

**Special Issue: Age and Growth of Chondrichthyan Fishes: New Methods,  
Techniques and Analysis**

# **Developments in environmental biology of fishes 25**

Series Editor

DAVID L.G. NOAKES

# **Special Issue: Age and Growth of Chondrichthyan Fishes: New Methods, Techniques and Analysis**

**Editor:**

**Carlson, John K. (Volume editor), National Marine Fisheries Service, Panama City, USA  
Goldman, Kenneth J. (Volume editor), Alaska Department of Fish and Game, Homer, USA**

Reprinted from *Environmental Biology of Fishes*, Volume 77 (3-4) 2006

A C.I.P catalogue record for this book is available from the Library of Congress

ISBN-10 1-4020-5569-2

ISBN-13 978-1-4020-5569-0

---

Published by Springer,  
P.O. Box 17, 3300 AA Dordrecht, The Netherlands

Sold and distributed in North, Central and South America  
By Springer,  
101 Philip Drive, Norwell, MA 02061, USA

In all other countries, sold and distributed  
By Springer,  
P.O. Box 322, 3300 AH Dordrecht, The Netherlands

<http://www.springer.com>  
*Printed on acid-free paper*

All Rights Reserved

© 2006 Springer

No part of the material protected by this copyright notice may be reproduced or utilized in any form or by any means, electric or mechanical, including photocopying, recording or by any information storage and retrieval system, without written permission from the copyright owner.

Printed in the Netherlands

## CONTENTS

Special Issue: Age and Growth of Chondrichthyan Fishes: New Methods,  
Techniques and Analysis

Guest Editors: Carlson, John K. & Goldman, Kenneth J.

Acknowledgment of referees	209–210
Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting by G.M. Cailliet, W.D. Smith, H.F. Mollet & K.J. Goldman	211–228
Age and growth of the sandbar shark, <i>Carcharhinus plumbeus</i> , in Hawaiian waters through vertebral analysis by J.G. Romine, R.D. Grubbs & J.A. Musick	229–239
A re-examination of the age and growth of sand tiger sharks, <i>Carcharias taurus</i> , in the western North Atlantic: the importance of ageing protocols and use of multiple back-calculation techniques by K.J. Goldman, S. Branstetter & J.A. Musick	241–252
Comparing external and internal dorsal-spine bands to interpret the age and growth of the giant lantern shark, <i>Etmopterus baxteri</i> (Squaliformes: Etmopteridae) by S.B. Irvine, J.D. Stevens & L.J.B. Laurenson	253–264
The potential use of caudal thorns as a non-invasive ageing structure in the thorny skate ( <i>Amblyraja radiata</i> Donovan, 1808) by M.J. Gallagher, M.J. Green & C.P. Nolan	265–272
Terminology for the ageing of chondrichthyan fish using dorsal-fin spines by M.W. Clarke & S.B. Irvine	273–277
Do differences in life history exist for blacktip sharks, <i>Carcharhinus limbatus</i> , from the United States South Atlantic Bight and Eastern Gulf of Mexico? by J.K. Carlson, J.R. Sulikowski & I.E. Baremore	279–292
Evidence of two-phase growth in elasmobranchs by M. Araya & L.A. Cubillos	293–300
Two Bayesian methods for estimating parameters of the von Bertalanffy growth equation by K.I. Siegfried & B. Sansó	301–308
A critical appraisal of marginal increment analysis for assessing temporal periodicity in band formation among tropical sharks by R. Lessa, F.M. Santana & P. Duarte-Neto	309–315
Elemental signatures in the vertebral cartilage of the round stingray, <i>Urobatis halleri</i> , from Seal Beach, California by L.F. Hale, J.V. Dudgeon, A.Z. Mason & C.G. Lowe	317–325
Bomb dating and age validation using the spines of spiny dogfish ( <i>Squalus acanthias</i> ) by S.E. Campana, C. Jones, G.A. McFarlane & S. Myklevoll	327–336
Investigations of $\Delta^{14}\text{C}$ , $\delta^{13}\text{C}$ , and $\delta^{15}\text{N}$ in vertebrae of white shark ( <i>Carcharodon carcharias</i> ) from the eastern North Pacific Ocean by L.A. Kerr, A.H. Andrews, G.M. Cailliet, T.A. Brown & K.H. Coale	337–353
Application of bomb radiocarbon chronologies to shortfin mako ( <i>Isurus oxyrinchus</i> ) age validation by D. Ardizzone, G.M. Cailliet, L.J. Natanson, A.H. Andrews, L.A. Kerr & T.A. Brown	355–366
Validated age and growth estimates for the shortfin mako, <i>Isurus oxyrinchus</i> , in the North Atlantic Ocean by L.J. Natanson, N.E. Kohler, D. Ardizzone, G.M. Cailliet, S.P. Wintner & H.F. Mollet	367–383
Validated age and growth of the sandbar shark, <i>Carcharhinus plumbeus</i> (Nardo 1827) in the waters off Western Australia by R.B. McAuley, C.A. Simpfendorfer, G.A. Hyndes, R.R. Allison, J.A. Chidlow, S.J. Newman & R.C.J. Lenanton	385–400
Analysis of variability in vertebral morphology and growth ring counts in two Carcharhinid sharks by A.N. Piercy, T.S. Ford, L.M. Levy & F.F. Snelson Jr	401–406
Morphometric minefields—towards a measurement standard for chondrichthyan fishes by M.P. Francis	407–421

