ELASMOBRANCHS

Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting

Gregor M. Cailliet · Wade D. Smith · Henry F. Mollet · Kenneth J. Goldman

Abstract Validated age and growth estimates are important for constructing age-structured population dynamic models of chondrichthyan fishes, especially those which are exploited. We review age and growth studies of chondrichthyan fishes, using 28 recent studies to identify areas where improvements can be made in describing the characteristics of ageing structures (both traditional and novel) utilized to estimate ages of sharks, rays, and chimaeras. The topics identified that need consistency include the: (1) terminology used to describe growth features; (2) methods used to both verify and validate age estimates from chondrichthyan calcified structures, especially edge and marginal increment analyses; and (3) the functions used to produce and describe growth parameters, stressing the incorporation of size at birth (L_0) and multiple functions to characterize growth characteristics, age at maturity and longevity.

Introduction

In recent years, there have been many advances in the quantitative study of age and growth of chondrichthyan fishes (Cailliet and Goldman 2004). Several new hard parts have been shown to provide valid assessments of age in some species, and new techniques for validation (e.g. bomb carbon) are becoming more widely known and applied. Moreover, the importance of assessing the precision and accuracy of counts on ageing structures, and the differences in growth models and their fits to data, are becoming more widely recognized. The book chapter cited above in a book entitled ''Biology of Sharks and their Relatives,'' edited by Carrier et al. (2004), reviewed the field of age and growth in this group of fishes up to 2003. Although it has been less than two years since this publication, numerous papers on these subjects have been published, in addition to several papers not covered in the 2004 review chapter.

Since then, we have found five papers that were missed and 23 new publications that covered age and growth of chondrichthyan fishes. These papers covered the life histories of three species

G. M. Cailliet (✉) · W. D. Smith · H. F. Mollet
Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, CA 95039, USA
e-mail: cailliet@mlml.calstate.edu

K. J. Goldman
Alaska Department of Fish and Game, 3298 Douglas Place, Homer, AK 99603, USA

of chimaeras (Francis and Maolagáin 2000, 2001, 2004; Moura et al. 2004), three species of rays (Coelho and Erzini 2002; Neer and Thompson 2005; White and Potter 2005), nine species of skates (Gallagher et al. 2004; Henderson et al. 2004; Francis and Maolagáin 2005; Gedamke et al. 2005; Sulikowski et al. 2005a, b), two species of mackerel shark (Malcolm et al. 2001; Campana et al. 2005), and ten species of ground or requiem sharks (Yamaguchi et al. 1998; Lombardi-Carlson et al. 2003; Oshitani et al. 2003; Cruz-Martinez et al. 2004; Ivory et al. 2004; Joung et al. 2004, 2005; Lessa et al. 2004; Neer and Thompson 2004; Santana and Lessa 2004; Carlson and Baremore 2005; Manning and Francis 2005; Neer et al. 2005).

We reviewed the 28 new or missed papers mentioned above, analyzing the approaches that were taken in them to help identify key problems, if any, still existing in the methods involved in chondrichthyan age and growth studies. We were specifically interested in determining how these authors handled issues like the terminology of growth patterns, verification and validation techniques (focusing on edge characteristics and marginal increment analyses), and growth function fitting (how the von Bertalanffy (1938) growth function was fit and what other functions might have also been useful). At the end of each section, we provide recommendations that will hopefully guide researchers on how to proceed with each type of growth-related analysis.

Cailliet and Goldman (2004) and Goldman (2004) provided many guidelines on how to approach the subjects mentioned above. However, since many of these recent papers used a variety of different approaches, we have chosen to use the variability encountered in them to suggest ways to unify the field so that future papers might use suitable, and hopefully similar, approaches in their assessment of chondrichthyan life history parameters. Considerable variability and inconsistency were found in the: (1) terminology used for growth patterns in these structures; (2) methods used to verify and validate age estimates, including whether or not statistical analyses were applied; and (3) growth function fitting and parameter estimation.

Calcified structures and terminology used for chondrichthyan growth studies

Most age and growth studies of sharks, rays, and chimaeras utilize growth patterns in vertebral centra, dorsal fin spines (especially for those species which do not have suitably calcified centra and/or live in deep-sea habitats), and more recently in skates, caudal thorns (Cailliet and Goldman 2004). These structures tend to accumulate calcified growth material as they age, thus producing concentric areas that often have characteristics reflecting the time of year (season) in which this material is being deposited. Of the papers we recently reviewed, all used calcified structures, including vertebral centra (23 of the studies), dorsal spines (four), and caudal thorns (two).

In the field of fish ageing, there have been several attempts to synthesize the terminology used to describe growth features so that it is consistent among studies, one of the earliest being Wilson et al. (1987). Recently, Panfili et al. (2002) provided a comprehensive review in their ''Manual of Fish Sclerochronology.'' However, this excellent review, with its glossary, is focused more on bony fish ageing, involving the use of otoliths and scales, which are not appropriate for chondrichthyan fishes.

It is important to distinguish between growth patterns that reflect seasonal growth and those, when combined, that may reflect annual (yearly) growth. Therefore, we first need to distinguish the length of time a particular growth pattern reflects. Panfili et al. (2002), for example, discussed daily growth rings, a phenomenon that has not yet been found in chondrichthyans. For these fishes, the first distinction is whether a term reflects a season (i.e., summer or winter patterns; but this may not always be the same in all species) or a year (i.e., an annual pattern, which requires some sort of validation, discussed later). As Panfili et al. (2002) noted, the term *annulus* ''has traditionally been used to designate yearly marks even though the term is derived from the Latin ''anus,'' meaning ring, not from ''annus,'' which means year.'' For the seasonal growth pattern, Panfili et al. (2002) synonymized the words *band*, *ring*, *increment*, and *mark*, something that we feel confuses researchers.

We would prefer to have a standardized terminology that all, or at least the majority of chondrichthyan researchers, should follow.

Cailliet and Goldman (2004) and Goldman (2004) tried to be consistent with their terminology, suggesting that "band" be used for seasonal periods (e.g. opaque bands tending to be deposited in summer and translucent bands tending to be deposited in winter months) and either "ring" or "annulus" be used for those growth patterns demonstrated or assumed to represent a year's period. Cailliet and Goldman (2004) stated that "the most commonly distinguishable banding pattern in sectioned centra when viewed microscopically is one of wide bands separated by distinct narrow bands," and also that the "terms opaque and translucent are commonly used to describe these bands." An additional characterization of chondrichthyan growth bands was applied by Officer et al. (1996, 1997) based upon their relative extent of mineralization; these were identified as "hypermineralized bands."

Although there is often regularity in the width of bands, this can still be a potentially misleading generalization. For broader discussions, we feel that it is important to modify such statements saying "there is often a consistency in the wide/narrow pattern." The width of these opaque and translucent bands can be particularly exaggerated during the early years, and later, as growth slows, widths of these bands become more similar to each other. In fact, opaque and translucent bands may be narrower than translucent bands and/or vice versa in "older" fish. In addition, the relative widths of these bands may not remain consistent throughout the life of the animal. It is the deposition of opaque and translucent bands that is usually more consistent seasonally. Therefore, bands should be described and identified for their optical qualities, rather than dimensions such as band widths, which can be highly variable.

While reviewing the papers published since Cailliet and Goldman (2004), we found that many terms and combinations of terms were used. In the 28 studies reviewed, seasonal patterns were termed "band" (18 studies), "ring" and "zone" (4 each), "increment" (1), and in one publication, not defined at all. The terms used to represent annual patterns in these studies were "band"

(7 studies), "band pair" (5), "annulus" (plural annuli), "ring" (in one of these, "growth ring") and "increment" (3 each), while 7 studies did not provide a definition. This supports our assertion that there is a need for consistency in the future use of terminology.

Indeed, years ago Cailliet et al. (1985) suggested counting *band pairs*, defined as one opaque and one translucent *band* combined, in their study of white shark, *Carcharodon carcharias*, growth. Martin and Cailliet (1988) added the term *rings*, which referred to the fine features within and making up either opaque or translucent bands (see Fig. 1 for a recent example). These fine rings have rarely been reported in chondrichthyans. Officer et al. (1996, 1997) identified these features as "minor increments" or "fine check marks" in gummy, *Mustelus antarcticus*, and school shark, *Galeorhinus galeus*, vertebrae, and similar rings were found in vertebral centra of the blue stingray, *Dasyatis chrysonota* (Cowley 1997), smooth hound, *M. mustelus* (Goosen and Smale 1997), and sandtiger sharks, *Carcharias taurus* (Goldman et al. 2006).

