As with scales, consistent measurement axes must be established and adhered to while recording growth measurements.

Box 15.4 Continued

Table Hypothetical walleye with a length at capture (L_c) of 610 mm and scale radius at capture (S_c) of 4.91 mm. Scale radii (S_i) at previous annuli are presented and lengths at these annuli (L_i) are back-calculated using equation (15.3). Annual growth increment can then be calculated.

Age (*i*)	S_i and S_c (mm)	L_i and L_c (mm)	Annual growth increment (mm)
1	1.78	221.1	166.5
2	3.12	387.6	79.5
3	3.76	467.1	57.2
4	4.22	524.3	42.2
5	4.56	566.5	23.6
6	4.75	590.1	
Capture (*c*)	4.91	610	

Whereas the Dahl–Lea method is common, the relationship between fish length and hard structure radius is typically not this simple. For example, fish hatch at lengths that are greater than 0 mm, and their hard structures, or increments on their hard structures, do not always begin to form upon hatching (e.g., larval fish lack scales until they reach a specific length). Therefore, the relationship between fish size and hard structure radius does not always extend through the origin, as required for the Dahl–Lea method. In these cases, the Fraser–Lee method (equation 15.4) can be used to assign the intercept a nonzero value. Further, the slope of the relationship for an individual fish in equation (15.4) is calculated as the slope of the line connecting two data points for that fish—(S_c, L_c) and (0, a). The slope is $(L_c - a)/S_c$, where S_c is the radius of the hard structure at capture, L_c is the length of the fish at capture, and a is the intercept of the regression of fish length on hard structure radius (a simply equals zero for the Dahl–Lea method). Values of a are commonly estimated using empirical data. Alternatively, standardized values of a have been established for some species (Table 15.1).

If the length of a walleye at capture is 610 mm, its scale radius at capture is 4.91 mm, and the intercept (a) of the regression of fish length on scale radius is 55.0 mm (standard a-value for walleye; Table 15.1), then the slope ($[L_c - a]/S_c$) is 113.0. Given the following scale radii (S_i) to previous annuli, the lengths of the fish at those previous annuli (L_i) are as follows.

(Box continues)

Otoliths also contain information on previous growth of individuals such that back-calculated lengths at age can be estimated. However, the characteristic that makes them so useful for aging (i.e., deposition of marks with little or no somatic growth) suggests that caution should be used when interpreting past growth of fish based on otoliths, particularly at older ages. Growth estimates from otoliths are commonly derived using a combination of length-at-age (i.e., at capture) data

Box 15.4 Continued

Table For the same hypothetical walleye as above, lengths of fish at previous annuli (L_i) are back-calculated using equation (15.4). Annual growth increment can then be calculated.

Age (i)	S_i and S_c (mm)	L_i and L_c (mm)	Annual growth increment (mm)
1	1.78	256.2	151.4
2	3.12	407.6	72.3
3	3.76	479.9	52.0
4	4.22	531.9	38.4
5	4.56	570.3	21.5
6	4.75	591.8	
Capture (c)	4.91	610	

A graphical representation of these calculations is provided below (also see Figure 15.17). A figure depicting the Dahl–Lea method would be similar except that the intercept would pass through the origin.

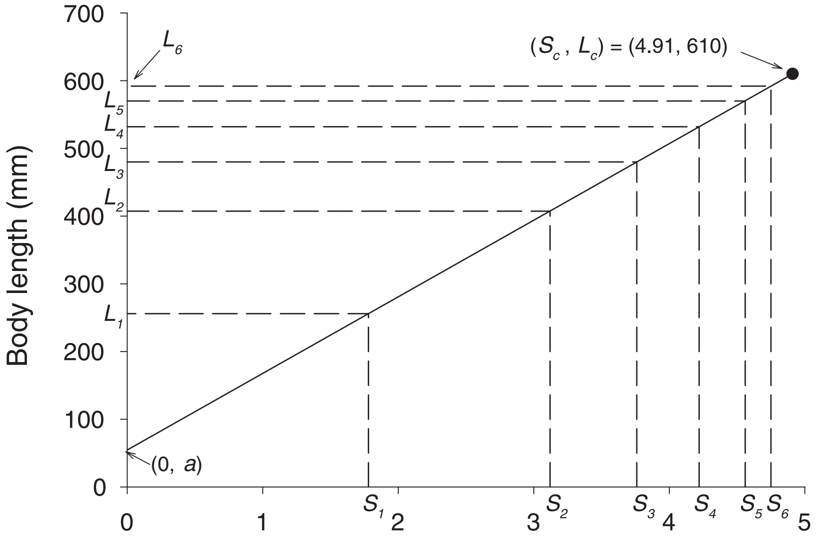

Figure Growth of hypothetical walleye based on the Fraser–Lee method of back-calculation. Corresponding S_i and L_i are noted on axes.

Fisheries scientists often calculate mean age-specific back-calculated lengths from estimated back-calculated lengths at age of individual fish to assess fish populations. The first step is to estimate mean back-calculated length at age of a year-class or age-group. In the

(Box continues)

Box 15.4 Continued

following table, the mean back-calculated length at age 1 of 15 sampled and aged age-1 fish was 253.2 mm. For age-2 fish, the mean back-calculated length at age 1 was 251.0 mm and at age 2 was 379.5 mm. After conducting these calculations for each year-class, a table of mean back-calculated lengths at age by year-class is produced.

Table Mean back-calculated lengths at age (mm) for six year-classes.

Age	Year-class	Number in sample (*w*)	Mean back-calculated lengths at age (mm) 1	2	3	4	5	6
1	2005	15	253.2					
2	2004	56	251.0	379.5				
3	2003	35	256.9	397.6	463.5			
4	2002	28	252.8	415.2	483.1	534.3		
5	2001	10	250.9	403.8	470.7	529.8	566.4	
6	2000	4	254.3	404.8	474.3	533.1	561.2	591.1

This information is useful, especially when comparing growth among age-classes, but scientists often desire estimates of the overall mean back-calculated lengths at age for all of the age-classes in an entire sample. One method to obtain these estimates is simply to take the overall average of the back-calculated lengths at age of *all* fish in the sample. An equivalent method is to use a weighted average of the mean back-calculated length at age data presented in the table above. Calculation thereof requires calculation of weighted means by first multiplying the number of fish in each year-class by their mean back-calculated lengths at each age. The sum of these products for each age is divided by the sum of the number of back-calculated lengths at age (i.e., the weights) resulting in an overall mean back-calculated length for each age.

(Box continues)

and growth models (section 15.4.3.3), particularly for daily growth of larval fish (Stevenson and Campana 1992). Similar to other hard structures, preparation of otoliths for growth analysis can be time consuming because care must be taken so that every structure is prepared in the same manner. A number of processing techniques are available, but a common technique is to crack or section otoliths along a transverse plane and measure along an axis extending from the nucleus to the dorsal or ventral edge of the otolith (Figure 15.16; Rutherford et al. 1995; Stunz et al. 2000; Stafford et al. 2002). Measurements are typically recorded along a straight line. Alternative measurement techniques are used if otolith morphology prevents a straight-line measurement axis (Oliveira and McCleave 2002; Watari et al. 2005). Regardless of the specific sectioning techniques and measurement axes, axes must be standardized among individuals in the sample if increments are to be used in growth analyses.

Growth estimates from the other hard structures referred to in section 15.2.3.2 (e.g., cleithra and opercles) are usually obtained using length-at-age data and growth models. Because these

Box 15.4 Continued

Table Weighted mean back-calculated lengths at age for six year-classes.

Year-class and statistic	Number in sample (w)	Weighted mean back-calculated lengths at age					
		1	2	3	4	5	6
2005	15	3,798.0					
2004	56	14,056.0	21,252.0				
2003	35	8,991.5	13,916.0	16,222.5			
2002	28	7,078.4	11,625.6	13,526.8	14,960.4		
2001	10	2,509.0	4,038.0	4,707.0	5,298.0	5,664.0	
2000	4	1,017.2	1,619.2	1,897.2	2,132.4	2,244.8	2,364.4
Σ(weighted mean back-calculated length at age)		37,450.1	52,450.8	36,353.5	22,390.8	7,908.8	2,364.4
Σ(w)		148	133	77	42	14	4
Overall mean back-calculated length at age		253.0	394.4	472.1	533.1	564.9	591.1

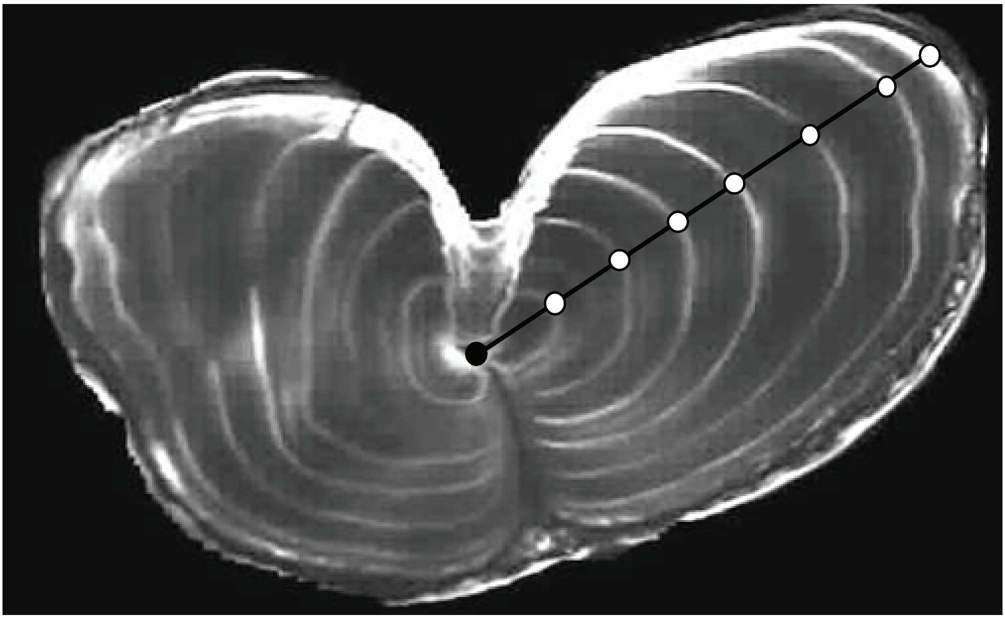

Figure 15.15 Cross section of a dorsal spine from an age-7 walleye. White circles indicate annuli. Because this fish was sampled in early spring before annulus formation, the seventh annulus is the spine edge (image courtesy of Joseph Larscheid, IDNR).