## Acknowledgment of referees

Published online: 17 October 2006  
© Springer Science+Business Media B.V. 2006

The guest editors would like to acknowledge the following referees for taking the time out of their schedules to review manuscripts for this volume.

Referee	Institution
Allen Andrews	Moss Landing Marine Laboratories
Andre Punt	University of Washington
Andrew Piercy	Florida Museum of Natural History
Ashley Williams	James Cook University
Brian Gervelis	National Marine Fisheries Service
Christina Conrath	Florida Museum of Natural History
Colin Simpfendorfer	Mote Marine Laboratory
Craig Kestelle	National Marine Fisheries Service
David Ebert	Moss Landing Marine Laboratories
David Kulka	Department of Fisheries & Oceans-Canada
David Milton	CSIRO Marine Research-Australia
R. Dean Grubbs	Virginia Institute of Marine Science
Enric Cortes	National Marine Fisheries Service
Greg Skomal	Massachusetts Division of Marine Fisheries
Henry Mollet	Monterey Bay Aquarium
Ivy Baremore	University of Florida
Referee	Institution
Jack Musick	Virginia Institute of Marine Science
James Gelsleichter	Mote Marine Laboratory
James Hobbs	University of California, Davis
James Sulikowski	Florida Museum of Natural History
Jason Romine	Virginia Institute of Marine Science
Jody Spence	University of Victoria
John Hoenig	Virginia Institute of Marine Science

Referee	Institution
Joshua Loefer	South Carolina Department of Natural Resources
Julie Neer	National Marine Fisheries Service
Kate Siegfried	University of California, Santa Cruz
Linda Lombardi	National Marine Fisheries Service
Lisa Kerr	University of Maryland
Lisa Natanson	National Marine Fisheries Service
Lori Hale	National Institute of Water and Atmospheric Research-New Zealand
Malcolm Francis	Port Elizabeth Museum-South Africa
Malcolm Smale	National Marine Fisheries Service
Marta Nammack	Irish Sea Fisheries Board
Michael Gallagher	National Marine Fisheries Service
Peter Sheridan	Fisheries Science Services Marine Institute-Ireland
Rick Officer	National Institute of Water and Atmospheric Research-New Zealand
RICC Francis	Department of Fisheries & Oceans-Canada
Rich Beamish	Western Australian Fisheries and Marine Research Laboratories
Rory McAuley	National Marine Fisheries Service
Sarah Gaichas	Deakin University-Australia
Sarah Irvine	Alaska Department of Fish and Game
Scott Meyer	

Referee	Institution
Steve Campana	Bedford Institute of Oceanography-Canada
Todd Gedamke	Virginia Institute of Marine Science
Warren Joyce	Bedford Institute of Oceanography-Canada
Wade Smith	Moss Landing Marine Laboratories
Yiota Apostolaki	Center for Environment, Fisheries and Aquaculture Science-Lowestoft, England



### Acknowledgment of financial support

This publication and travel to the symposium for some participants was supported in part by the National Sea Grant College, Program of the U.S. Department of Commerce's National Oceanic and Atmospheric Administration under NOAA Grant # NA04OAR4170038, project # W05-23PD, through the California Sea Grant College Program; and in part by the California State Resources Agency. Funding was also provided by the American Elasmobranch Society, the National Marine Fisheries Service-Southeast Fisheries Science Center, and the Florida Aquarium. The views expressed herein do not necessarily reflect the views of any of those organizations.