Recommendations

For clarity and consistency, we suggest that chondrichthyan fish agers use the following
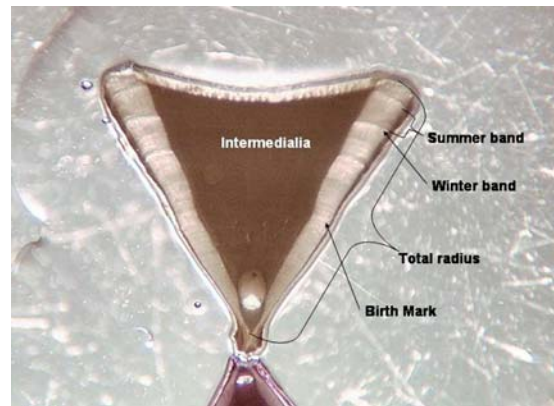

Fig. 1 A thin-sectioned vertebral centrum from an estimated 3.5+ year old spinner shark (*Carcharhinus brevipinna*) is shown (from Carlson and Baremore 2005). Centrum features, including the birthmark, opaque and translucent bands, band pairs, are identified. Also notable is the marginal increment of the ultimate band and the finer rings within the structure

terminology: (1) "Opaque" or "translucent bands" (following Cailliet et al. 1983); (2) "band pairs" (often referred to as annuli and/or rings, sensu Cailliet and Goldman (2004) and Goldman (2004)), comprising one opaque and one translucent band; and (3) "increments" which are measurements of partial to complete growth bands or band pairs (which should be specifically defined by authors). These terms should not be confused with other terminology such as "checks" or "discontinuous bands" (Panfili et al. 2002), although these also appear as translucent and opaque features. We remind investigators that the method of preparation and examination of an ageing structure (e.g. stained vs. unstained, radiographed vs. microphotographed, and viewed using reflected vs. transmitted light) alter the optical properties of calcified structures. Therefore, features characterized as opaque or translucent may vary depending upon methodology. Finally, we propose that future studies ascertain whether bands classified as "opaque" are hyper- or hypomineralized.

Verification and precision analysis

Panfili et al. (2002) defined "verification" as confirming "the consistency of the interpretation of age, i.e., the repeatability and/or precision of a numerical interpretation that may be independent of age." They further define "precision" as "the closeness of repeated measurements of the same quantity." They then pointed out that this can be between or within readers or laboratories. The techniques commonly used to verify age estimates were presented by Campana (2001) for fishes in general and by Cailliet and Goldman (2004) and Goldman (2004) for use on chondrichthyans.

Most of the 28 recently reviewed studies presented evidence that verified or assessed precisions of age estimates. The Index of Average Percent Error (Beamish and Fournier 1981, sometimes also including D and V of Chang 1982) was presented in 13 of these papers, while percentage agreement (Beamish and Fournier 1981; Cailliet et al. 1990; Kimura and Lyons 1991; Campana 2001; Cailliet and Goldman 2004) and age–bias curves (Campana et al. 1995) each were

reported in six papers. Combinations of the various verification and precision assessments were common (11 studies). This approach of combining various assessments is a good one because when more than one method produces similar results it gives additional strength to the conclusions.

However, Hoenig et al. (1995) demonstrated that there can be differences in precision that APE indices obscure because they assume that the variability among observations of individual fish can be averaged over all age groups and that this variability can be expressed in relative terms. Additionally, APE indices do not result in values that are independent of the age estimates, do not test for systematic differences, do not distinguish all sources of variability (such as differences in precision with age) and do not take experimental design among studies into account (i.e., number of times each sample was read in each study.

Within a given ageing study, APE indices may serve as good relative indicators of precision within and between readers provided that each reader ages each vertebra the same number of times. However, even this appears only to tell us which reader was less variable, not which one was better or if either were biased. Bias is a more critical issue than precision, particularly in long-lived chondrichthyan fishes. We prefer also using Goldman's (2004) method for assessing precision, in which the percent agreement within and between readers is calculated, with individuals divided into appropriate length or disc width groups (e.g., 5–10 cm increments). This can be done with sexes separate and/or combined. Biases can then be assessed using contingency table methods (Bowker 1948; Hoenig et al. 1995). We feel that there is validity in using percent agreement with individuals grouped by length as a test of precision because it does not rely on ages (which have been estimated or assessed), but rather on empirical length measurements. Of course, age could be used if, and only if, validation of absolute age for all available age classes had been achieved.

Recommendations

Chondrichthyan life history researchers should continue to apply precision analyses in their

ageing studies, and should, whenever possible, use multiple methods. In addition, within- or between-reader age–bias curves should be employed, including frequencies and levels of agreements superimposed on these curves (Fig. 2), and contingency tables.
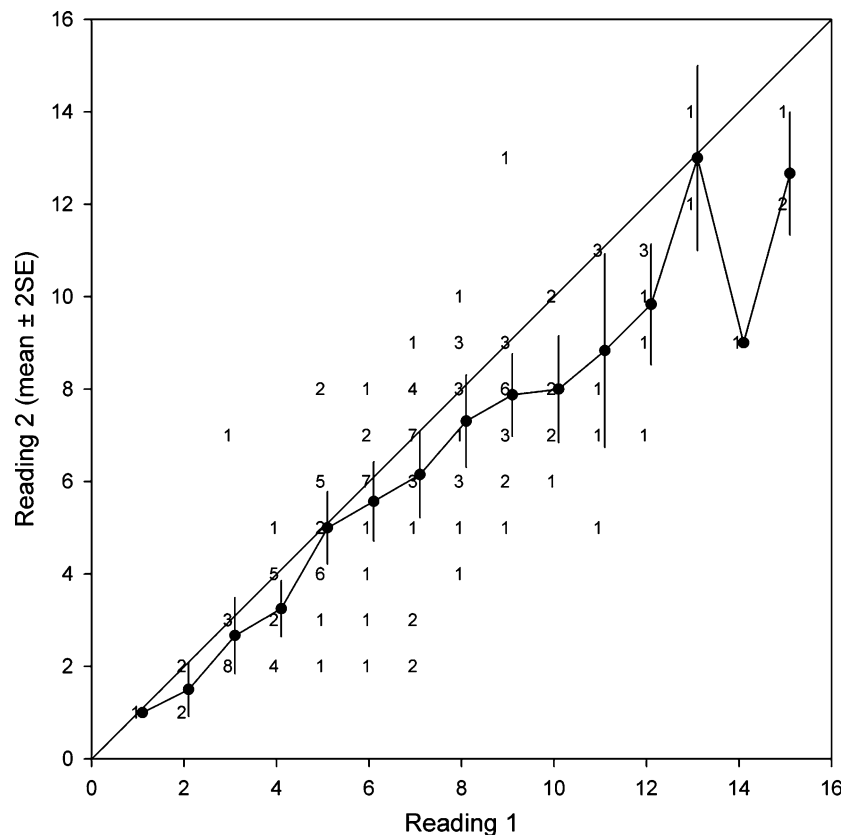
Validation analysis

Panfili et al. (2002) defined "accuracy" as "the closeness of the estimate of a quantity (measured or computed value) to its true value." Thus, to document or test accuracy is to validate that the growth zones being counted represent some temporal unit such as season or year. Again, the techniques commonly used to validate age estimates were presented by Campana (2001) for fishes in general and by Cailliet and Goldman (2004) and Goldman (2004) for use on chondrichthyans.

Campana (2001) included at least eight approaches, all clearly summarized and listed, in order of choice. These were: (1) release of known age and marked fish; (2) bomb radiocarbon; (3) mark-recapture of chemically tagged fish; (4) radiochemical dating; (5) discrete length modes sampled for age structures; (6) natural date-specific markers; (7) marginal increment analysis; and (8) captive rearing (with and without oxytetracycline or OTC). While radiochemical dating has proven to be quite useful for bony fish otoliths (see Andrews et al. 1999, 2005; Stevens et al. 2004 for examples), its assumptions are invalid for cartilaginous chondrichthyan skeletons and it cannot be used on this group of fishes (Welden et al. 1987).

According to Cailliet and Goldman (2004), the techniques most commonly used on chondrichthyan fishes were marginal increment analysis, size frequency modal analysis, release of known-age, marked fish, mark-recapture of chemically tagged fish, and captive rearing. Also, one study

Fig. 2 An intra-reader age–bias plot that also incorporates age-specific agreements from a contingency table of thorn band counts for *Amblyraja georgiana* (from Francis and Maolagáin 2005). Numbers represent number of skates, and dots with error bars are the mean counts of reading 2 (±2 standard errors) relative to reading 1 (offset by +0.1 bands for clarity) for 119 readings. The diagonal line indicates a one-to-one relationship

was published by Campana et al. (2002) utilizing bomb radiocarbon age validation techniques for the porbeagle, *Lamna nasus*, and one vertebral centrum of the shortfin mako, *Isurus oxyrinchus*. While this exciting new validation approach is quite promising, it is also highly technical and expensive, thus no new papers have been published to date. However, three papers were presented at this symposium, which appear in these proceedings (see Ardizzone et al. 2006; Campana et al. 2006; Kerr et al. 2006)

In our review of the recent literature (Cailliet and Goldman 2004), including the more recent 28 studies, validation studies have not been very common for chondrichthyan fishes. This is mainly because of their limited accessibility, large size and mobility, and the difficulty of obtaining monthly, or even seasonal, samples. As a result, almost half of the 28 studies (13) did not report any age validation results, and the rest used a variety of tools.