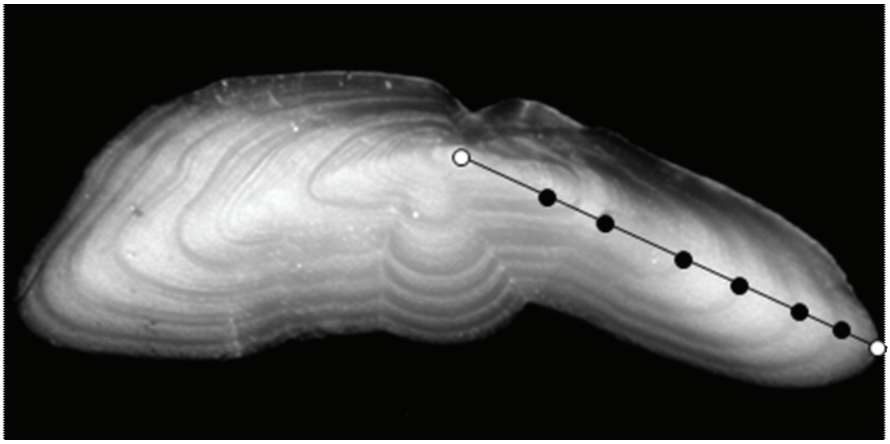

Figure 15.16 Example of a sectioned sagittal otolith from an age-6 Atlantic cod. The white circle near the center of the otolith indicates the nucleus, the black circles indicate annuli, and the white circle towards the outside of the otolith indicates the edge (image courtesy of Steven Campana, BIO).

structures are less commonly used than are otoliths, fin rays, spines, and scales for back-calculation purposes, we recommend that readers seek additional information on common methods for identifying and measuring growth increments on these structures.

A variety of techniques is available to obtain measurements from hard structures. Growth marks are typically measured to the outer edge of the mark (i.e., edge away from the center of the structure). One method for measuring growth marks is to measure the structure directly by use of an ocular micrometer. With this technique, a scale, otolith, or other structure is viewed with a dissecting or compound microscope. The distances from some standardized starting point (e.g., focus or nucleus) to the edge and to each growth ring are measured by means of the ocular micrometer and recorded along an established measurement axis. Microfiche readers or microprojectors are commonly used for scales (section 15.2.3.2; Figure 15.5); the scale image is projected onto a screen, the rings are counted, and annuli are marked on a piece of paper. Marks on the paper can then be measured with a ruler, a digitizing tablet, or an image analysis system. Another common method is to take a picture of the structure with a camera attached to a microscope. Printed images of the structure can then be measured with a ruler or digitizer (Marwitz and Hubert 1995; Bariche 2005; Rypel 2008). Alternatively, digital images can be captured using a microscope and camera attached to a computer (Figure 15.5). By means of image analysis software, measurements are obtained and stored digitally. An important aspect of all techniques is that the magnification is recorded so that measurements are related to the measurement scale used to measure body length.

Back-calculated length-at-age estimation techniques. After hard structures have been aged and annular or daily growth measurements have been obtained, the next step is to back-calculate the length of individual fish at previous ages (Box 15.4). The two primary types or categories of back-calculation that have been used by fisheries scientists are direct regression and proportional methods. Direct regression techniques are mentioned only because some readers may encounter these techniques in the literature. However, direct regression techniques should be avoided because they discard growth information, ignore variation in hard structure size among individuals, and frequently overestimate back-calculated length at age (see Carlander 1981 and Francis 1990 for critiques). Rather, back-calculation techniques that are based on the proportional relationship between individual fish body size and the size of its hard structures are recommended (Francis 1990; Ricker 1992). Although numerous variations exist, we will focus on the most common methods.

The Dahl–Lea, or direct proportion, method for estimating back-calculated length at previous age is used when the relation between fish length and hard structure radius (e.g., focus to edge of scale) is linear and has an intercept that does not differ from the origin (i.e., through the origin; Figure 15.17). In such a situation, growth of the hard structure is directly proportional to body growth. Based on this relationship, length at previous ages can be calculated as

$$L_i = L_c(S_i / S_c), \tag{15.3}$$

where L_i is the back-calculated length of the fish when the *i*th increment was formed, L_c is the length of the fish at capture, S_i is the radius of the hard structure at the *i*th increment, and S_c is the radius of the hard structure at capture (Ricker 1975).

The equation represents a set of all possible lines passing through the origin (Figure 15.17). To back-calculate the length of an individual fish, we use the line that passes through the origin and the point S_c, L_c (note that this point is different for each fish). A primary assumption of this method that must be verified is that the regression between fish length and hard structure radius has its intercept at the origin. If the intercept differs from the origin, errors in back-calculated growth can result, and another technique should be used. The Dahl–Lea method is not usually used with scales but is common for fin rays, spines, and otoliths (Schramm et al. 1992).

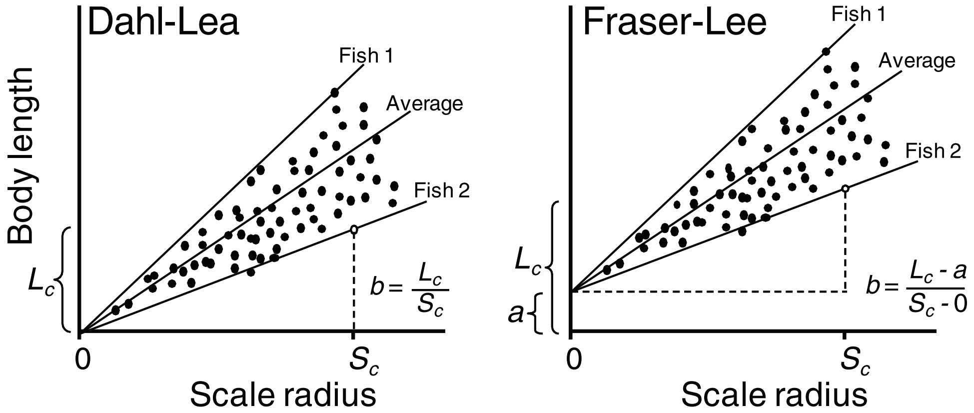

Figure 15.17 A comparison of how the Dahl–Lea and Fraser–Lee methods back-calculate body length from distances between the focus and each annulus on a hard structure for each fish. Back-calculated lengths at age *i* are calculated for individual fish as described by equations (15.3) and (15.4). Each fish has its own slope (*b*), which is estimated from a two-point regression. In the case of the Dahl–Lea equation, one point is (S_c, L_c) and the other is (0, 0). For the Fraser–Lee equation, one point is also (S_c, L_c) but the other is (0, *a*) (see Box 15.4). The radius of the hard structure at capture (S_c) and the length of the fish at capture (L_c) is the same in both equations. The intercept parameter (*a*) is zero for the Dahl–Lea equation and nonzero for the Fraser–Lee method.

The Fraser–Lee method of back-calculation was developed in response to observations that body length versus hard-structure radius relationships often fail to pass through the origin (Figure 15.17). It is now one of the most widely used back-calculation techniques. The equation for estimating back-calculated length at previous age is

$$L_i = ((L_c - a)/S_c)\ S_i + a, \tag{15.4}$$

where a is the intercept parameter and the other variables are defined above.

The slope of the Fraser–Lee equation, $(L_c - a)/S_c$, is calculated for each fish as the slope of a line connecting two points: (S_c, L_c) and $(0, a)$. The value of a is calculated as the intercept of the regression of fish length at capture on hard-structure radius at capture for a range of fish sizes of the species being examined (Figure 15.18). When a equals 0, the Fraser–Lee equation is equivalent to the Dahl–Lea method. The meaning of a has been debated extensively. Some have suggested that a is the length of the fish when it first forms the hard structure. However, a can be negative, leading many to argue that a cannot be given a morphological interpretation. Perhaps the most appropriate interpretation is the statistical interpretation of a as the best value that will predict L_c in the regression of fish length on hard-structure radius. To help keep any bias in age estimates caused by this parameter consistent among scientists, standard a-values have been developed (e.g., Table 15.1). Alternatively, an a-value can be empirically estimated for the sample. When an a-value is empirically derived from a sample, care must be taken to ensure that fish across the entire distribution of fish lengths are included, particularly small fish (e.g., Hudson and Bulow 1984).

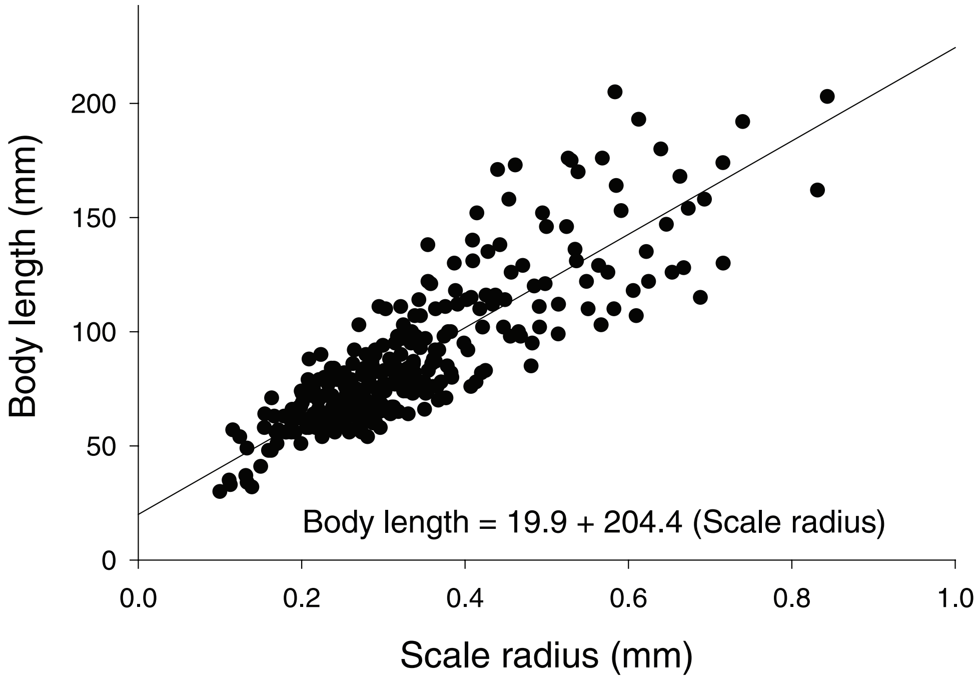

Figure 15.18 Body length versus scale radius relationship for 286 creek chubs sampled from a stream in eastern Kansas. The intercept parameter, a, of the regression equation is used in the Fraser–Lee equation for back-calculating length at previous ages.

Table 15.1 Standard intercept values (i.e., *a*-values) of the fish length to scale radius relationship used for estimating back-calculated length at age with the Fraser–Lee method. All values are from Carlander (1982) except for white bass (Beck et al. 1997).

Species	Standard *a* (mm)
Centrarchidae	
Bluegill	20
Black crappie	35
Green sunfish	10
Largemouth bass	20
Pumpkinseed	25
Rock bass	25
Smallmouth bass	35
Warmouth	20
White crappie	35
Moronidae	
White bass	40
Percidae	
Yellow perch	30
Walleye	55

The direct proportion and Fraser–Lee methods are the most widely used back-calculation techniques. However, they are not the only back-calculation methods, nor are they always appropriate for all species and structures. Most additional back-calculation techniques have the same general form and differ only by slight modifications to slope and intercept values (Table 15.2; see Bartlett et al. 1984, Ogle et al. 1996, and Morita and Matsuishi 2001 for additional methods and discussion). Depending on the relation between fish length and hard structure radius, these equations may or may not result in identical back-calculated lengths at age (Francis 1990; Ricker 1992). Pierce et al. (1996) compared mean back-calculated lengths at age of pumpkinseeds and golden shiners calculated using three different back-calculation equations (Fraser–Lee, one based on the body proportional hypothesis, and one based on the scale proportional hypothesis) and found that estimates were nearly identical among the three techniques. Michaletz et al. (2009) evaluated the accuracy and precision of several back-calculation techniques for estimating growth of channel catfish by use of pectoral spines and otoliths. They found substantial differences in the accuracy of back-calculation models that were a function of the axis from which structure measurements were taken.