### Special acknowledgements

The guest editors extend their appreciation to George Burgess, Jeff Carrier, John Morrissey, Julie Neer, Ilze Berzins, Russell Moll, Alex

Chester, Nancy Thompson, Michelle Heupel, and Colin Simpfendorfer for helping with various aspects of the symposium. We also thank Lori Hale and Dana Bethea for assisting with the edits to all the manuscripts. Finally, our appreciation goes to Suzanne Mekking, Martine van Bezooijen, and David Noakes for working with us on getting this volume published in *Environmental Biology of Fishes*.

# 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

Received: 2 June 2006 / Accepted: 22 June 2006 / Published online: 29 September 2006  
© Springer Science+Business Media B.V. 2006

**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.

**Keywords** Age validation · Precision analysis · Chondrichthyes · Growth · Longevity · Vertebrae

## 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.

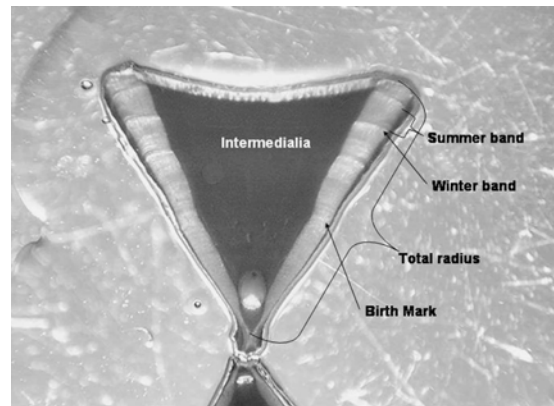
While reviewing the papers published since Cailliet and Goldman (2004), we found that many terms and combinations of terms were used. In the 28 studies reviewed, seasonal patterns were termed “band” (18 studies), “ring” and “zone” (4 each), “increment” (1), and in one publication, not defined at all.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