Edge analysis

As discussed by Cailliet and Goldman (2004) and Goldman (2004), edge analysis characterizes the margin of a structure used for ageing over time in many different individuals to discern seasonal changes in growth. These structures have traditionally been vertebral centra, but this approach could equally apply to spines, thorns and neural arches. Edge analysis involves qualitatively characterizing the margin of the calcified structure as opaque or translucent, light or dark, wide or narrow, or a combination of these features.

In our examination of the recent literature we found that 6 of the 13 studies applied centrum edge analysis as a validation method. One approach was categorizing the edges simply as opaque or translucent (four studies), while the others categorized the edges as one of three grades (two studies).

The use of edge analysis was introduced by Holden and Vince (1973), who determined the timing of band deposition and validated the annual formation of one opaque and translucent band (one band pair) in whole vertebral centra of *Raja clavata* in conjunction with OTC mark recapture. However, they warned that the timing

of opaque band formation did not necessarily coincide with the time that they become visible at the edge of the centrum. In their study, recognition of centrum edge types was commonly obscured by remaining vertebral connective tissue. Prompted by this earlier study, Tanaka and Mizue (1979) sectioned vertebral centra to enhance band clarity and determine the periodicity of band formation. Three grades of band development were classified from centrum edges. These grades were based on the optical qualities and width of the ultimate band (I: dark; II: light, narrow; III: light, broad) in relation to the month of capture.

Identifications of edge types may be influenced by many factors. The optical qualities of an ageing structure vary with preparation (e.g. thickness of section), species, its dimensions, and lighting methods. Edge types of stained vertebrae may be more difficult to interpret because of the accumulation of stain at the sample–resin interface. Inter-annual environmental variation may also alter the pattern of band formation and reduce the resolution of the technique. The experience level of those estimating ages and inconsistent criteria for assigning edge grades may further introduce variability and subjectivity into the analysis. It is therefore critical to include only samples of good condition and clarity and to carefully and consistently examine the edges of an ageing structure.

Despite the subjectivity associated with this approach, edge analysis has frequently been used in chondrichthyan ageing studies. The percent frequency of opaque and translucent bands has been compared with month or season of specimen capture (e.g. Roussouw 1984; Kusher et al. 1992; Wintner et al. 2002), and Tanaka and Mizue's (1979) approach has been adopted in numerous studies (e.g. Yudin and Cailliet 1990; Carlson et al. 1999). Following modified edge analysis methods introduced in teleost ageing studies (Anderson et al. 1992; Vilizzi and Walker 1999), Smith (2005) classified four distinct edge categories: narrow translucent, broad translucent, narrow opaque and broad opaque. The width of the forming band (broad/narrow) was determined based on proportional development in relation to the previous like band. Although this approach

may not be well suited for small-bodied species or may become more complicated among the largest/oldest specimens, the consideration of four general edge types can provide enhanced details pertaining to seasonal patterns of band formation. When combined with additional techniques, such as Marginal Increment Analysis (MIA), edge analysis can provide valuable corroborative evidence to validate the periodicity of band formation.

Marginal increment analysis

MIA provides a useful, semi-direct (Panfili et al. 2002) method of validating the periodicity of band formation. It is the most commonly employed validation technique among chondrichthyan age and growth studies (Cailliet and Goldman 2004; Goldman 2004). Like edge analysis, MIA requires the recognition and identification of the band type forming on the outer edge of an ageing structure. Typically, the width of the ultimate, developing band (or band pair) is compared to the width of the last fully formed band pair and mean values of these ratios are related to the month of capture. Trends in the periodicity of band formation can be compared by size class, pooled age classes, select age classes (e.g. White et al. 2001; Sulikowski et al. 2005a), or season (Neer and Thompson 2005), but should ideally be restricted to individual age classes (Campana 2001). Specimens estimated to be age 0 cannot be included in MIA because they lack fully formed band pairs.

Campana (2001) identified MIA as one of the most difficult and likely to be abused methods of validation. However, Parsons (1993) successfully established the applicability and resolution of MIA in chondrichthyan growth studies by validating the annual deposition of a single band pair within the vertebral centra of *Sphyrna tiburo* using MIA in conjunction with captive, known-age and OTC-injected recaptured specimens. Although the incorporation of MIA into elasmobranch ageing studies has increased markedly since Parsons' (1993) study, the technique had previously been applied for many years. In his pioneering work, Ishiyama (1951) was the first to present a formula for MIA and examine ratios of ultimate and penultimate marginal widths between months of capture to determine the season of band formation. This attempt, however, was largely overlooked.

More recent authors (e.g. Killam and Parsons 1989; Simpfendorfer 1993; Natanson et al. 1995; Loefer and Sedberry 2003; Santana and Lessa 2004; Goldman and Musick 2006) have applied MIA as a validation technique, but few have provided examples of the formulae used to calculate these values or explicit details of this technique. Consequently, ambiguous and inconsistent terminology associated with MIA may have restricted the effective use, interpretation, and comparative value of these analyses among many elasmobranch ageing studies.

Four publications are commonly cited in association with chondrichthyan MIA and each offer seemingly different approaches and terminology:

(1) Natanson et al. (1995): MIR = $(VR–R_n)/(R_n–R_{n-1})$, in which MIR is the Marginal Increment Ratio, VR is the vertebral radius, R_n is the radius of the ultimate band or band pair, and R_{n-1} is the radius of the next to last complete band pair;

(2) Conrath et al. (2002): MIR = MW/PBW, in which MIR remains as previously defined, MW is the margin width, and PBW is the previous band pair width;

(3) Lessa et al. (2004): MI = $VR–R_n$, in which MI is termed the marginal increment, VR is the vertebral radius, and R_n is the radius of the last complete band or band pair.

(4) Branstetter and Musick (1994) apply the term ''relative marginal increment analysis,'' but did not provide a formula or figure to describe the calculation. In their description of MIA, the authors' definitions of the terms ''band'' and ''ring'' were unclear and they proceeded to use them interchangeably making it somewhat difficult to interpret the features to which they were referring. Ambiguity associated with only the presentation of text and terminology may result in differing interpretations as to what features (e.g. bands or band pairs, opaque bands or translucent bands, broad or narrow bands, etc.) should be measured and compared.

Of these four methods, the one detailed by Natanson et al. (1995) has been the most widely cited and originated from Hayashi's (1976) study of marginal increment formation in the otoliths of the red tilefish, *Branchiostegus japonicus*. Each of the techniques described by Branstetter and Musick (1994), Natanson et al. (1995) and Conrath et al. (2002) calculate relative MIRs because the width of the outermost band pair (or band) is divided by the last fully formed band pair, making the marginal increment proportional to the previous growth band, but not necessarily to other fish of different ages. Alternatively, Santana and Lessa (2004) presented a variation that reports the mean relative MIRs by expressing absolute marginal increments as a percentage following Crabtree and Bullock (1998). In contrast, Lessa et al.'s (2004) approach does not provide values of the marginal width. Instead, their formula provides a secondary estimate of vertebral radius minus the ultimate band pair. This approach should not be used as a semi-direct validation method.

If the MIA methods of Branstetter and Musick (1994), Natanson et al. (1995) and Conrath et al. (2002) are interpreted and calculated correctly, they will provide the same result. These methods are not distinct and reflect the most commonly applied form of MIA in teleost ageing studies. The modification presented by Conrath et al. (2002) provides a simplification that directly compares the widths of the ultimate and penultimate band pairs. Secondarily determining width of the penultimate band pair (or band) by subtracting measurements from the vertebral radius introduces additional measurement error into calculations. The percent marginal increment applied by Santana and Lessa (2004) generates an interesting assessment of increment patterns but may inhibit the ability to assess the significance of these trends using most common statistical methods because values are expressed as a percentage. Therefore, we feel using the simplification of MIA as described by Conrath et al. (2002) is the most appropriate technique for validating the temporal periodicity of band deposition among chondrichthyans.

When considering preparation techniques for structures used in age determination and valida-

tion, especially MIA, we caution against the use of whole vertebrae. This is mainly because there can be error measuring straight lines on a concave surface. Many authors (e.g. Kusher et al. 1992) have discussed the potential drawbacks of ageing whole vertebrae and stressed the advantages of sectioning these structures so as to more easily discern the growth zones, especially from older fishes.