The biologically modified Fraser–Lee equation is somewhat unique in that it explicitly uses biologically derived values to obtain estimates of back-calculated length at age (Campana 1990; Ricker 1992). This technique was originally developed to account for the observation that otolith size is often disproportionate to fish size (Campana 1990), which violates the primary assumption necessary to back-calculate length at age accurately from hard structures. The method has provided accurate back-calculated length estimates for larval and juvenile fish, but its usefulness for estimating annual growth and for structures other than otoliths remains to be investigated (see Ricker 1992 for additional discussion).

Table 15.2 Examples of linear and nonlinear techniques used to back-calculate length of fish at previous ages. All equations have the following parameters in common: L_i = back-calculated length at the ith increment; L_c = length at capture; S_i = radius of the hard structure at the ith increment; S_c = radius of the hard structure at capture. Additional parameters are listed in the third column.

Method	Equation	Parameter description	Reference
		Linear methods	
Dahl–Lea	$L_i = (S_i/S_c)L_c$		Ricker (1975)
Fraser–Lee	$L_i = a + [(L_c - a)/S_c]S_i$	a = intercept of L_c on S_c	Ricker (1975)
Scale proportional hypothesis or Hile	$L_i = (-b/c) + \{[L_c + (b/c)]/S_c\}S_i$	b = intercept of S_c on L_c; c = slope of S_c on L_c	Francis (1990)
Body proportional hypothesis or Whitney and Carlander	$L_i = [(a + dS_i)/(a + dS_i)]L_c$	a = intercept of L_c on S_c; d = slope of L_c on S_c	Francis (1990)
Biologically modified Fraser–Lee	$L_i = L_c + [(S_i - S_c)(L_c - L_0)]/(S_c - S_0)$	L_0 and S_0 = length of fish (L_0) and hard-structure size (S_0) at the initiation of proportionality between fish and hard-structure growth	Campana (1990)
		Nonlinear methods	
Monastyrsky	$L_i = (S_i/S_c)^v L_c$	v = constant from $L_c = \mu S_c^v$	Francis (1990)
Quadratic	$L_i = L_c[(a + bS_i + cS_i^2)/(a + bS_c + cS_c^2)]$	a, b, and c = constants from $L_c = a + bS_c + cS_c^2$	Francis (1990)

The Weisberg method (Weisberg and Frie 1987; Weisberg 1993; Weisberg et al. 2010) is more of an analytical process than an explicit back-calculation technique, but it can be used to obtain estimates of back-calculated lengths at age. Two versions of the technique have been proposed. The first technique, described in Weisberg (1993), uses fixed-effects linear models to separate variation in growth caused by environmental factors from that caused by the age of a fish. Models are fit to hard structure increments and results are translated into back-calculated lengths. Maceina (1992) describes a similar approach. More recently, Weisberg et al. (2010) described a technique similar to Weisberg (1993) that uses mixed-effects models instead of fixed-effects models. The new approach yields results similar to previous techniques but overcomes many of the shortcomings associated with fixed-effects approaches (e.g., within-fish correlations were ignored and among-study comparisons could not be made).

Based on the diversity of methods and continuous discussion of back-calculation techniques in the literature, it is apparent that the development of back-calculation techniques is a dynamic and often complex component of fisheries science. In most situations, estimating back-calculated lengths by means of the Dahl–Lea or Fraser–Lee methods is probably appropriate, but scientists should validate results whenever possible.

Lee's phenomenon. Lee's phenomenon occurs when back-calculated lengths at age of older year-classes are consistently smaller than those of younger year-classes (Ricker 1975; Table 15.3). A number of explanations for Lee's phenomenon have been proposed, including (1) older fish are slower-growing survivors of their year-class and have experienced reduced vulnerability to predation or fishing morality; (2) the ratio of fish length to hard structure size varies with fish growth; (3) the sampling gear is selective for fast-growing individuals of the youngest ages; (4) the aging technique is faulty; and (5) the intercept parameter or back-calculation technique is biased. If true, explanation 1 may provide important insight into processes influencing the population. If explanation 2 is true, detailed studies and complex back-calculation techniques may be required to provide reliable growth information. Validation of aging techniques and adequate sampling would help reduce problems associated with sampling and aging bias (explanations 3 and 4). Techniques have been proposed for evaluating whether Lee's phenomenon is caused by back-calculation error (Gutreuter 1987; Newman and Weisberg 1987; Smale and Taylor 1987), and methods for eliminating it include using biologically derived intercept values (Campana 1990) or measuring increments from only the two or three most recent growth years (Gutreuter 1987).

Table 15.3 Mean back-calculated lengths at age of bluegill by year-class illustrate Lee's phenomenon. Younger year-classes in the sample appear to have faster growth at younger ages (e.g., mean length at age 1) than do older year-classes.

		Mean back-calculated lengths at age (mm)					
Age	Year-class	1	2	3	4	5	6
1	1993	90.5					
2	1992	85.3	113.6				
3	1991	78.9	112.2	139.6			
4	1990	75.9	108.9	133.8	150.3		
5	1989	66.2	96.0	129.1	147.5	160.3	
6	1988	59.7	92.2	126.2	145.4	156.6	166.2

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

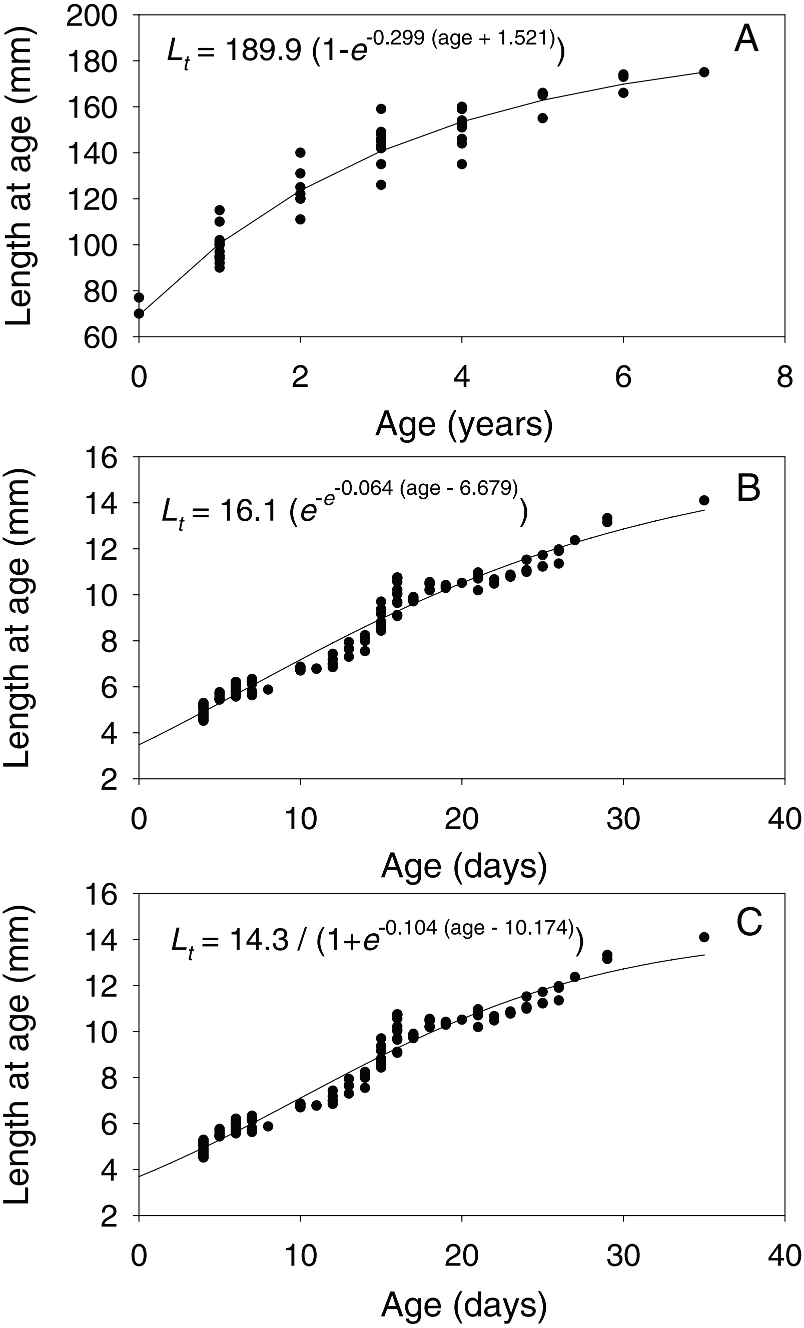

Figure 15.19 Examples of von Bertalanffy (**A**; creek chub), Gompertz (**B**; larval white bass), and logistic (**C**; larval white bass) growth models.

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

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

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

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

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;

Werner and Gilliam 1984). Pauly (1987) stressed the need for size-specific analyses because size-specific techniques are more biologically interpretable than are age-based models. Compared with age-specific techniques, few studies have used size-specific analysis techniques, perhaps because of a strong tradition of age-specific analyses, an unawareness of size-specific methods, or perceived complexity of analytical techniques. Regardless, size-specific growth analyses complement traditional age-specific techniques and can provide a more detailed understanding of factors influencing growth.

As with all growth analyses, size-specific analyses vary from simple to complex, but the basic premise is the same for all methods. The focus of size-specific growth analysis is on the size rather than the age of a fish; however, size-specific techniques also rely on back-calculated length-at-age data. First, the growth histories of individual fish are determined by back-calculation (Box 15.5). Then, annual growth increments of all individuals in the sample are plotted against their initial lengths at the beginning of the year. A regression model may be fitted to the data, but because these models are typically curvilinear, the statistical techniques may be complex. The resulting regression model can then be used to interpret growth. For instance, annual growth can be estimated for different sizes of fish, such as the size at which fish switch from one prey type to another, reach sexual maturity, reach a size suitable for recreational or commercial harvest, or correspond to size structure indices (Chapter 14). Excellent examples of this approach can be found in Osenberg et al. (1988), Neumann et al. (1994), Putman et al. (1995), Gutreuter et al. (1999), and Shoup et al. (2007). Although similar inferences may result from age-specific analyses, size-specific techniques are often more biologically interpretable and may elucidate patterns not observed by age-specific methods. Ideally, fisheries scientists should conduct both age- and size-specific analyses to provide the best possible assessment of growth.