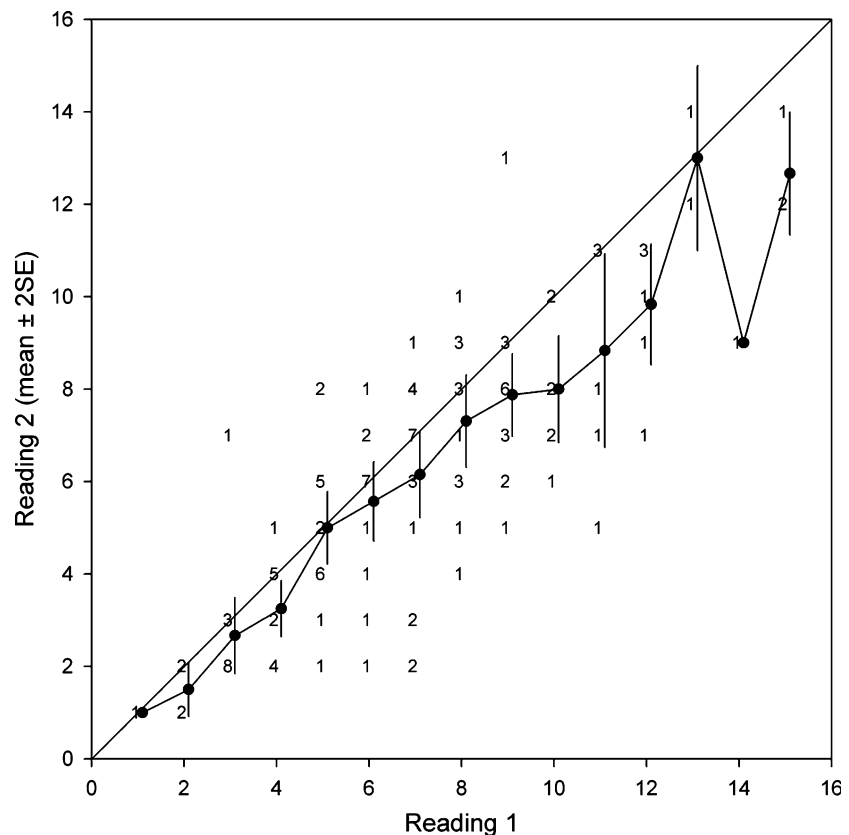
**Validation analysis**

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 oxy-tetracycline 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 ( $\pm 2$  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*<sub>0</sub> vs. *t*<sub>0</sub> 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*<sub>∞</sub> is the theoretical asymptotic length, *L*<sub>0</sub> 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:

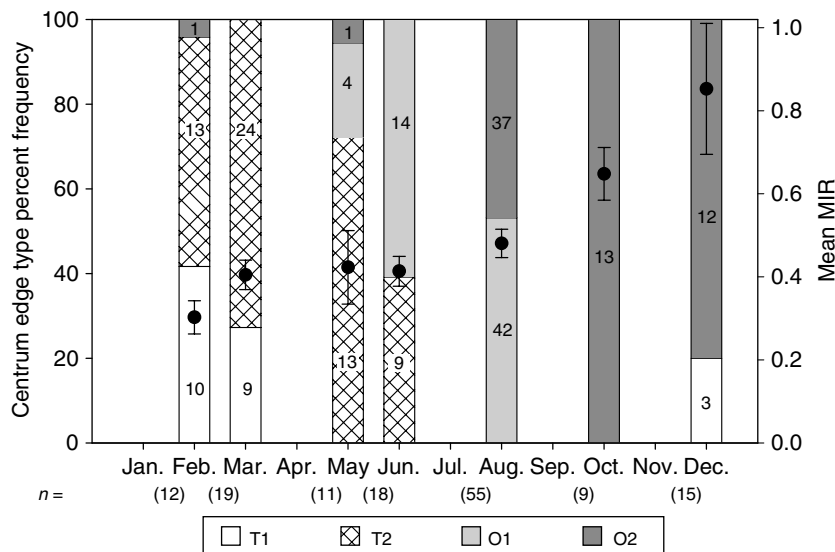
$$L(t) = L_{\infty} \left( 1 - e^{-k(t-t_0)} \right),$$

where *t*<sub>0</sub> 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  $\eta$  (eta) is the build-up (anabolic),  $\kappa$  (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)  $\pm 1$  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  $\eta$  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  $L_\infty$ ,  $k$ , and  $L_0$  to an equation with the parameters  $L_\infty$ ,  $k$ , 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  $L_\infty$  is given by:

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

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:

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

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  $L_\infty$ ,  $k$ , 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 Dykhuizen and Mollet 1992; Neer and Thompson 2005). This modification can often significantly alter the other VBGF parameters. For example, it could decrease  $L_\infty$  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  $k$ ,  $L_\infty$ , 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  $L_\infty$ .

## 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 chondrichthyan 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  $L_\infty$  (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).

**Acknowledgements** We dedicate this paper to all our graduate students and colleagues who have made it possible for us to keep up with the studies of fish age and growth, especially those who helped generate and evaluate ageing techniques. We really appreciate the efforts of John Carlson and Ken Goldman in putting together the slate of symposium speakers (and contributors to this volume) at the Joint Meeting of Ichthyologists and Herpetologists and American Elasmobranch Society Annual Meeting in 2005 entitled “Age and Growth of Chondrichthyan Fishes: New Methods, Techniques, and Analyses” in Tampa, Florida, 6–11 July, 2005. We appreciate the constructive comments on this manuscript by Colin Simpfendorfer, Jack Musick and several other anonymous reviewers. We acknowledge John Carlson, Ivy Baremore, Malcolm Francis, and C.O. Maolagáin for allowing us to use their figures. This study was supported by funds from NOAA/NMFS to the National Shark Research Consortium.

## 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 peelii* (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: Woiniski 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, (*Amblyraja 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-Llomas 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
- Hoening 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