MIA typically tests the null hypothesis that a single band pair is deposited annually within the ageing structure of a study species. Given that initial assumption, it is imperative that measurements incorporated into these analyses consist of the last fully-formed band pair (one translucent and one opaque band) and the ultimate forming band or band pair. Measurement of opaque or translucent bands alone would not adequately test this null hypothesis. If more than one band pair is formed each year, or no pattern is evident whatsoever, it will be revealed in such analyses.

Following MIA, statistical analyses should be applied to the resulting data set to determine if significant differences exist among months. Too frequently, authors have relied on visual assessments of potential trends in marginal increment formation based solely on graphical representation of the data. Adequate statistical analyses include parametric single factor ANOVA (e.g. Carlson et al. 2003) and non-parametric Kruskal–Wallis one-way ANOVA (e.g. Simpfendorfer et al. 2000). The required assumptions for parametric analyses (i.e., equality of variances and normality) should be tested to determine if ANOVA is appropriate. As a result, transformation of mean marginal increment data may be necessary to perform ANOVA (e.g. Neer et al. 2005). Likewise, power analysis should be applied to assess the adequacy of sample size and potential for statistical error. Few authors have tested (or reported testing) their marginal increment data to ensure that parametric analyses were appropriate. Because non-parametric approaches may be more robust in cases of unequal sample sizes, inequality of variances, or departures from normality (e.g. Zar 1996), Kruskal–Wallis tests on ranks may be particularly well suited for marginal increment data.

Although rarely included, post-hoc tests should be applied to determine the source and extent of

variation if significant differences are detected in mean marginal increment ratios among months. Tukey and Newman–Keuls are the most commonly used parametric tests for this purpose and modifications of each are available in the common event of unequal sample sizes (Zar 1996; Santana and Lessa 2004). Equivalent procedures are available for non-parametric evaluations, including the Nemenyi and Dunn tests (Zar 1996; Smith 2005). The approach of Dunn (1964) may be more applicable as it does not require equal sample sizes. The ability to identify which monthly or seasonal mean marginal increment ratios are significant from one another may enhance conclusions on the timing of band deposition and the environmental or biological factors that are associated with these events.

In our review of the recent 28 studies, authors used a version of marginal increment analysis in 12 studies. However, of those studies using MIA, only four attempted any statistical analyses to determine if observed variation in the mean marginal increment ratios differed significantly among months or seasons. These statistics included one factor ANOVA (3 studies), the Tukey test (1 study), and non-parametric ANOVA or the Kruskal–Wallace test (1 study).

Recommendations

For edge analysis, researchers should consider using several grades based upon the optical qualities and width of the ultimate band. It is also essential that only samples of good condition and clarity are used. Structures should be sectioned for use with both edge and marginal increment analyses because characterization and measurement of the critical areas of the margin will be more precise. We also feel that researchers need to develop and apply statistical analyses to categorical edge data, perhaps including log-likelihood ratios, Kolmogorov–Smirnov goodness of fit tests, and frequency distribution analysis, among other possibilities (e.g. Zar 1996; Cappo et al. 2000).

For both edge and marginal increment analysis, we support recent recommendations that trends in the periodicity of band formation be analyzed separately by size class, pooled age classes, selected age classes, and seasons. We also support combining edge analysis with other techniques (e.g. MIA) to strengthen the interpretation of band formation periodicity (Fig. 3).

The simplification of MIA as described by Conrath et al. (2002) is the most appropriate technique for validating the temporal periodicity of band deposition among chondrichthyans. Statistical analyses for MIA are necessary to insure that the edge dimensions really vary significantly with season. These should include tests to determine whether parametric or non-parametric statistics would be most appropriate for a given study. If significant differences among months or seasons are detected, appropriate post-hoc tests should be applied to identify the temporal source of this variation.

L_0 vs. t_0 and other aspects of the von Bertalanffy growth function (VBGF)

The VBGF (von Bertalanffy 1934, 1938, 1960) is the most commonly used growth function in chondrichthyan age and growth studies:

$$L(t) = L_\infty - (L_\infty - L_0)\,e^{-kt},$$

where $L(t)$ is length as a function of time (t), L_∞ is the theoretical asymptotic length, L_0 is the size at birth, and k is the rate constant. The function that has consistently been presented as von Bertalanffy's (1934) growth function (e.g. Ricker 1979; Gulland 1983; Hilborn and Walters 1992; Haddon 2001) represents a modification of the original formula and is:

$$L(t) = L_\infty\left(1 - e^{-k(t-t_0)}\right),$$

where t_0 is the theoretical time at zero length and the other parameters are as previously defined. Von Bertalanffy (1934) obtained his growth function by integrating the differential equation:

$$dw/dt = \eta\,w^{2/3} - \kappa\,w,$$

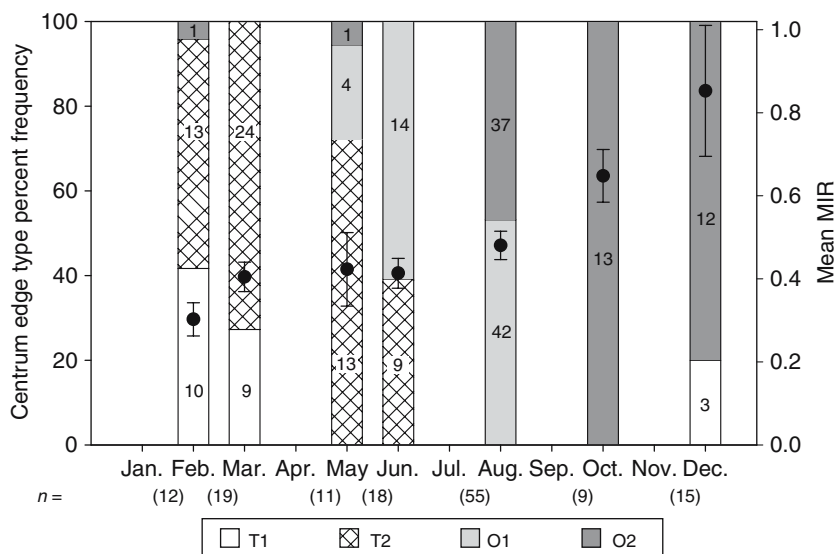where η (eta) is the build-up (anabolic), κ (kappa) is the break-down (catabolic) physiological

Fig. 3 Monthly variation among four centrum edge types ($n = 205$) and mean monthly marginal increment ratios (MIR) ±1 standard error ($n = 139$) determined from pooled sexes and size classes of the diamond stingray, *Dasyatis dipterura* (from Smith 2005). Values within the histogram represent the number of samples included in monthly centrum edge analyses. Sample sizes incorporated into the marginal increment analysis are listed in parentheses below the x-axis

parameter, and *w* is mass (weight). The constant of integration is determined by the value of $w(t)$ at time zero (y-axis intercept) or $L(t)$, and not some imaginary, negative time when $w(t) = 0$ or $L(t) = 0$ (x-axis intercept). His differential equation applied to mass, but the first step in this integration is the substitution method $y = w^{1/3}$ and this first mathematical step can be interpreted biologically to produce a differential equation for length if we substitute with $L = qw^{1/3}$ where q is a constant. The integration of the differential equation also shows that it is convenient to use the parameter $L_\infty = 3q(\eta/k)$ which is inversely proportional to the rate constant k (where $k = \kappa/3$). The steady state value $L\ (t = \infty) = L_\infty$ is determined by both η and k, while the time it takes to reach the final length from birth is determined by k alone.

It was Beverton (1954) who first used t_0 instead of L_0 as the third parameter in the VBGF. He mathematically transformed the VBGF with the parameters L_∞, k, and L_0 to an equation with the parameters L_∞, k, and t_0 to simplify yield calculations. He stated in Lecture 9 on p. 43: "It must be remembered that the constant t_0 is largely artificial, insofar as it defines the age at

which the organism would be of zero length if it grew throughout life with the same pattern of growth as in the post-larval phase." The VBGF with t_0 as the third parameter was also used in Beverton and Holt (1957), and they also stated on p. 34: "In practice, the constant t_0 must be regarded as quite artificial." Nevertheless, this led to widespread but unfortunate use of the VBGF with t_0 as the third parameter in age and growth studies. Holden (1974) incorrectly assumed that t_0 had biological meaning for elasmobranchs (i.e., gestation period), but it does not (Pratt and Casey 1990; Van Dykhuizen and Mollet 1992).