15.4.3.5 Growth Standards

A primary reason for conducting an age and growth analysis is to compare growth of fish in a population through time or among populations. Comparisons can be made to regional or statewide mean back-calculated lengths at age (or mean lengths at age) to determine whether fish are growing faster or slower than in other regional water bodies (Carlander 1969, 1977, 1997). Such comparisons can be made in terms of standard percentiles (Table 15.4; Hubert 1999). For example, if the mean back-calculated length at age 5 of a channel catfish population is 400 mm, then it would be in the upper 75th percentile of growth, indicating relatively fast growth compared with other North American channel catfish populations (Table 15.4). In addition to channel catfish, percentile values of growth have been developed for a number of North American freshwater fishes (Quist et al. 2003; Jackson and Hurley 2005; Jackson et al. 2008).

Growth indices may also be used to make comparisons among populations. For instance, Casselman and Crossman (1986) compiled growth information on about 500 individual muskellunge from populations across Canada and the USA. They estimated age-specific standard lengths (and weights) by means of a von Bertalanffy growth model. A relative growth index was then estimated as the observed length (multiplied by 100) divided by the standard length (i.e., predicted length from the von Bertalanffy model) for a given age (estimated in the same manner as relative weight, W_r; Chapter 14). Similar growth standards were proposed for a number of North American freshwater fishes (Quist et al. 2003; Jackson and Hurley 2005; Jackson et al. 2008). In addition to these techniques, a number of other standards could be

Box 15.5 Size-Specific Growth Analysis

Size-specific growth analysis techniques focus on growth as it relates to the size of fish rather than the age of fish. For example, determination that an age-1 fish grew 151 mm over the course of a year would result from an age-specific analysis whereas determination that a 200-mm fish grew 50 mm during a year would be the result of a size-specific analysis. Size-specific analyses typically use the same data as used in age-specific analyses.

The first step is to establish the initial lengths of the fish and their subsequent growth. Back-calculated lengths at age of three individual fish are presented below in the first table. Annual initial lengths and growth increments calculated from the back-calculated lengths at age are shown in the second table. In this example, we assume that each fish was 5 mm long at hatch and that this length represents the initial length during the first growing year of each fish.

Table Back-calculated lengths at age.

	Back-calculated length at age (mm)		
Age	Fish 1	Fish 2	Fish 3
1	120	154	82
2	281	296	234
3	335	359	319
4	357		362
5	366		373
6			380

Table Initial lengths (IL, mm) and annual growth increments (AGI, mm).

Fish 1		Fish 2		Fish 3	
IL	AGI	IL	AGI	IL	AGI
5	115	5	149	5	77
120	161	154	142	82	152
281	54	296	63	234	85
335	22			319	43
357	9			362	11
				373	7

Because the back-calculated length at age 1 of Fish 1 was 120 mm, its annual growth increment was 115 mm during its first year of life. During its second growth year, Fish 1 had an initial length of 120 mm (5 mm + 115 mm; back-calculated length at age 1) and grew 161 mm. Additional growth increments are calculated similarly. Plotting annual growth increments against annual initial lengths of all three fish yields the figure below. An overall growth model, in this case a quadratic model, can then be fit to the data.

(Box continues)

Box 15.5 Continued

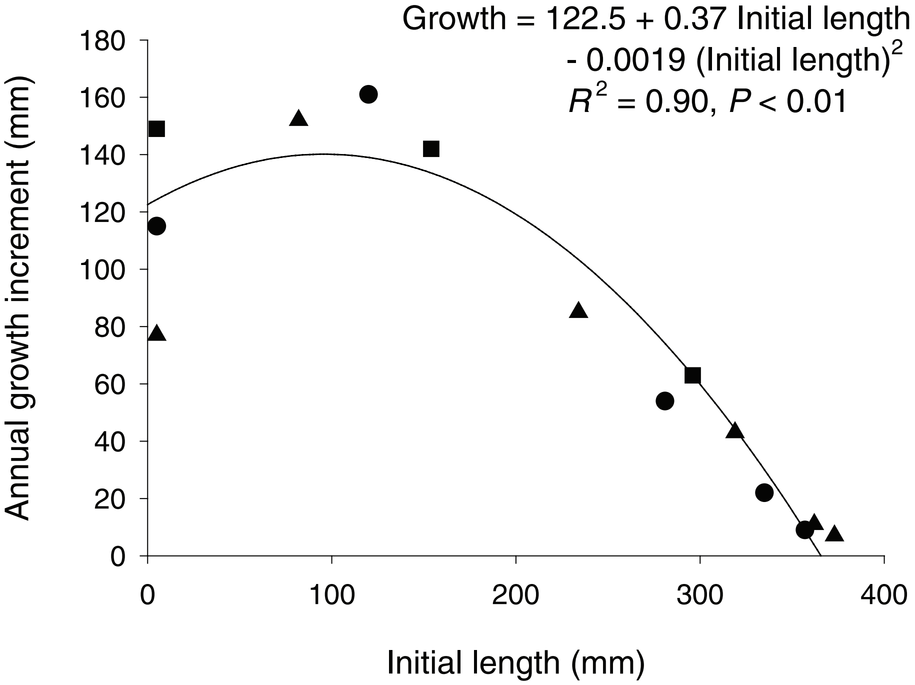

Figure Growth model (regression) based on growth data for three fish (different symbols represent different fish).

Estimates of growth of different sizes of fish can be estimated from the equation. Lengths of interest generally correspond to lengths at which major life history changes occur, such as the size at sexual maturity, recruitment to recreational or commercial fisheries (e.g., minimum length regulations or gear restrictions), switch to piscivory, or standard length categories (Chapter 14). In this example, a 100-mm fish has a predicted annual growth increment of 141 mm, a 200-mm fish has a predicted annual growth increment of 121 mm, and a 300-mm fish has a predicted annual growth increment of 63 mm. If multiple populations are sampled (e.g., from different sample sites), growth models can be fit to each population and growth of different sizes of fish can be compared or estimates can be used in further analyses (e.g., relationships with prey abundance or habitat characteristics).

used. For instance, the 50th percentile of growth (as proposed by Hubert 1999) could be used as a standard length for calculation of a growth index (rather than a standard estimated from a von Bertalanffy growth equation). Gutreuter (1987) suggested that growth standards based on size-specific growth increments might be useful. Regardless, comparing growth among and within populations will remain an important component of age and growth analyses, as will be the development of new methods for extracting the maximum amount of insight from age and growth information.

Table 15.4 Standard growth percentiles (mean length, mm) for age-3 to age-10 channel catfish in North America (modified from Hubert 1999).

	Percentiles						
Age (years)	5th	10th	25th	50th	75th	90th	95th
3	172	192	211	238	282	310	331
4	217	243	268	291	332	387	396
5	240	271	307	341	386	444	476
6	291	316	353	386	429	504	537
7	303	331	388	434	479	567	596
8	331	353	417	469	513	595	620
9	340	379	456	504	547	628	669
10	363	387	505	554	597	665	703

15.5 VALIDATION AND VERIFICATION OF MARKS ON HARD STRUCTURES

A necessary component of any age and growth analysis is an evaluation of the technique by both validation and verification. Although these terms are sometimes used interchangeably in the literature, they have different meanings when applied to age and growth analyses. Validation refers to the accuracy of the age or growth estimate, whereas verification refers to precision (Beamish and McFarlane 1983; Chapter 2; but see Kalish et al. 1995). Despite the demonstrated importance of validation, literature reviews in 1983 (Beamish and McFarlane 1983) and 2001 (Campana 2001) both found that documentation of validation in age and growth studies was lacking. These reviews included validation of absolute age as well as validation across age-classes (rather than for a single age-class). Lack of validation can cause costly errors, as demonstrated for walleye pollock by Beamish and McFarlane (1995; also see Beamish and McFarlane 1983 for examples with white sucker and Pacific ocean perch). In particular, mortality estimates based on incorrect age estimates can lead to setting regulations or quotas that result in overexploitation. Given the importance of the resources with which we are working, accuracy of age and growth information is important if we are to understand fisheries and thereby make the best possible management decisions.

A wide array of methods has been used to validate both annular and daily ages of fishes (Geffen 1992; Campana 2001; Durham and Wilde 2008; Schill et al. 2010). The most common methods used for annular aging have been marginal-increment analysis (see Campana 2001 and Isely and Grabowski 2007 for additional discussion) and mark–recapture of wild fish. The most often used approaches for daily increment analysis have been captive rearing in the laboratory or under controlled field conditions, often with some sort of chemical marking (see Campana 2001 for a thorough discussion). A technique used to validate ages of old fish is the analysis of radiocarbon (^{14}C) markers in otoliths, which resulted from widespread nuclear weapons testing in the 1950s and 1960s (Kalish 1993; Campana et al. 2006). Regardless of the technique, one benefit of validating hard-structure age estimates from specimens of known age is that it can assist readers in determining exactly what an annual or daily ring is, as opposed to the appearance of accessory marks, checks, or other anomalies. This is particularly important in the study of daily otolith increments, where formation of subdaily rings is common and a great deal of experience is required to distinguish true daily rings (Campana 1992; Geffen 1992). Regardless of the technique used for validation, both the frequency of increment formation as well as the age at first increment formation must be identified; without the latter component, ages may all be incorrect by some unknown constant amount.

Validation of back-calculation is difficult and has been rarely conducted, requiring that the observed lengths of individual fish, or groups of fish, be compared with those generated by back-calculation (Francis 1990). Typically this is attempted by comparing mean back-calculated lengths of a cohort of fish with mean lengths of another cohort. However, comparison among cohorts is often not appropriate because among-cohort variation in growth rates caused by different growing conditions can be great (Francis 1990). The preferred validation method is to compare measured and back-calculated lengths of the same individuals. A few examples exist, particularly with the use of marked individuals (e.g., Smedstad and Holm 1996; Horppila and Nyberg 1999; Klumb et al. 1999a, 1999b; Borkholder and Edwards 2001; Nitschke et al. 2001; Panfili and Tomás 2001; Neilson et al. 2003; Michaletz et al. 2009).

A measure of the precision of a fish-aging technique (i.e., verification) is best obtained by having two or more readers independently count the annular or daily rings. The independence of the readers prevents any bias that could occur if the counts obtained by one reader were known to the other reader(s). In addition, readers must be unaware of fish lengths to preclude assigning older ages to larger fish or similar ages to similar-sized fish. Aging fish without length information may be a bit frustrating, but the resulting age determination will be a more valid and objective statistic because systematic bias is minimized. Verification accomplished solely by a single reader making multiple independent counts on the same structure is not recommended. Whereas this approach will certainly lead to decreased variation compared with using more than one reader, it verifies only that the single reader is consistent in his or her reading technique across fish (or that the reader's biases are consistent across fish) and will still reflect other biases that may be present. As such, accuracy of the estimates may suffer. Systematic biases may also exist when two or more readers read the same hard structures. To test for this, counts by multiple readers can be directly compared using regression analysis, paired t-tests, or the nonparametric Wilcoxon matched-pairs rank test. A more sensitive approach is the age bias graph, in which the mean age (including some estimate of precision) determined by one reader is graphed as a function of the mean age (including some estimate of precision) determined by the other reader (Campana et al. 1995). Visual determination of systematic biases among readers is thereby relatively easy to identify.