We also note that the rate constant k has units of reciprocal time and is difficult to interpret. It is easier to interpret k in terms of half-lives (ln $2/k$) with units of time. The time it takes to reach the fraction x of L_∞ is given by:

$$t_x = 1/k \ln\left[(L_\infty - L_0)/(L_\infty(1 - x))\right].$$

If, for example, we use $x = 0.95$ (Ricker 1979), we also need to specify L_0 (for example $0.2L_\infty$), then we can interpret $t_{0.95}$ as a longevity estimate as given by:

$$t_{0.95} = 2.77/k = 4.0 \ln 2/k (4 \text{ half} - \text{lives}).$$

Fabens ([1965](#)) defined longevity based on $x = 0.9933$, assumed $L_0 = 0$, and obtained:

$$t_{0.99} = 5/k = 7.21 \ln 2/k,$$

for 7.2 half-lives. This shows that there is a considerable range for the definition of longevity depending on the value of x postulated.

It does not matter which 3-parameter VBGF is used for fitting length vs. age data as they are mathematically equivalent. However, the equation with L_0 as the third parameter has major advantages. Size at birth of elasmobranchs is often well defined and known. It is therefore easy to judge whether the fitted L_0 is a reasonable value. If the parameters L_∞, k, and t_0 are used as fitting parameters for elasmobranch age and growth studies, then L_0 should at least be calculated ($L_0 = L_\infty(1 - e^{kt_0})$). If the calculation of L_0 is omitted, one cannot evaluate how reasonable the fitted t_0 might be; they often are quite excessive (i.e., a t_0 value that is far too large or far too small) and this is an indication that an unreasonable calculated L_0 will result. Despite the advantages of using L_0 instead of t_0 as the third parameter in the VBGF, few papers dealing with elasmobranch growth have used it (e.g. Aasen [1963](#); Cailliet et al. [1992](#); Van Dykhuizen and Mollet [1992](#); Mollet et al. [2002](#)). We are not sure why t_0 remained the preferred third parameter in most publications over the last 20 or more years, except that it is convenient.

Some authors have dealt with the lack of biological reality involved with estimating t_0 by fixing or anchoring the VBGF with an estimate of L_0 from known or estimated size-at-birth values (e.g. Van Dykhuisen and Mollet [1992](#); Neer and Thompson [2005](#)). This modification can often significantly alter the other VBGF parameters. For example, it could decrease L_∞ and also increase the mean square error (MSE) and the standard error of the estimate (SEE) of the function. The 2-parameter VBGF with L_0 fixed as only one value can ignore what is often highly variable and sometime rapid early juvenile

growth rates. Thus, all known values of L_0 should be used.

In our review of the 28 most recent chondrichthyan growth studies, almost all estimated growth parameters using the VBGF, and most (25 studies) also used the 3-parameter solution solving for k, L_∞, and t_0 but not L_0). However, three studies (Carlson and Baremore [2005](#); Neer et al. [2005](#); Santana and Lessa [2004](#)) also used a two-parameter solution, using a fixed (or average) L_0 to anchor the model, solving only for k and L_∞.

Recommendations

Our recommendation is to use L_0 instead of t_0, whenever possible, because it can be biologically meaningful (Cailliet and Goldman [2004](#)). We suggest that t_0 should never be used to estimate meaningful life history parameters of chondrichthyans (e.g. gestation period). If a three-parameter fit for the VBGF is used that incorporates t_0, researchers should check to see whether the resulting, calculated L_0 value crosses the y-axis within the range of observed length at birth.

Multiple growth functions: biological relevance, quality of fit, and convenience

It is often important and even necessary, to use more than one growth function to adequately characterize the growth of a given species. Yet, as previously stated, a single form of the VBGF (after Beverton [1954](#)) has primarily been applied in chondrichthyan ageing studies. However, serious limitations and reservations have been identified with the growth function (e.g. Knight [1968](#); Roff [1980](#); Moreau [1987](#)), including a limited ability to reflect early growth (Gamito [1998](#)). Some of the criticisms applied to the VBGF are also relevant to many growth functions in general (e.g. assumption of asymptotic growth). Appropriate models should be selected on the indication of biological reality, statistical basis of their fit, convenience (Moreau [1987](#)), and, as models of increased complexity are applied, parsimony (e.g. Burnham and Anderson [2002](#); Spiegelhalter et al. [2002](#); Guthery et al. [2005](#)). If an investigator's

objective is to express the growth characteristics of a species in quantitative terms, it is imprudent and may be counter-productive to base this description on a single, exclusive model.

Numerous models have been developed to describe growth characteristics based on size-at-age estimates or mark-recapture data (e.g. Ricker 1979; Baker et al. 1991; Haddon 2001). The VBGF itself has been modified, including two-parameter fits based on known size-at-birth (e.g. Van Dykhuizen and Mollet 1992), weight-at-age estimates (Fabens 1965), a generalized four-parameter form (Pauly 1979), or ''near-linear'' reparamaterizations developed to improve statistical properties of the model (e.g. Ratkowsky 1986; Hernandez-Llamas and Ratkowsky 2004). Polynomial functions have been suggested and applied as alternatives to the VBGF, but the resulting parameters provide no correlate for biological evaluation (Knight 1968; Chen et al. 1992). Flexible models, such as Richards (1959) and Schnute (1981), provide formulations that are capable of expressing more than one model form. Growth models have also been developed that incorporate the influences of ontogenetic or strong seasonal changes in growth trajectories (Soriano et al. 1992; Porch et al. 2002). However, it is outside the scope of this review to summarize each of the many available growth models and detail their characteristics. Instead, we emphasize that a single universal model is unlikely to adequately describe the growth of all chondrichthyans and encourage the fitting of multiple functions to enhance descriptions of growth.

Moreau (1987, p. 81) stated that ''the main criteria for choosing a growth curve are quality of fit and convenience.'' Goodness of fit is best evaluated using several criteria. Coefficients of determination (r^2) have been the primary and often sole measure of model fit among chondrichthyan ageing studies. However, this approach may not be well suited for non-linear models (e.g. Kvålseth 1985). Recommended methods of evaluating model performance include the lowest residual MSE (also referred to as residual variance) or SEE, examination or comparison of residuals, and level of significance (e.g. $P < 0.05$) (Ratkowsky 1983; Neter et al. 1996). These measures used separately or in combination, are

valuable whether considering single or multiple models. Although the potential for misinterpreting the quality of fit based on analysis of residuals alone increases when sample sizes are relatively small, plots of standardized residuals vs. predicted age allow a rapid means of identifying outliers within a dataset. Such outliers could, in turn, disproportionately influence estimates of MSE or SEE (Ratkowsky 1983). Because standardized residuals are normalized by their standard deviation, these plots and related analyses provide useful means of comparing fit between models generated from differing size-at-age (e.g. total length, disc width, weight) variables. Convenience is also an important factor in model selection. Specific models may be preferred for comparison with other studies, application to additional fishery models, or for indirect estimation of mortality and other life history correlates (e.g. Jensen 1996).

Regardless of the quality of fit and need for convenient models, the extent to which a given growth function produces reasonable biological estimates must remain a primary factor in model selection. Goodness of fit, used alone, could lead to choosing an inappropriate growth function. Using a combination of fit and a biological interpretation of one or more of the parameters, such as L_0 (from t_0 if necessary), longevity (from k), and L_∞ (directly), may ensure that the most biologically meaningful growth function is chosen.

In our review of the 28 most recent chondrichthyan growth studies, most applied only the VBGF (25 studies). However, four studies (Carlson and Baremore 2005; Neer et al. 2005; Neer and Thompson 2005; Santana and Lessa 2004) also fit their data to alternate growth functions (Ricker 1979), including the Gompertz (3 studies), logistic (3 studies), modified VBGF using a fixed L_0 based on a known size-at-birth (2 studies), Richards (2 studies), and Schnute (1 study) models (e.g. Winsor 1932; Ricker 1979; Schnute 1981). In each of these four studies, goodness of fit was evaluated by one or more measures other than the coefficients of determination (r^2).

Alternative models to the VBGF have been demonstrated to provide improved fits or generate more biologically reasonable representations

of chondrichthyan growth in some studies. Gompertz and logistic models have been reported to produce significantly better fits to weight-at-age estimates than other model forms for *Rhinoptera bonasus* (Neer and Thompson 2005) and *Carcharhinus limbatus* (Killam and Parsons 1989), respectively. A logistic model fit to total length-at-age was presented as the most appropriate descriptor of growth for *Raja binoculata* (Zeiner and Wolf 1993). In some instances (Neer and Cailliet 2001), alternative growth functions provided the best fit to observed size-at-age data but were not reported because of the convenience and recognition of using the VBGF. Although the traditional VBGF may be an unsuitable descriptor of growth for species which do not attenuate toward an asymptote with increasing age, data quality, sample size, and dispersion of data across size-classes influence model performance, and subsequent selection. These examples illustrate the value of evaluating alternative models.

Recommendations

Although the VBGF may often provide a suitable description of growth, we encourage the use of multiple growth models to evaluate the growth characteristics of a given species. We also recommend that one should certainly consider convenience (i.e., the ability to compare parameters between sexes and among studies, locations, or species) and fit (i.e., using numerous growth functions, statistically examining them, and choosing those that best fit the actual size-at-age data) when characterizing growth for a given species. This approach is needed, considering that not all species follow the same growth function and different stages of their lives may undergo different characteristic growth patterns (Moreau 1987; Prince et al. 1991; Soriano et al. 1992; Hernandez-Llamas and Ratkowsky 2004). Finally, we encourage authors to consider and fit alternate metrics of body size for use with various growth models. For example, it may be more relevant to use girth, disc width, and/or weight rather than total length for angel sharks (Natanson and Cailliet 1990) and many species of batoids.

Summary and conclusions

Since validated age and growth estimates are important for constructing age-structured population dynamic models of chondrichthyan fishes, we have reviewed the field of age and growth on these fishes, briefly summarizing 28 recent studies either missed or new since the publication of the summary chapter on chondrichthyan ageing by Cailliet and Goldman (2004). We used these recent studies to identify areas where improvements can be made in describing the characteristics of ageing structures (both traditional and novel) utilized to estimate ages of sharks, rays, and chimaeras. The topics identified that we believe would be improved through greater consistency include the: (1) terminology used to describe growth features, promoting the use of the terms bands and band pairs; (2) methods used to both verify and validate age estimates from chondrichthyan calcified structures, especially edge and marginal increment analyses, and including statistical analyses; (3) the functions used to produce and interpret growth model parameters, stressing the incorporation of size at birth (L_0); and (4) use of multiple functions to characterize chondrichthyan growth, age at maturity, and longevity. Finally, we also strongly urge chondrichthyan agers to consult, review and incorporate established and novel methods used in age and growth studies of other organisms, including bony fishes (e.g. Campana 2001; Panfili et al. 2002).

References

Aasen O (1963) Length and growth of the porbeagle (*Lamna nasus*, Bonnaterre) in the North West Atlantic. Rep Norwegian Fish Mar Investig 13(6):20–37

Anderson JR, Morison AK, Ray D (1992) Age and growth of the Murray cod, *Maccullochella peeli* (Perciformes: Percichthyidae), in the Lower Murray-Darling Basin, using thin-sectioned otoliths. Aust J Mar Freshw Res 43:983–1013

Andrews AH, Cailliet GM, Coale KH (1999) Age and growth of the Pacific grenadier (*Coryphaenoides acrolepis*) with age estimate validation using an improved radiometric ageing technique. Can J Fish Aquat Sci 56:1339–1350

Andrews AH, Burton EJ, Kerr LA, Cailliet GM, Coale KH, Lundstrom CC, Brown TA (2005) Bomb radiocarbon and lead-radium disequilibria in otoliths of bocaccio rockfish (*Sebastes paucispinis*): a determination of age and longevity for a difficult-to-age fish. Proceedings of the 3rd international symposium on otolith research and application. Marine Freshw Res 56:517–528

Ardizzone, D, Cailliet GM, Natanson LJ, Andrews AH, Kerr LA, Brown TA (2006) Application of bomb radiocarbon chronologies to shortfin mako (*Isurus oxyrinchus*) age validation. In: Carlson JK, Goldman KJ (eds) Age and growth of chondrichthyan fishes: new methods, techniques and analyses. Special Volume from symposium of the American Elasmobranch Society, July 2005. Environ Biol Fish (in press)

Baker TT, Lafferty R, Quinn II TJ (1991) A general growth model for mark-recapture data. Fish Res 11:257–281

Beamish RJ, Fournier DA (1981) A method for comparing the precision of a set of age determinations. Can J Fish Aquat Sci 38:982–983

von Bertalanffy L (1934) Untersuchungen ueber die Gesetzlichkeit des Wachstums. Wilhelm Roux' Arch Entwick Organ 131:613–652

von Bertalanffy L (1938) A quantitative theory of organic growth (inquiries on growth laws II). Hum Biol 10:181–213

von Bertalanffy L (1960) Principles and theory of growth. In: Wowinski WW (ed) Fundamental aspects of normal and malignant growth. Elsevier, Amsterdam, pp 137–259

Beverton RJH (1954) Notes on the use of theoretical models in the study of the dynamics of exploited fish populations. United States Fishery Laboratory, Beaufort, North Carolina, Miscellaneous Contribution (2), 159 pp

Beverton RJH, Holt SJ (1957) On the dynamics of exploited fish populations. United Kingdom Ministry of Agriculture and Fisheries, Fisheries Investigations (Series 2) 19, 533 pp

Bowker AH (1948) A test for symmetry in contingency tables. J Am Stat Assoc 43:572–574

Branstetter S, Musick JA (1994) Age and growth estimates for the sand tiger in the northwestern Atlantic ocean. Trans Am Fish Soc 123:242–254

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York, 488 pp

Cailliet GM, Goldman KJ (2004) Age determination and validation in chondrichthyan fishes. In: Carrier J, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press LLC, Boca Raton, FL, pp 399–447

Cailliet GM, Martin LK, Kusher D, Wolf P, Welden BA (1983) Techniques for enhancing vertebral bands in age estimation of California elasmobranchs. In: Prince ED, Pulos LM (eds) Proceedings international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, sharks. NOAA Tech. Rep. NMFS 8, pp 157–165

Cailliet GM, Natanson LJ, Welden BA, Ebert DA (1985) Preliminary studies on the age and growth of the white shark, *Carcharodon carcharias*, using vertebral bands. S Calif Acad Sci Mem 9:49–60

Cailliet GM, Yudin KG, Tanaka S, Taniuchi T (1990) Growth characteristics of two populations of *Mustelus manazo* from Japan based upon cross-readings of vertebral bands. In: Pratt HL Jr, Gruber SH, Taniuchi T (eds) Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. NOAA Technical Report (90), pp 167–176

Cailliet GM, Mollet HF, Pittenger GG, Bedford D, Natanson LJ (1992) Growth and demography of the pacific angel shark (*Squatina californica*), based upon tag returns off California. Aust J Mar Freshw Res 43:1313–1330

Campana SE (2001) Accuracy, precision, and quality control in age determination, including a review of the use and abuse of age validation methods. J Fish Biol 59:197–242

Campana SE, Annand CM, McMillan JI (1995) Graphical and statistical methods for determining the consistency of age determinations. Trans Am Fish Soc 124:131–138

Campana SE, Natanson LJ, Myklevoll S (2002) Bomb dating and age determination of large pelagic sharks. Can J Fish Aquat Sci 59:450–455

Campana SE, Marks L, Joyce W (2005) The biology and fishery of shortfin mako sharks (*Isurus oxyrinchus*) in Atlantic Canadian waters. Fish Res 73:341–352

Campana SE, Jones C, McFarlane GA, Myklevoll S (2006) Bomb dating and age determination of spiny dogfish. In: Carlson JK, Goldman KJ (eds) Age and growth of chondrichthyan fishes: new methods, techniques and analyses. Special Volume from symposium of the American Elasmobranch Society, July 2005. Environ Biol Fish (in press)

Cappo M, Eden P, Newman SJ, Robertson S (2000) A new approach to validation of periodicity and timing of opaque zone formation in the otoliths of eleven species of *Lutjanus* from the central Great Barrier Reef. Fish Bull 98:474–488

Carlson JK, Baremore IE (2005) Growth dynamics of the spinner shark (*Carcharhinus brevipinna*) off the United States southeast and Gulf of Mexico coasts: a comparison of methods. Fish Bull 103:280–291

Carlson JK, Cortes E, Bethea DM (2003) Life history and population dynamics of the finetooth shark (*Carcharhinus isodon*) in the northeastern Gulf of Mexico. Fish Bull 101:281–292

Carlson JK, Cortes E, Johnson AG (1999) Age and growth of the blacknose shark, *Carcharhinus acronotus*, in the eastern Gulf of Mexico. Copeia 1999:684–691

Carrier J, Musick JA, Heithaus MR (eds) (2004) Biology of sharks and their relatives. CRC Press LLC, Boca Raton, FL, 596 pp

Chang WYB (1982) A statistical method for evaluating the reproducibility of age determination. Can J Fish Aquat Sci 39:1208–1210

Chen Y, Jackson DA, Harvey HH (1992) A comparison of von Bertalanffy and polynomial functions in modelling fish growth data. Can J Aquat Sci 49:1228–1235

Coelho R, Erzini K (2002) Age and growth of the undulate ray, *Raja undulata*, in the Algarve (southern Portugal). J Mar Biol Assoc UK 82:987–990

Conrath CL, Gelsleichter J, Musick JA (2002) Age and growth of the smooth dogfish (*Mustelus canis*) in the northwest Atlantic Ocean. Fish Bull 100:674–682