Aging fish is an inherently subjective practice (Beamish and McFarlane 1995; Campana 2001; Buckmeier 2002; Morison et al. 2005). For example, accuracy of 36 fisheries professionals aging the same set of 50 known-age largemouth bass otoliths differed greatly, with biases existing for individual readers and accuracy differing between ages assigned to younger and older fish (Buckmeier 2002). Typical approaches to eliminate such among-reader variability are addition of a third independent reader, resolution of differences by discussion (Alves et al. 2002; Bariche 2005), or use of among-reader variation to correct for precision errors (Richards et al. 1992).

15.6 ADDITIONAL CONSIDERATIONS AND RESOURCES

The following sections provide information on emerging techniques associated with age and growth analyses and resources that aid in conducting age and growth analyses.

15.6.1 Integration of Age and Growth Information with Microchemistry of Hard Structures

Microchemical characteristics of hard structures have been quantified and used in stock identification, reconstruction of movement patterns, and mass marking (Coutant and Chen 1993; Outridge et al. 1995; Campana 1999; Veinott et al. 1999). Microchemical analyses of whole otoliths (Begg et al. 1998) and otolith cores (Hobbs et al. 2005) have been used to discriminate among local spawning populations. Movement patterns have been studied using elemental composition of fin rays and spines (Veinott et al. 1999; Arai et al. 2002), scales (Wells et al. 2003), and otoliths (Arai and Miyazaki 2001). The resolution of measurement is to a point at which fine-scale microchemical characteristics of the hard structure can be linked with temporal patterns, providing a potential way to link age, growth, and habitat use during a fish's life history (Secor et al. 1995; Milton et al. 2000; Swearer et al. 2003; Allen et al. 2009; Smith and Whitledge 2010). A great deal of research has been conducted to quantify the relations among concentrations of some important elements in fish otoliths (e.g., Sr, which is related to salinity; Kraus and Secor 2004) and environmental history of fish (see review in Campana 2005). Whereas countless questions remain, this is a rapidly developing and important area of research, particularly relative to fish early life history.

15.6.2 Resources for Conducting Age and Growth Analyses

Numerous data capturing and analysis techniques have been discussed in the preceding sections. Nearly all of the techniques can be easily carried out by hand, by use of spreadsheet programs, or by statistical analysis software programs. Fortunately, a number of fisheries-specific, commercially available software packages are available to assist with database management and age and growth analyses. The following is an overview of commonly used and readily available resources and is not meant to be an exhaustive list. In addition, presentation of commercially available software programs does not indicate endorsement by the authors or editors, nor can we assure that all calculations produced by software packages are accurate. Those using software packages should become familiar with the correct analytical techniques and validate the calculations of all programs.

The use of age–length keys is a common practice for estimating population age structure and mean length at age. Calculations conducted by hand or by means of a spreadsheet program can be difficult for those wishing to assign ages to un-aged individuals in a sample (see sections 15.3 and 15.4.3.1). Isermann and Knight (2005) provide programming code for those using SAS (SAS Institute, Cary, North Carolina) and the software program Fisheries Analysis and Modeling Simulator (FAMS; Slipke and Maceina 2001; available from the American Fisheries Society Fisheries Information and Technology Section [AFS–FITS]) that can be used to assign ages to un-aged fish in a sample.

A number of fisheries-specific software programs are available to obtain growth measurements from hard structures. The program FISHCAL89-DISBCAL89 (available from AFS–FITS) has been used extensively to digitize and store growth measurements (e.g., from marked strips of paper as described in section 15.4.3.2). However, the program is DOS-based and not user-friendly, and has not been updated for many years. The program FishBC (available from AFS–FITS) was developed as an updated version of FISHCAL89-DISBCAL89 and allows users to input growth measurements from a digitizing tablet directly. Another program available to fisheries professionals is WinFin, developed by and available from the Nebraska Game and Parks Commission. This program allows measurements (e.g., on paper strips) to be digitized using a computer monitor. All of these programs are relatively inexpensive or free to fisheries professionals but are somewhat limited in their use because measurements from structures must be digitized from a photograph or strip of paper (except for FishBC, which has image analysis capabilities). Such an approach is common for scales but not for other structures. Rather, other hard structures are usually viewed and measured using an image analysis system, whereby the computer uses image analysis software to capture images and record measurements. Some image analysis software packages provide routines that help identify growth marks based on spectral analyses. In our experience, such routines often over- or underestimate ages and sometimes mark annuli in the wrong location. Whereas these routines are useful for some structures and species, scientists clearly must not rely on the software to make aging and measurement decisions. An additional benefit of image analysis software is that it has a number of other uses, such as measuring larval fish, counting and measuring eggs, or measuring prey items collected as part of food habits investigations. The hardware and software for such a system can be expensive but may be justified if age and growth studies are standard practice.

Back-calculation of growth can be estimated using FISHCALC89-DISBCAL89, WinFin, or FishBC. These programs use the Fraser–Lee method and provide estimates for individuals and mean back-calculated lengths at age, as well as estimates of annual growth increments. Programs designed to conduct the Weisberg method of growth analysis are discussed in Weisberg et al. (2010). Whereas growth models (e.g., von Bertalanffy and Gompertz) are typically fit using statistical analysis programs (see Isely and Graboswki 2007 for an example using SAS), a few fisheries-specific software packages provide methods for fitting growth models. The programs FAMS and FISHPARM (available from AFS–FITS) can be used to fit von Bertalanffy growth models. The program FISHPARM can also be used to provide parameter estimates for a variety of other common growth models, including Gompertz, logistic, exponential, and quadratic growth models. In addition, Haddon (2001) provides examples for fitting growth models (e.g., von Bertalanffy and logistic) by means of spreadsheet programs.

15.7 CONCLUSIONS

The concept of age and growth is relatively simple, but it should be evident that methods of collecting, preparing, reading, measuring, and analyzing data each have their own benefits, limitations, idiosyncrasies, and complexities. As such, fisheries scientists should maintain consistency throughout the process to maintain a high level of data quality. When age and growth surveys are conducted correctly (e.g., adequately large and unbiased samples, accurate age estimates, and proper growth analyses), age and growth information provides a wealth of information that far outweighs the cost of collection.

15.8 REFERENCES

Admassu, D., and J. M. Casselman. 2000. Otolith age determination for adult tilapia, *Oreochromis niloticus* L. from Lake Awassa (Ethiopian rift valley) by interpreting biannuli and differentiating biannual recruitment. Hydrobiologia 418:15–24.

Albrechtsen, K. 1968. A dyeing technique for otolith age reading. Journal of Conservation 32:278–280.

Allen, P. J., J. A. Hobbs, J. J. Cech, Jr., J. P. Van Eenennaam, and S. I. Doroshov. 2009. Using trace elements in pectoral fin rays to assess life history movements in sturgeon: estimating age at initial seawater entry in Klamath River green sturgeon. Transactions of the American Fisheries Society 138:240–250.

Alves, A., P. de Barros, and M. R. Pinho. 2002. Age and growth studies of bigeye tuna *Thunnus obesus* from Madeira using vertebrae. Fisheries Research 54:389–393.

Arai, T., A. V. Levin, A. N. Boltunov, and N. Miyazaki. 2002. Migratory history of the Russian sturgeon *Acipenser guldenstadti* in the Caspian Sea, as revealed by pectoral fin spine Sr:Ca ratios. Marine Biology 141:315–319.

Arai, T., and N. Miyazaki. 2001. Use of otolith microchemistry to estimate the migratory history of the Russian sturgeon, *Acipenser guldenstadti*. Journal of the Marine Biological Association of the UK 81:709–710.

Bagenal, T. B. 1974. The ageing of fish. Unwin Brothers, Surrey, UK.

Bagenal, T. B., and F. W. Tesch. 1978. Age and growth. Pages 101–136 *in* T. B. Bagenal, editor. Methods for assessment of fish production in freshwater, 3rd edition. Blackwell Scientific Publications, Oxford, UK.

Bariche, M. 2005. Age and growth of Lessepsian rabbitfish from the eastern Mediterranean. Journal of Applied Ichthyology 21:141–145.

Bartlett, J. R., P. F. Anderson, R. Williams, and D. M. Ellis. 1984. The use of analysis of covariance (ANCOVA) in the back-calculation of growth in fish. Journal of Fish Biology 24:201–213.

Beamish, R. J. 1979. Differences in age of Pacific hake (*Merluccius productus*) using whole and sections of otoliths. Journal of the Fisheries Research Board of Canada 36:141–151.

Beamish, R. J., and G. A. McFarlane. 1983. The forgotten requirement for age validation in fisheries biology. Transactions of the American Fisheries Society 112:735–743.

Beamish, R. J., and G. A. McFarlane. 1995. A discussion of the importance of aging errors, and an application to walleye pollock: the world's largest fishery. Pages 545–565 *in* D. H. Secor, J. M. Dean, and S. E. Campana, editors. Recent developments in fish otolith research. University of South Carolina Press, Columbia.

Beamish, R. J., G. A. McFarlane, and A. Benson. 2006. Longevity overfishing. Progress in Oceanography 68:289–302.

Beck, H. D., D. W. Willis, and J. M. Francis. 1997. A proposed standard intercept for the white bass body length–scale radius relationship. North American Journal of Fisheries Management 17:488–492.

Beckman, D. W., and C. A. Wilson. 1995. Seasonal timing of opaque zone formation in fish otoliths. Pages 27–43 *in* D. Secor, J. M. Dean, and S. E. Campana, editors. Recent developments in fish otolith research. University of South Carolina Press, Columbia.

Begg, G. A., M. Cappo, D. S. Cameron, S. Boyle, and M. J. Sellin. 1998. Stock discrimination of school mackerel, *Scomberomorus queenslandicus*, and spotted mackerel, *Scomberomorus munroi*, in coastal waters of eastern Australia by analysis of minor and trace elements in whole otoliths. Fishery Bulletin 96:653–666.

Begg, G. A., S. E. Campana, A. J. Fowler, and I. M. Suther. 2005. Otolith research and application: current directions in innovation and implementation. Marine and Freshwater Research 56:477–483.

Bettoli, P. W., and L. E. Miranda. 2001. A cautionary note about estimating mean length at age with subsampled data. North American Journal of Fisheries Management 21:425–428.

Birkeland, C., and P. K. Dayton. 2005. The importance in fishery management of leaving the big ones. Trends in Ecology and Evolution 20:356–358.

Borkholder, B. D., and A. J. Edwards. 2001. Comparing the use of dorsal fin spines with scales to back-calculate length-at-age estimates in walleyes. North American Journal of Fisheries Management 21:935–942.

Brennan, J. S., and G. M. Cailliet. 1989. Comparative age-determination techniques for white sturgeon in California. Transactions of the American Fisheries Society 118:296–310.

Brett, J. R. 1979. Environmental factors and growth. Page 599–675 *in* W. S. Hoar, D. J. Randall, and J. R. Brett, editors. Fish physiology, volume 8: bioenergetics and growth. Academic Press, New York.

Brown, P., C. Green, K. P. Sivakumaran, D. Stoessel, and A. Giles. 2004. Validating otolith annuli for annual age determination of common carp. Transactions of the American Fisheries Society 133:190–196.

Buckmeier, D. L. 2002. Assessment of reader accuracy and recommendations to reduce subjectivity in age estimation. Fisheries 27(11):10–14.