Cowley PDS (1997) Age and growth of the blue stingray *Dasyatis chrysonota chrysonota* from the Southern Eastern Cape coast of South Africa. S Afr J Mar Sci 18:31–38

Crabtree RE, Bullock LH (1998) Age, growth, and reproduction of black grouper, *Mycteroperca bonaci*, in Florida waters. Fish Bull 96:735–753

Cruz-Martinez A, Chiappa-Carrara S, Arenas-Fuentes V (2004) Age and growth of the bull shark, *Carcharhinus leucas*, from southern Gulf of Mexico. E-J Northw Atlant Fish Sci 35(13):1–10

Dunn OJ (1964) Multiple contrasts using ranks sums. Technometrics 6:241–252

Fabens AJ (1965) Properties and fitting of the von Bertalanffy growth curve. Growth 29:265–289

Francis MP, Maolagáin CÓ (2000) Age and growth of ghost sharks. Final Research Report for Ministry of Fisheries Research Project GSH1999/01 Objective 1, National Institute of Water and Atmospheric Research, pp 1–27

Francis MP, Maolagáin CÓ (2001) Development of ageing techniques for dark ghost shark (*Hydrolagus novaezelandiae*). Final Research Report for Ministry of Fisheries Research Project MOF2000/03C, National Institute of Water and Atmospheric Research, pp 1–18

Francis MP, Maolagáin CÓ (2004) Feasibility of ageing pale ghost sharks (*Hydrolagus bemisi*). Final Research Report for Ministry of Fisheries Research Project GSH2002/01 Objective 2, National Institute of Water and Atmospheric Research, pp 1–11

Francis MP, Maolagáin CÓ (2005) Age and growth of the Antarctic skate, (A*mblyraja georgiana*), in the Ross Sea. Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Science 12:183–194

Gallagher MJ, Nolan CP, Jeal F (2004) Age, growth and maturity of the commercial ray species from the Irish Sea. E-J Northw Atlant Fish Sci 35(10):22

Gamito S (1998) Growth models and their use in ecological modeling: an application to a fish population. Ecol Model 113:83–94

Gedamke T, DuPaul WD, Musick JA (2005) Observations on the life history of the barndoor skate, *Dipturus laevis*, on George Bank (western North Atlantic). E-J Northw Atlant Fish Sci 35(10):13

Goldman KJ (2004) Age and growth of elasmobranch fishes. In: Musick JA, Bonfil R (eds) Elasmobranch fisheries management techniques. Asia Pacific Economic Cooperation, Singapore, 370 pp, pp 97–132

Goldman KJ, Branstetter S, Musick JA (2006) A re-examination of the age and growth of sand tiger sharks, *Carcharias taurus*, in the western North Atlantic: the importance of ageing protocols and use of multiple back-calculation techniques. In: Carlson JK, Goldman KJ (eds) Special volume from symposium of the American Elasmobranch Society, July 2005. Environ Biol Fish (in press)

Goldman KJ, Musick JA (2006) Growth and maturity of salmon sharks in the eastern and western North Pacific, with comments on back-calculation methods. Fish Bull 104:278–292

Goosen AJJ, Smale MJ (1997) A preliminary study of age and growth of the smoothhound shark *Mustelus mustelus* (Triakidae). S Afr J Mar Sci 18:85–91

Gulland JA (1983) Fish stock assessment. A manual of basic methods. FAO/Wiley Ser Food Agric 1:86–97

Guthery FS, Brennan LA, Peterson MJ, Lusk JJ (2005) Information theory in wildlife science: critique and viewpoint. J Wildlife Manage 69(2):457–465

Haddon M (2001) Chapter 8: Growth of individuals. In: Modeling and quantitative measures in fisheries. Chapman and Hall/CRC, Boca Raton, FL, pp 187–246

Hayashi Y (1976) Studies on the growth of the red tilefish in the east China Sea – 1. A foundational consideration for age determination from otoliths. Bull Jpn Soc Sci Fish 42(11):1237–1242

Henderson AC, Arkhipkin AI, Chtcherbich JN (2004) Distribution, growth and reproduction of the white-spotted skate *Bathyraja albomaculata* (Norman, 1937) around the Falkland Islands. E-J Northw Atlant Fish Sci 35(1):1–10

Hernandez-Lllamas A, Ratkowsky DA (2004) Growth of fishes, crustaceans and molluscs: estimation of the von Bertalanffy, Logistic, Gompertz and Richards curves and a new growth model. Mar Ecol Prog Ser 282:237–244

Hilborn R, Walter CJ (1992) Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York, 570 pp

Hoenig JM, Morgan MJ, Brown CA (1995) Analyzing differences between two age determination methods by tests of symmetry. Can J Fish Aquat Sci 52:364–368

Holden MJ (1974) Problems in the rational exploitation of elasmobranch populations and some suggested solutions. In: Jones EH (ed) Sea fisheries research. Logos, London, pp 187–215

Holden MJ, Vince MR (1973) Age validation studies on the centra of *Raja clavata* using tetracycline. J Conseil Int Explor Mer 35:13–17

Ishiyama R (1951) Studies on the rays and skates belonging to the family Rajidae, found in Japan and adjacent regions. 2. On the age-determination of Japanese black skate *Raja fusca* Garman (Preliminary Report). Bull Jpn Soc Fish 16(12):112–118

Ivory P, Jeal F, Nolan CP (2004) Age determination, growth and reproduction in the lesser-spotted dogfish, *Scyliorhinus canicula*. E-J Northw Atlant Fish Sci 35(2):20

Jensen AL (1996) Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Can J Fish Aquat Sci 54:987–989

Joung SJ, Liao YY, Chen CT (2004) Age and growth of sandbar shark, *Carcharhinus plumbeus*, in northeastern Taiwan waters. Fish Res 70:83–96

Joung SJ, Liao YY, Liu KM, Chen CT, Leu LC (2005) Age, growth and reproduction of the spinner shark, *Carcharhinus brevipinna*, in the northeastern waters of Taiwan. Zool Stud 44(1):102–110

Kerr LA, Andrews AH, Cailliet GM, Brown TA, Coale KH (2006) Investigations of radiocarbon and stable carbon and nitrogen ratios in vertebrae of white shark (*Carcharodon carcharias*) from the eastern North Pacific Ocean. In: Carlson JK, Goldman KJ (eds) Age and growth of chondrichthyan fishes: New methods, techniques and analyses. Special volume from symposium of the American Elasmobranch Society, July 2005. Environ Biol Fish (in press)

Killam KA, Parsons GR (1989) Age and growth of the blacktip shark, *Carcharhinus limbatus*, near Tampa Bay, Florida. Fish Bull 87:845–857

Kimura DK, Lyons JJ (1991) Between-reader bias and variability in the age-determination process. Fish Bull 89:53–60

Knight W (1968) Asymptotic growth: an example of nonsense disguised as mathematics. J Fish Res Board Can 25(6):1303–1307

Kusher DI, Smith SE, Cailliet GM (1992) Validated age and growth of the leopard shark, *Triakis semifasciata*, with comments on reproduction. Environ Biol Fish 35:187–203

Kvålseth TO (1985) Cautionary note about r^2. Am Stat 39(4):279–285

Lessa R, Santana FM, Hazin FH (2004) Age and growth of the blue shark *Prionace glauca* (Linnaeus, 1758) off northeastern Brazil. Fish Res 66:19–30

Loefer JK, Sedberry GR (2003) Life history of the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) (Richardson, 1836) off the southeastern United States. Fish Bull 101:75–88

Lombardi-Carlson LA, Cortes E, Parsons GR, Manire CA (2003) Latitudinal variation in life-history traits of bonnethead sharks, *Sphyrna tiburo*, (Carcharhinifor-

mes, Sphyrnidae), from the eastern Gulf of Mexico. Mar Freshw Res 54:875–883

Malcolm H, Bruce BD, Stevens JD (2001) A review of the biology and status of white sharks in Australian waters. Report to Environment Australia, Marine Species Protection Program, CSIRO Marine Research, Hobart, 81 pp

Manning MJ, Francis MP (2005) Age and growth of the blue shark (*Prionace glauca*) from the New Zealand exclusive economic zone. New Zealand Fisheries Assessment report 2005/26, 52 pp

Martin LK, Cailliet GM (1988) Age and growth of the bat ray, *Myliobatis californica*, off central California. Copeia 1988(3):762–773

Mollet HF, Ezcurra JM, O'Sullivan JB (2002) Captive biology of the pelagic stingray, *Dasyatis violacea* (Bonaparte, 1832). Mar Freshw Res 53:531–541

Moreau J (1987) Mathematical and biological expression of growth in fishes: recent trends and further developments. In: Summerfelt RC, Hall GE (eds) Age and growth of fish. Iowa State University Press, Ames, pp 81–113