Buckmeier, D. L., E. R. Irwin, R. K. Betsill, and J. A. Prentice. 2002. Validity of pectoral spines and otoliths for estimating ages of channel catfish. North American Journal of Fisheries Management 22:934–942.

Buktenica, M. W., S. F. Girdner, G. L. Larson, and C. D. McIntire. 2007. Variability of kokanee and rainbow trout food habits, distribution, and population dynamics, in an ultraoligotrophic lake with no manipulative management. Hydrobiologia 574:235–264.

Buxton, C. D., and J. R. Clarke. 1989. The growth of *Cymatoceps nastutus* (Teleostei: Sparidae) with comments on diet and reproduction. South African Journal of Marine Science 8:57–65.

Cailliet, G. M., and K. J. Goldman. 2004. Age determination and validation in chondrichthyan fishes. Pages 339–447 *in* J. C. Carrier, J. A. Music, and M. R. Heithaus. Biology of sharks and their relatives. CRC Press, Boca Raton, Florida.

Campana, S. E. 1990. How reliable are growth back-calculations based on otoliths? Canadian Journal of Fisheries and Aquatic Sciences 47:2219–2227.

Campana, S. E. 1992. Measurement and interpretation of the microstructure of fish otoliths. Pages 59–71 *in* D. K. Stevenson and S. E. Campana, editors. Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117.

Campana, S. E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188:263–297.

Campana, S. E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59:197–242.

Campana, S. E. 2005. Otolith science entering the 21st century. Marine and Freshwater Research 56:485–495.

Campana, S. E., M. C. Annand, and J. I. McMillan. 1995. Graphical and statistical methods for determining the consistency of age determinations. Transactions of the American Fisheries Society 124:131–138.

Campana, S. E., and P. D. F. Hurley. 1989. An age- and temperature-mediated growth model for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae in the Gulf of Maine. Canadian Journal of Fisheries and Aquatic Sciences 46:603–613.

Campana, S. E., and C. M. Jones. 1992. Analysis of otolith microstructure data. Pages 73–100 *in* D. K. Stevenson and S. E. Campana, editors. Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117.

Campana, S. E., C. Jones, G. A. McFarlane, and S. Myklevoll. 2006. Bomb dating and age validation using the spines of spiny dogfish (*Squalus acanthias*). Environmental Biology of Fishes 77:327–336.

Campana, S. E., and J. D. Nielson. 1985. Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Sciences 42:1014–1032.

Carlander, K. D. 1969. Handbook of freshwater fishery biology, volume one. Iowa State University Press, Ames.

Carlander, K. D. 1977. Handbook of freshwater fishery biology, volume two. Iowa State University Press, Ames.

Carlander, K. D. 1981. Caution on the use of the regression method of back-calculating lengths from scale measurements. Fisheries 6(1):2–4.

Carlander, K. D. 1982. Standard intercepts for calculating lengths from scale measurement for some centrarchid and percid fishes. Transactions of the American Fisheries Society 111:332–336.

Carlander, K. D. 1997. Handbook of freshwater fishery biology, volume three. Iowa State University Press, Ames.

Carline, R. F., B. L. Johnson, and T. J. Hall. 1984. Estimation and interpretation of proportional stock density for fish populations in Ohio impoundments. North American Journal of Fisheries Management 4:139–154.

Casselman, J. M. 1983. Age and growth assessment of fish from their calcified structures—techniques and tools. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service Technical Report 8:1–17.

Casselman, J. M. 1987. Determination of age and growth. Pages 209–242 *in* A. H. Weatherly and H. S. Gill, editors. The biology of fish growth. Academic Press, New York.

Casselman, J. M., and E. J. Crossman. 1986. Size, age, and growth of trophy muskellunge and muskellunge–northern pike hybrids—the cleithrum project, 1979–1983. Pages 93–110 *in* G. E. Hall, editor. Managing muskies, a treatise on the biology and propagation of muskellunge in North America. American Fisheries Society, Special Publication 15, Bethesda, Maryland.

Cassoff, R. M., S. E. Campana, and S. Myklevoll. 2007. Changes in baseline growth and maturation parameters of Northwest Atlantic porbeagle, *Lamna nasus*, following heavy exploitation. Canadian Journal of Fisheries and Aquatic Sciences 64:19–29.

Cayre, P. M., and T. Diouf. 1983. Estimating age and growth of little tunny, *Euthynnus alletteratus*, off the coast of Senegal, using dorsal fin spine sections. Pages 105–110 *in* E. D. Prince and L. M. Pulos, editors. Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks. NOAA (National Oceanic and Atmospheric Administration) Technical Report NMFS 8, National Marine Fisheries Service, Southeast Fisheries Center, Miami.

Christensen, J. M. 1964. Burning otoliths, a technique for age determination of soles and other fish. Journal of Conservation 29:73–81.

Collins, M. R., and T. I. J. Smith. 1996. Sturgeon fin ray removal is nondeleterious. North American Journal of Fisheries Management 16:939–941.

Cotter, A. J. R., L. Burt, C. G. M. Paxton, C. Fernandez, S. T. Buckland, and J. X. Pan. 2004. Are stock assessment methods too complicated? Fish and Fisheries 5:235–254.

Coutant, C. C., and C. H. Chen. 1993. Strontium microstructures in scales of freshwater and estuarine striped bass (*Morone saxatilis*) detected by laser ablation mass spectroscopy. Canadian Journal of Fisheries and Aquatic Sciences 50:1318–1323.

Daugherty, D. J., T. M. Sutton, and R. W. Greil. 2003. Life history characteristics, population structure, and contributions of hatchery and wild steelhead in a Lake Huron tributary. Journal of Great Lakes Research 29:511–520.

DeVries, D. R., and R. V. Frie. 1996. Determination of age and growth. Pages 483–512 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

DiCenzo, V. J., and P. W. Bettoli. 1995. Verification of daily ring deposition in the otoliths of young-of-year spotted bass. Transactions of the American Fisheries Society 124:633–636.

Durham, B. W., and G. R. Wilde. 2008. Validation of daily growth increment formation in the otoliths of juvenile cyprinid fishes from the Brazos River, Texas. North American Journal of Fisheries Management 28:442–446.

Everhart, W. H., and W. D. Youngs. 1981. Principles of fishery science, 2nd edition. Cornell University Press, Ithaca, New York.

Fey, D. P., G. E. Bath Martin, J. A. Morris, and J. A. Hare. 2005. Effect of type of otolith and preparation technique on age estimation of larval and juvenile spot (*Leiostomus xanthurus*). Fishery Bulletin 103:544–552.

Francis, R. I. C. C. 1990. Back-calculation of fish length: a critical review. Journal of Fish Biology 36:883–902.

Geffen, A. J. 1992. Validation of otolith increment deposition rate. Pages 101–113 *in* D. K. Stevenson and S. E. Campana, editors. Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117.

Gerking, S. D., and R. R. Raush. 1979. Relative importance of size and chronological age in the life programme of fishes. Archiv fur Hydrobiologie Beiheft Ergebnisse der Limnologie 13:181–194.

Gutreuter, S. 1987. Considerations for estimation and interpretation of annual growth rates. Pages 115–126 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Gutreuter, S., A. D. Bartels, K. Irons, and M. B. Sandheinrich. 1999. Evaluation of the flood-pulse concept based on statistical models of growth of selected fishes of the Upper Mississippi River system. Canadian Journal of Fisheries and Aquatic Sciences 56:2282–2291.

Guy, C. S., and D. W. Willis. 1995. Population characteristics of black crappies in South Dakota waters: a case for ecosystem-specific management. North American Journal of Fisheries Management 15:754–765.

Haake, P. W., C. A. Wilson, and J. M. Dean. 1982. A technique for the examination of otoliths by SE with application to larval fishes. Pages 12–15 *in* C. F. Bryan, J. V. Conner, and F. M. Truesdale, editors. Proceedings of the 5th annual larval fish conference, Lousiana State University Press, Baton Rouge.

Haddon, M. 2001. Modeling and quantitative methods in fisheries. Chapman and Hall, New York.

Hales, L. S., and M. C. Belk. 1992. Validation of otolith annuli of bluegills in a southeastern thermal reservoir. Transactions of the American Fisheries Society 121:828–830.

Harrison, E. J., and W. F. Hadley. 1979. A comparison of the use of cleithra to the use of scales for age and growth studies. Transactions of the American Fisheries Society 108:452–456.

He, J. X., L. G. Rudstam, J. L. Forney, A. J. VanDeValk, and D. J. Stewart. 2005. Long-term patterns in growth of Oneida Lake walleye: a multivariate and stage-explicit approach for applying the von Bertalanffy growth function. Journal of Fish Biology 66:1459–1470.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Kluwer Academic Publishers, Norwell, Massachusetts.

Hobbs, J. A., Q. Yin, J. Burton, and W. A. Bennett. 2005. Retrospective determination of natal habitats for an estuarine fish with otolith strontium isotope ratios. Marine and Freshwater Research 56:655–660.

Hoenig, J. M., and D. M. Heisey. 1987. Use of a log-linear model with the EM algorithm to correct estimates of stock composition and to convert length to age. Transactions of the American Fisheries Society 116:232–243.

Horppila, J., and K. Nyberg. 1999. The validity of different methods in the backcalculation of the lengths of roach—a comparison between scales and cleithra. Journal of Fish Biology 54:489–498.

Hoxmeier, R. J. H., D. D. Aday, and D. H. Wahl. 2001. Factors influencing precision of age estimation from scales and otoliths of bluegills in Illinois reservoirs. North American Journal of Fisheries Management 21:374–380.

Hsieh, C. H., C. S. Reiss, J. R. Hunter, J. R. Beddington, R. M. May, and G. Sugihara. 2006. Fishing elevates variability in the abundance of exploited species. Nature (London) 443:859–862.

Hubert, W. A. 1999. Standards for assessment of age and growth data for channel catfish. Journal of Freshwater Ecology 14:313–326.

Hudson, W. F., and F. J. Bulow. 1984. Relationships between squamation chronology of the bluegill, *Lepomis macrochirus* Rafinesque, and age–growth models. Journal of Fish Biology 24:459–469.

Hughes, T. C., C. E. Lowie, and J. M. Haynes. 2005. Age, growth, relative abundance, and scuba capture of a new or recovering spawning population of lake sturgeon in the lower Niagara River, New York. North American Journal of Fisheries Management 25:1263–1272.

Irvine, S. B., J. D. Stevens, and L. J. B. Laurenson. 2006. Surface bands on deepwater squalid dorsal-fin spines: an alternative method for aging *Centroselachus crepidater*. Canadian Journal of Fisheries and Aquatic Sciences 63:617–627.

Isaac, V. J. 1990. The accuracy of some length-based methods for fish population studies. International Center for Living Aquatic Resources Management Technical Report 27, Manila.

Isely, J. J., and T. B. Grabowski. 2007. Age and growth. Pages 187–228 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Isermann, D. A., and C. T. Knight. 2005. A computer program for age–length keys incorporating assignment to individual fish. North American Journal of Fisheries Management 25:1153–1160.

Isermann, D. A., W. L. McKibbin, and D. W. Willis. 2002. An analysis of methods for quantifying crappie recruitment variability. North American Journal of Fisheries Management 22:1124–1135.

Itoh, T., Y. Shiina, S. Tsuji, F. Endo, and N. Tezuka. 2000. Otolith daily increment formation in laboratory reared larval and juvenile bluefin tuna *Thunnus thynnus*. Fisheries Research 66:834–839.

Jackson, J. J., and K. L. Hurley. 2005. Relative growth of white crappie and black crappie in the United States. Journal of Freshwater Ecology 20:461–467.

Jackson, J. R. 2007. Earliest references to age determination of fishes and their early application to the study of fisheries. Fisheries 32:321–328.

Jackson, Z. J., M. C. Quist, and J. G. Larscheid. 2008. Growth standards for nine North American fish species. Fisheries Management and Ecology 15:107–118.

Jearld, A., Jr. 1983. Age determination. Pages 301–324 *in* L. A. Nielsen and D. L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

Johnson, B. L., and D. B. Noltie. 1997. Demography, growth, and reproductive allocation in stream-spawning longnose gar. Transactions of the American Fisheries Society 126:438–466.

Jones, C. M. 1992. Development and application of the otolith increment technique. Pages 1–11 *in* D. K. Stevenson and S. E. Campana, editors. Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117.

Jones, C. M. 2000. Fitting growth curves to retrospective size-at-age data. Fisheries Research 46:123–129.

Kalish, J. M. 1993. Pre- and postbomb radiocarbon in fish otoliths. Earth and Planetary Science Letters 114:549–554.

Kalish, J. M., R. J. Beamish, E. B. Brothers, J. M. Casselman, R. I. C. C. Francis, H. Mosegaard, J. Panfili, E. D. Prince, R. E. Thresher, C. A. Wilson, and P. J. Wright. 1995. Glossary for otolith studies. Pages 723–729 *in* D. H. Secor, J. M. Dean, and S. E. Campana, editors. Recent developments in fish otolith research. University of South Carolina Press, Columbia.

Kaufmann, K. W. 1981. Fitting and using growth curves. Oecologia 49:293–299.

Kimura, D. K. 1977. Statistical assessment of the age–length key. Journal of the Fisheries Research Board of Canada 34:317–324.

Klumb, R. A., M. A. Bozek, and R. V. Frie. 1999a. Proportionality of body to scale growth: validation of two back-calculation models with individually tagged and recaptured smallmouth bass and walleyes. Transactions of the American Fisheries Society 128:815–831.

Klumb, R. A., M. A. Bozek, and R. V. Frie. 1999b. Validation of the Dahl–Lea and Fraser–Lee back-calculation models by using oxytetracycline-marked bluegills and bluegill × green sunfish hybrids. North American Journal of Fisheries Management 19:504–514.

Koch, J. D., and M. C. Quist. 2007. A technique for preparing fin rays and spines for age and growth analysis. North American Journal of Fisheries Management 27:781–784.

Koch, J. D., W. Schreck, and M. C. Quist. 2008. Standardized removal and sectioning locations for shovelnose sturgeon fin rays. Fisheries Management and Ecology 15:139–145.

Kraus, R. T., and D. H. Secor. 2004. Incorporation of strontium into otoliths of an estuarine fish. Journal of Experimental Marine Biology and Ecology 302:85–106.

Krueger, K. L., and W. A. Hubert. 1997. Irregularly shaped otoliths from saugers prevent back-calculation of length at previous ages in Wyoming. North American Journal of Fisheries Management 17:769–772.

Larkin, P. A., J. G. Terpenning, and R. R. Parker. 1956. Size as a determinant of growth rate in rainbow trout *Salmo gairdneri*. Transactions of the American Fisheries Society 86:84–96.

Leigh, G. M., and W. S. Hearn. 2000. Changes in growth of juvenile southern bluefin tuna (*Thunnus maccoyii*): an analysis of length-frequency data from the Australian fishery. Marine and Freshwater Research 51:143–154.

Lein, G. M., and D. R. DeVries. 1998. Paddlefish in the Alabama River drainage: population characteristics and the adult spawning migration. Transactions of the American Fisheries Society 127:441–454.

Lentsch, L. D., and J. S. Griffith. 1987. Lack of first-year annuli on scales: frequency of occurrence and predictability in trout of the western United States. Pages 177–188 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Logsdon, D. E. 2007. Use of unsectioned dorsal spines for estimating walleye ages. North American Journal of Fisheries Management 27:1112–1118.

MacDonald, P. D. 1987. Analysis of length-frequency distributions. Pages 371–384 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Maceina, M. J. 1992. A simple regression model to assess environmental effects on fish growth. Journal of Fish Biology 41:557–565.

Maceina, M. J. 1997. Simple application of using residuals from catch-curve regressions to assess year-class strength in fish. Fisheries Research 32:115–121.

Maceina, M. J., J. Boxrucker, D. L. Buckmeier, R. S. Gangl, D. O. Lucchesi, D. A. Isermann, J. R. Jackson, and P. J. Martinez. 2007. Current status and review of freshwater fish aging procedures used by state and provincial fisheries agencies with recommendations for future directions. Fisheries 32:329–340.

MacInnis, A. J., and L. D. Corkum. 2000. Age and growth of round goby *Neogobius melanostomus* in the upper Detroit River. Transactions of the American Fisheries Society 129:852–858.

Mackay, W. C., G. R. Ash, and H. J. Norris, editors. 1990. Fish aging methods for Alberta. R. L. & L. Environmental Services Ltd. in association with Alberta Fish and Wildlife Division and University of Alberta, Edmonton.

Marwitz, T. D., and W. A. Hubert. 1995. Precision of age estimates of Wyoming walleyes from different calcified structures. Prairie Naturalist 27:41–49.

Mayhew, J. K. 1969. Age and growth of flathead catfish in the Des Moines River, Iowa. Transactions of the American Fisheries Society 98:118–120.

McBride, R. S., M. L. Hendricks, and J. E. Olney. 2005. Testing the validity of Cating's (1953) method for age determination of American shad using scales. Fisheries 30(10):10–18.

McFarlane, G. A., and R. J. Beamish. 1987. Validation of the dorsal spine method of age determination for spiny dogfish. Pages 287–300 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

McFarlane, G. A., J. King, and M. W. Saunders. 2002. Preliminary study on the use of neural arches in the age determination of bluntnose sixgill sharks (*Hexanchus griseus*). Fishery Bulletin 100:861–864.

Meeuwig, M. H., and J. M. Bayer. 2005. Morphology and aging precision of statoliths from larvae of Columbia River basin lampreys. North American Journal of Fisheries Management 25:38–48.

Michaletz, P. H. 2005. Does pectoral spine extraction cause mortality to channel catfish? North American Journal of Fisheries Management 25:533–535.

Michaletz, P. H., D. M. Nicks, and E. W. Buckner, Jr. 2009. Accuracy and precision of estimate of back-calculated channel catfish lengths and growth increments using pectoral spines and otoliths. North American Journal of Fisheries Management 29:1664–1675.

Milton, D. A., C. D. Tenakanai, and S. R. Chenery. 2000. Can the movements of barramundi in the Fly River Region, Papua New Guinea be traced in their otoliths? Estuarine, Coastal and Shelf Science 50:855–868.

Miranda, L. E. 2002. Establishing size-based mortality caps. North American Journal of Fisheries Management 22:433–440.

Miranda, L. E., and P. W. Bettoli. 2007. Mortality. Pages 229–277 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Morales-Nin, B. 1992. Determination of growth in bony fishes from otolith microstructure. FAO (Food and Agriculture Organization of the United Nations) Fisheries Technical Paper 322, Rome.

Morales-Nin, B. 2001. Mediterranean deep-water fish age determination and age validation: the state of the art. Fisheries Research 51:377–383.

Morison, A. K., J. Burnett, W. J. McCurdy, and E. Moksness. 2005. Quality issues in the use of otoliths for fish age estimation. Marine and Freshwater Research 56:773–782.

Morita, K., and T. Matsuishi. 2001. A new model of growth back-calculation incorporating age effect based on otoliths. Canadian Journal of Fisheries and Aquatic Sciences 25:1805–1811.

Moss, J. H., D. A. Beauchamp, A. D. Cross, K. W. Myers, E. V. Farley, Jr., J. M. Murphy, and J. H. Helle. 2005. Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. Transactions of the American Fisheries Society 134:1313–1322.

Natanson, L. J., J. J. Mello, and S. E. Campana. 2002. Validated age and growth of the porbeagle shark

(*Lamna nasus*) in the western North Atlantic Ocean. Fishery Bulletin 100:266–278.

Neer, J. A., and G. M. Cailliet. 2001. Aspects of the life history of the Pacific electric ray, *Torpedo californica* (Ayres). Copeia 2001:842–847.

Neilson, J. D., W. T. Stobo, and P. Perley. 2003. Age and growth of Canadian east coast pollock: comparison of results from otolith examination and mark–recapture studies. Transactions of the American Fisheries Society 132:536–545.

Neumann, R. M., D. W. Willis, and D. D. Mann. 1994. Evaluation of largemouth bass slot length limits in two small South Dakota impoundments. Prairie Naturalist 26:15–32.

Newman, R. M., and S. Weisberg. 1987. Among- and within-fish variation of scale growth increments in brown trout. Pages 159–176 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Nitschke, P., J. Burnett, and B. C. Kelly. 2001. Age and growth verification for cunner in western Cape Cod Bay, Massachusetts, using tag-recapture data. Transactions of the American Fisheries Society 130:1150–1163.

Ogle, D. H., R. C. Pruitt, G. R. Spangler, and M. J. Cyterski. 1996. A Bayesian approach to assigning probabilities to fish ages determined from temporal signatures in growth increments. Canadian Journal of Fisheries and Aquatic Sciences 53:1788–1794.

Oliveira, K. 1996. Field validation of annular growth rings in the American eel, *Anguila rostrata*, using tetracycline-marked otoliths. Fishery Bulletin 94:186–189.

Oliveira, K., and J. D. McCleave. 2002. Sexually different growth histories of the American eel in four rivers in Maine. Transactions of the American Fisheries Society 131:203–211.

Osenberg, C. W., E. E. Werner, G. G. Mittelbach, and D. J. Hall. 1988. Growth patterns in bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) sunfish: environmental variation and the importance of ontogenetic niche shifts. Canadian Journal of Fisheries and Aquatic Sciences 45:17–26.

Outridge, P. M., G. Veinott, and R. D. Evans. 1995. Laser ablation ICP-MS analysis of incremental biological structures: archives of trace-element accumulation. Environmental Review 3:160–170.

Owens, R. W., and N. M. Pronin. 2000. Age and growth of pike (*Esox lucius*) in Chivyrkui Bay, Lake Baikal. Journal of Great Lakes Research 26:164–173.

Panella, G. 1974. Otolith growth patterns: an aid in age determination in temperate and tropical fishes. Pages 28–39 *in* T. B. Bagenal, editor. The ageing of fish. Unwin Brothers, Surrey, UK.

Panella, G. 1980. Growth patterns in fish sagittae. Pages 519–560 *in* D. C. Rhoads and R. A. Lutz, editors. Skeletal growth of aquatic organisms. Plenum, New York.