Moura T, Figueiredo I, Bordalo Machado P, Serrano Gordo L (2004) Growth pattern and reproductive strategy of the holocephalan *Chimaera monstrosa* along the Portuguese continental slope. J Mar Biol Assoc UK 84:801–804

Natanson LJ, Cailliet GM (1990) Vertebral growth zone deposition in Pacific angel sharks. Copeia 1990(4):1133–1145

Natanson LJ, Casey JG, Kohler NE (1995) Age and growth estimates for the dusky shark, *Carcharhinus obscurus*, in the western North Atlantic Ocean. Fish Bull 93:116–126

Neer JA, Cailliet GM (2001) Aspects of the life history of the Pacific electric ray, *Torpedo californica* (Ayres). Copeia 2001(3):842–847

Neer JA, Thompson BA (2004) Aspects of the biology of the finetooth shark, *Carcharhinus isodon*, in Louisiana waters. Gulf Mexico Sci 2004(1):108–113

Neer JA, Thompson BA (2005) Life history of the cownose ray, *Rhinoptera bonasus*, in the northern Gulf of Mexico, with comments on geographic variability in life history traits. Environ Biol Fish 73:321–331

Neer JA, Thompson BA, Carlson JK (2005) Age and growth of *Carcharhinus leucas* in the northern Gulf of Mexico: incorporating variability in size at birth. J Fish Biol 66:1–14

Neter J, Kutner MH, Nachtsheim CJ, Wasserman W (1996) Applied linear statistical models: a unified practical approach, 4th edn. Irwin, Chicago, IL, 1408 pp

Officer RA, Gason AS, Walker TI, Clement JG (1996) Sources of variation in counts of growth increments in vertebrae from gummy shark, *Mustelus antarcticus*, and school shark, *Galeorhinus galeus*: implications for age determination. Can J Fish Aquat Sci 53:1765–1777

Officer RA, Day RW, Clement JG, Brown LP (1997) Captive gummy sharks, *Mustelus antarcticus*, form hypermineralised bands in their vertebrae during winter. Can J Fish Aquat Sci 54:2677–2683

Oshitani S, Nakano H, Tanaka S (2003) Age and growth of the silky shark *Carcharhinus falciformis* from the Pacific Ocean. Fish Sci 69:456–464

Panfili J, de Pontual H, Troadec H, Wright PJ (eds) (2002) Manual of fish schlerochronology. Ifremer-IRD coedition, Brest, France, 464 pp

Parsons GR (1993) Age determination and growth of the bonnethead shark *Sphyrna tiburo*: a comparison of two populations. Mar Biol 117:23–31

Pauly D (1979) Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula. Institut für Meereskunde an der Universität Kiel No. 63, 156 pp

Porch CE, Wilson CA, Nieland DL (2002) A new growth model for red drum (*Sciaenops ocellatus*) that accommodates seasonal and ontogenic changes in growth rates. Fish Bull 100:149–152

Pratt HL Jr, Casey JG (1990) Shark reproductive strategies as a limiting factor in directed fisheries, with a review of Holden's method of estimating growth parameters. In: Pratt HL, Gruber SH, Taniuchi T (eds) Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. NOAA Technical Report NMFS 90, pp 97–109

Prince ED, Lee DW, Zweifel JR, Brothers EB (1991) Estimating age and growth of young Atlantic blue marlin *Makaira nigricans* from otolith microstructure. Fish Bull 89:441–459

Ratkowsky DA (1983) Nonlinear regression modeling: a unified practical approach. Statistics: textbooks and monographs, vol 48. Marcel Dekker, Inc., New York, 276 pp

Ratkowsky DA (1986) Statistical properties and alternative parameterizations of the von Bertalanffy growth curve. Can J Fish Aquat Sci 43:742–747

Richard FJ (1959) A flexible growth function for empirical use. J Exp Bot 10(29):290–300

Ricker WE (1979) Growth rates and models. In: Hoar WS, Randall DJ, Brett JR (eds) Fish physiology, vol VIII. Bioenergetics and Growth, pp 677–743

Roff DA (1980) A motion for the retirement of the von Bertalanffy function. Can J Fish Aquat Sci 37:127–129

Roussouw GJ (1984) Age and growth of the sand shark, *Rhinobatos annulatus*, in Algoa Bay, South Africa. J Fish Biol 25:213–222

Santana FM, Lessa R (2004) Age determination and growth of the night shark (*Carcharhinus signatus*) off the northeastern Brazilian coast. Fish Bull 102:156–167

Schnute J (1981) A versatile growth model with statistically stable parameters. Can J Fish Aquat Sci 38:1128–1140

Simpfendorfer CA (1993) Age and growth of the Australian sharpnose shark, *Rhizoprionodon taylori*, from north Queensland, Australia. Environ Biol Fish 36(3):233–241

Simpfendorfer CA, Chidlow J, McAuley R, Unsworth P (2000) Age and growth of the whiskery shark, *Furgaleus macki*, from southwestern Australia. Environ Biol Fish 58:335–343

Smith WD (2005) Life history aspects and population dynamics of a commercially exploited stingray, *Dasyatis* dipterura. MS Thesis, Moss Landing Marine Laboratories and San Francisco State University, 221 pp

Soriano M, Moreau J, Hoenig JM, Pauly D (1992) New functions for the analysis of two-phase growth of juvenile and adult fishes, with application to Nile perch. Trans Am Fish Soc 131:486–493

Spiegelhalter DJ, Best NG, Carlin BP, van der Linde A (2002) Bayesian measures of model complexity and fit. J Roy Stat Soc B 64(4):583–639

Stevens MM, Andrews AH, Cailliet GM, Coale KH, Lundstrom CC (2004) Radiometric validation of age, growth, and longevity for the blackgill rockfish, *Sebastes melanostomus*. Fish Bull 102:711–722

Sulikowski JA, Kneebone J, Eizey S, Jurek J, Danley PD, Howell WH, Tsang PCW (2005a) Age and growth estimates of the thorny skate (*Amblyraja radiata*) in the western Gulf of Maine. Fish Bull 103:161–168

Sulikowski JA, Tsang PCW, Howel WH (2005b) Age and size at sexual maturity for the winter skate, *Leucoraja ocellata*, in the western Gulf of Maine based on morphological, histological, and steroid based analysis. Environ Biol Fish 72:429–441

Tanaka S, Mizue K (1979) Studies on sharks – XV. Age and growth of Japanese dogfish, *Mustelus manazo* Bleeker in the East China Sea. Bull Jpn Soc Sci Fish 45:43–50

Van Dykhuizen G, Mollet HF (1992) Growth, age estimation and feeding of captive sevengill sharks, *Notorynchus cepedianus*, at the Monterey Bay Aquarium. Aust J Mar Freshw Res 43:297–318

Vilizzi L, Walker KF (1999) Age and growth of the common carp, *Cyprinus carpio*, in the River Murray, Australia: validation, consistency of interpretation, and growth models. Environ Biol Fish 54:77–106

Welden BA, Cailliet GM, Flegal AR (1987) Comparison of radiometric with vertebral band age estimates in four California elasmobranchs. In: Summerfelt RC, Hall GE (eds) The age and growth of fish. The Iowa State University Press, Ames, pp 301–315

White WT, Platell ME, Potter IC (2001) Relationship between reproductive biology and age composition and growth in *Urolophus lobatus* (Batoidea: Urolophidae). Mar Biol 138:135–147

White WT, Potter IC (2005) Reproductive biology, size and age compositions and growth of the batoid, *Urolophus* paucimaculatus, including comparisons with other species of the Urolophidae. Mar Freshw Res 56:101–110

Wilson CA, Chairman, Glossary Committee (1987) Glossary. In: Summerfelt RC, Hall GE (eds) Age and growth of fish. Iowa State University Press, Ames, pp 527–530

Winsor CP (1932) The Gompertz curve as a growth curve. Proc Natl Acad Sci 18(1):1–8

Wintner SP, Dudley SFJ, Kistnasamy N, Everett (2002) Age and growth estimates for the Zambezi shark, *Carcharhinus leucas*, from the east coast of South Aftica. Mar Freshw Res 53:557–556

Yamaguchi A, Taniuchi T, Shimizu M (1998) Goegraphic variation in growth of the starspotted dogfish *Mustelus manazo* from five localities in Japan and Taiwan. Fish Sci 65:732–739

Yudin KG, Cailliet GM (1990) Age and growth of the gray smoothhound, *Mustelus californicus*, and the brown smoothhound, *M. henlei*, sharks from central California. Copeia 1990:191–204

Zar JH (1996) Biostatistical analysis, 3rd edn. Prentice Hall, NJ, 662 pp

Zeiner SJ, Wolf P (1993) Growth characteristics and estimates of age at maturity of two species of skates (*Raja binoculata* and *Raja rhina*) from Monterey Bay, California. NOAA Technical Report NMFS 115:87–99