Panfili, J., and J. Tomás. 2001. Validation of age estimation and back-calculation of fish length based on otolith microstructure in tilapias (Pisces, Cichlidae). Fishery Bulletin 99:139–150.

Parker, R. P., and P. A. Larkin. 1959. A concept of growth in fishes. Journal of the Fisheries Research Board of Canada 16:721–745.

Pauly, D. 1987. Application of information on age and growth of fish to fishery management. Pages 495–506 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Pierce, C. L., J. B. Rasmussen, and W. C. Leggett. 1996. Back-calculation of fish length from scales: empirical comparison of proportional methods. Transactions of the American Fisheries Society 125:889–898.

Popper, A. N., J. Ramcharitar, and S. E. Campana. 2005. Why otoliths? Insights from inner ear physiology and fish biology. Marine and Freshwater Research 56:497–504.

Przybylski, M., and E. Garcia-Berthou. 2004. Age and growth of European bitterling (*Rhodeus sericeus*) in the Wieprez-Krzna Canal, Poland. Ecohydrology and Hydrobiology 4:207–213.

Putman, J. H., C. L. Pierce, and D. M. Day. 1995. Relationships between environmental variables and size-specific growth rates of Illinois stream fishes. Transactions of the American Fisheries Society 124:252–261.

Quinn, T. J., II, and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Quist, M. C., C. S. Guy, R. D. Schultz, and J. L. Stephen. 2003. Latitudinal comparisons of walleye growth in North America and factors influencing growth of walleyes in Kansas reservoirs. North American

Journal of Fisheries Management 23:677–692.

Quist, M. C., Z. J. Jackson, M. R. Bower, and W. A. Hubert. 2007. Precision of hard structures used to estimate age of riverine catostomids and cyprinids in the upper Colorado River basin. North American Journal of Fisheries Management 27:643–649.

Radtke, R. L. 1989. Larval fish age, growth and body shrinkage: information available from otoliths. Canadian Journal of Fisheries and Aquatic Sciences 46:1884–1894.

Richards, L. J., J. T. Schnute, A. R. Kronlund, and R. J. Beamish. 1992. Statistical models for the analysis of aging error. Canadian Journal of Fisheries and Aquatic Sciences 49:1801–1815.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Ricker, W. E. 1979. Growth rates and models. Pages 677–743 *in* W. S. Hoar, D. J. Randall, and J. R. Brett, editors. Fish physiology, volume 8: bioenergetics and growth. Academic Press, New York.

Ricker, W. E. 1992. Back-calculation of fish lengths based on proportionality between scale and length increments. Canadian Journal of Fisheries and Aquatic Sciences 49:1018–1026.

Roa-Ureta, R. H. 2009. A likelihood-based model of fish growth with multiple length frequency data. Journal of Agricultural, Biological, and Environmental Statistics 15:416–429.

Roff, D. A. 1980. A motion to retire the von Bertalanffy function. Canadian Journal of Fisheries and Aquatic Sciences 37:127–129.

Rowell, K., K. W. Flessa, D. L. Dettman, M. J. Roman, L. R. Gerber, and L. T. Findley. 2008. Diverting the Colorado River leads to a dramatic life history shift in an endangered marine fish. Biological Conservation 141:1138–1148.

Rutherford, D. A., W. E. Kelso, C. F. Bryan, and G. C. Constant. 1995. Influence of physicochemical characteristics on annual growth increments of four fishes from the lower Mississippi River. Transactions of the American Fisheries Society 124:687–697.

Rypel, A. L. 2008. An inexpensive image analysis system for fish otoliths. North American Journal of Fisheries Management 28:193–197.

Salthaug, A. 2003. Dynamic age–length keys. Fisheries Bulletin 101:451–456.

Schill, D. J. 2009. Population studies of desert redband trout. Doctoral dissertation. University of Idaho, Moscow.

Schill, D. J., E. R. J. M. Mamer, and G. W. LaBar. 2010. Validation of scales and otoliths for estimating age of redband trout in high desert streams of Idaho. Environmental Biology of Fishes 89:319–332.

Schneidervin, R. W., and W. A. Hubert. 1986. A rapid technique for otolith removal from salmonids and catostomids. North American Journal of Fisheries Management 6:287.

Scholten, G. D., and P. W. Bettoli. 2005. Population characteristics and assessment of overfishing for an exploited paddlefish population in the lower Tennessee River. Transactions of the American Fisheries Society 134:1285–1298.

Schramm, H. L., Jr. 1989. Formation of annuli in otoliths of bluegills. Transactions of the American Fisheries Society 118:546–555.

Schramm, H. L., Jr., S. P. Malvestuto, and W. A. Hubert. 1992. Evaluation of procedures for back-calculation of lengths of largemouth bass aged by otoliths. North American Journal of Fisheries Management 12:604–608.

Scoppettone, G. G. 1988. Growth and longevity of the cui-ui and longevity of other catostomids and cyprinids in western North America. Transactions of the American Fisheries Society 117:301–307.

Secor, D. H., J. M. Dean, and E. H. Laban. 1991. Manual for otolith removal and preparation for microstructural examination. University of South Carolina, Baruch Institute for Marine Biology and Coastal Research Technical Report 91–1, Columbia.

Secor, D. H., J. M. Dean, and E. H. Laban. 1992. Otolith removal and preparation for microstructural examination. Pages 19–57 *in* D. K. Stevenson and S. E. Campana, editors. Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117.

Secor, D. H., A. Henderson-Arzapalo, and P. M. Piccoli. 1995. Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fishes? Journal of Experimental Marine Biology and Ecology 192:15–33.

Sharp, D., and D. R. Bernard. 1988. Precision of estimated ages of lake trout from five calcified structures. North American Journal of Fisheries Management 8:367–372.

Shoup, D. E., S. P. Callahan, D. H. Wahl, and C. L. Pierce. 2007. Size-specific growth of bluegill, largemouth bass and channel catfish in relation to prey availability and limnological variables. Journal of Fish Biology 70:21–34.

Simkiss, K. 1974. Calcium metabolism of fish in relation to aging. Pages 1–12 *in* T. B. Bagenal, editor. The ageing of fish. Unwin Brothers, Surrey, UK.

Slipke, J. W., and M. J. Maceina. 2001. Fisheries analyses and simulation tools (FAST 2.0). Department of Fisheries and Allied Aquacultures, Auburn University, Auburn, Alabama.

Smale, M. A., and W. W. Taylor. 1987. Sources of back-calculation error in estimating growth of lake whitefish. Pages 189–202 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Smedstad, O. M., and J. C. Holm. 1996. Validation of back-calculation formulae for cod otoliths. Journal of Fish Biology 49:973–985.

Smith, K. T., and G. W. Whitledge. 2010. Fin ray chemistry as a potential natural tag for smallmouth bass in northern Illinois rivers. Journal of Freshwater Ecology 25:627–635.

Smith, S. H. 1954. Method of producing plastic impressions of fish scales without using heat. Progressive Fish-Culturist 16:75–78.

Stafford, C. P., J. A. Stanford, F. R. Hauer, and E. B. Brothers. 2002. Changes in lake trout growth associated with *Mysis relicta* establishment: a retrospective analysis using otoliths. Transactions of the American Fisheries Society 131:994–1003.

Stevenson, D. K., and S. E. Campana, editors. 1992. Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Sciences 117.

Stevenson, F., and R. E. Day. 1987. Mortality and growth of channel catfish following extraction of a pectoral spine. North American Journal of Fisheries Management 7:443–445.

Stunz, G. W., T. L. Linton, and R. L. Colura. 2000. Age and growth of southern flounder in Texas waters, with emphasis on Matagorda Bay. Transactions of the American Fisheries Society 129:119–125.

Summerfelt, R. C., and G. E. Hall, editors. 1987. Age and growth of fish. Iowa State University Press, Ames.

Suzuki, K., and S. Kimura. 1990. A bibliography on methods of aging fishes (1926–1988). Annual Report of the Toba Aquarium 2:45–94.

Swearer, S. E., G. E. Forrester, M. A. Steele, A. J. Brooks, and D. W. Lea. 2003. Spatio-temporal and interspecific variation in otolith trace-elemental fingerprints in a temperate estuarine fish assemblage. Estuarine, Coastal and Shelf Science 56:1111–1123.

Taubert, B. D. 1980. Reproduction of shortnose sturgeon (*Acipenser brevirostrum*) in Holyoke Pool, Connecticut River, Massachusetts. Copeia 1980:114–117.

Taylor, C. M., and R. J. Miller. 1990. Reproductive ecology and population structure of the plains minnow, *Hybognathus placitus* (Pisces: Cyprinidae), in central Oklahoma. American Midland Naturalist 123:32–39.

Tesch, F. W. 1971. Age and growth. Pages 98–130 *in* W. E. Ricker, editor. Methods for assessment of fish production in fresh waters. Blackwell Scientific Publications, London.

VanderKooy, S., and K. Guindon-Tisdel. 2003. A practical handbook for determining the ages of Gulf of Mexico fishes. Gulf States Marine Fisheries Commission, Ocean Springs, Mississippi.

Veinott, G., T. Northcote, M. Rosenau, and R. D. Evans. 1999. Concentrations of strontium in the pectoral fin rays of the white sturgeon (*Acipenser transmontanus*) by laser ablation sampling-inductively coupled plasma-mass spectrometry as an indicator of marine migrations. Canadian Journal of Fisheries and Aquatic Sciences 56:1981–1990.

Walsh, M. G., A. P. Maloy, and T. P. O'Brien. 2008. Comparison of rainbow smelt age estimates from fin rays and otoliths. North American Journal of Fisheries Management 28:42–49.

Watari, S., J. Yonezawa, S. Yamada, E. Tanaka, and T. Kitakado. 2005. Age and growth of yellowstriped butterfish, *Labracoglossa argentiventris*, around Izu Oshima Island. Fisheries Science 71:86–94.

Weisberg, S. 1993. A computer program for using hard-part increment data to estimate age and environmental effects in fish populations. University of Minnesota, Minnesota Sea Grant Program, St. Paul.

Weisberg, S., and R. V. Frie. 1987. Linear models for the growth of fish. Pages 127–143 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Weisberg, S., G. Spangler, and L. S. Richmond. 2010. Mixed effects models for fish growth. Canadian Journal of Fisheries and Aquatic Sciences 67:269–277.

Wells, B. K., B. E. Rieman, J. L. Clayton, D. L. Horan, and C. M. Jones. 2003. Relationships between water, otolith, and scale chemistries of westslope cutthroat trout from the Coeur d'Alene River, Idaho: the potential application of hard-part chemistry to describe movements in freshwater. Transactions of the American Fisheries Society 132:409–424.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15:393–425.

Westrheim, S. J., and W. E. Ricker. 1978. Bias in using an age–length key to estimate age-frequency distributions. Journal of the Fisheries Research Board of Canada 35:184–189.

Williamson, C. J., and J. E. Garvey. 2005. Growth, fecundity, and diets of newly established silver carp in the middle Mississippi River. Transactions of the American Fisheries Society 134:1423–1430.

Winemiller, K. O. 2005. Life history strategies, population regulation, and implications for fisheries management. Canadian Journal of Fisheries and Aquatic Sciences 62:872–885.