4-9-2015

Estimating Growth and Mortality in Elasmobranchs: Are we doing it correctly?

Brian J. Moe
Nova Southeastern University, brian.moe87@gmail.com

Follow this and additional works at: https://nsuworks.nova.edu/occ_stuetd

Part of the Marine Biology Commons, and the Oceanography and Atmospheric Sciences and Meteorology Commons

Share Feedback About This Item

This Thesis has supplementary content. View the full record on NSUWorks here:
https://nsuworks.nova.edu/occ_stuetd/42

NSUWorks Citation

https://nsuworks.nova.edu/occ_stuetd/42.

This Thesis is brought to you by the HCNSO Student Work at NSUWorks. It has been accepted for inclusion in HCNSO Student Theses and Dissertations by an authorized administrator of NSUWorks. For more information, please contact nsuworks@nova.edu.
Estimating Growth and Mortality in Elasmobranchs: Are we doing it correctly?

By

Brian James Moe

Submitted to the Faculty of
Nova Southeastern University Oceanographic Center
in partial fulfillment of the requirements for
the degree of Masters of Science with a specialty in:

Marine Biology

Nova Southeastern University
April 9, 2015
Abstract

The instantaneous mortality rate ($M$) is an important parameter in elasmobranch management and conservation, but is difficult to estimate directly. Thus, indirect estimates based on relatively easily obtained life history parameters are commonly used. Many indirect methods incorporate one or more parameters from the von Bertalanffy growth model (VBGM), which is often criticized for its inability to describe changes in growth associated with maturity. The Lester growth model (LGM) is a biphasic alternative to the VBGM that incorporates trade-offs between reproduction, growth, and survival, and may therefore more accurately estimate $M$. I used published data from 29 elasmobranch species to compare the performance of the LGM to four conventional growth models and nine conventional methods for indirectly estimating $M$. For three species ($Heterodontus portusjacksoni$, $Rhizoprionodon taylori$, and $Carcharhinus limbatus$), I obtained direct estimates of $M$ to evaluate the accuracy of indirect $M$ methods. According to AICc, the LGM was the best fitting model for 80.8% of datasets. Using one-sample t-tests, I found that five indirect $M$ methods (two of which are dependent on the LGM) consistently generated estimates of $M$ that were in close agreement with direct estimates. The most common methods in elasmobranch literature appear to be overestimating $M$ by factors of 1.34 – 1.91. However, further research is needed to verify these results across a wider range of species. Overall, I recommend using the LGM to describe the lifetime growth of sharks, and estimating $M$ by averaging across five indirect methods.

Keywords: Biphasic growth, Lester growth model, von Bertalanffy, elasmobranch, indirect mortality, lifetime growth
Acknowledgements

First off, I thank my committee; Paul Venturelli, Dave Kerstetter, and Richard Spieler. The guidance and feedback I have received from each of you throughout this process in invaluable. Richard, I am also extremely grateful for your willingness to taking me on as one of your students when I first arrived at NSU. You gave me a shot in your lab years ago, and although we had a scrap the project after a long drawn-out series of failures, it was a great opportunity. Despite of the death of hundreds of zebrafish larvae, it ultimately resulted in the continuation of my career as a fisheries ecologist at the FSU Coastal and Marine Lab. Additionally, I sincerely thank you for your role in bringing Paul on as an adjunct faculty as NSU to serve as my major advisor.

Paul, you have been a fantastic teacher, mentor, and friend to me over the years. You are the entire reason I have chosen to study population dynamics. Before taking your population dynamics course, I fully intended to pursue a career in fish physiology. However, through witnessing your passion for teaching and love of your research, I soon realized that fisheries population dynamics is the field I wanted to work in. I know you were a bit uncertain about taking me on as a student after I came to you with the idea of studying shark population dynamics (being that we were in landlocked Minnesota and you had never seen a non-captive shark before, let alone study them), but it somehow worked out great for both of us! Without your guidance and willingness to bring me into your lab, I would not be where I am now. For that I’m eternally grateful.

Additionally, this thesis was made possible largely by the gracious willingness of others to share their hard earned data. This study first took the form of an undergraduate independent research project during my final year at the University of Minnesota back in 2011, before finally transforming it into a thesis during the winter of 2013. And so, I have been collecting data used in this thesis for nearly 4.5 years. Thus, there are many people I would like to thank for sharing data and contributing to this study. To start, I thank Dean Grubbs and Jason Romine for being the first to share data with me. Your willingness to share length-at-age data for the sandbar shark effectively launched what would eventually become my thesis. I also thank, Nigel Lester and Robert Ramos for providing data on the
Port Jackson shark shortly thereafter. It was at this point that my small undergraduate project began to pick up momentum, and I began reaching out to others in an effort to increase the species richness of this study. Over the years I was able to expand my study to include a total of 29 species, of which raw data was generously provided for 10 species (in addition to the species already described). For their generous contributions of data, I thank Chip Cotton, Christina Conrath, Ken Goldman, Andrew Piercy, John Carlson, Beth Matta, Jon Dale, Walter Bubley, and Trey Driggers. None of this would have been possible without your generosity and willingness to lend a hand to a young scientist in need. I again thank Nigel Lester; this time for your assistance in the proper fitting of your growth model.

I also thank my friends and family. Mom and Dad, thank you so much for dealing with the fact that I don’t want to live in Minnesota. Your continued support though this entire process has been absolutely wonderful. I also thank my younger brother for all his support. Jacob thank you for listening to me vent (particularly during my first year here), and supporting me when things were going well. You are a marvelous brother. I thank my very large extended family for all the support you have given me, particularly the grandparents on both sides of the family. Lastly, my friends. Heather, you have been wonderful to me over the years. Thank you so much for being there for me during my time in South FL, and I apologize for making you read over drafts again, and again, and again, and again. Josh, Andrew, Hunter, Lauren, and Amber, you have all been great friends, and I thank you for your continued friendship and support (particularly in recent weeks).

Finally, I thank Chip Cotton for agreeing to bring me on in just a few short months as a Ph.D. student at the FSU CML. By accepting me as your future student, you gave me the final push I needed to put this thesis to rest.
Table of Contents

Chapter 1: General Introduction ................................................................................. 6
  Problem Statement ................................................................................................. 6
  Literature Review .................................................................................................. 7
  Conventional Growth Models in the Elasmobranch Literature ............................. 7
  The Lester Growth Model ..................................................................................... 9
  Indirect Mortality Estimation ............................................................................... 11
  Growth-Independent Methods ............................................................................ 11
  von Bertalanffy Growth-Dependent Methods ...................................................... 13
  Lester Growth-Dependent Methods .................................................................... 17
  Conclusion .............................................................................................................. 18

Chapter 2: Lifetime Growth of 29 Species of Elasmobranch ................................. 20
  Introduction .......................................................................................................... 20
  Methods .................................................................................................................. 22
  Data ........................................................................................................................ 22
  Growth Models ..................................................................................................... 22
  Model Selection ...................................................................................................... 25
  Results ..................................................................................................................... 25
  Discussion .............................................................................................................. 35

Chapter 3: Accurately Estimating Indirect Mortality: A Case Study of Three Species of Shark .................................................................................................................. 38
  Introduction .......................................................................................................... 38
  Methods .................................................................................................................. 39
  Data ........................................................................................................................ 39
  Indirect Mortality Methods ................................................................................... 40
  Mortality Comparison ........................................................................................... 44
  Results ..................................................................................................................... 44
  Discussion .............................................................................................................. 46

Chapter 4: Indirect Mortality of 29 Species of Elasmobranchs ............................... 49
  Introduction .......................................................................................................... 49
  Methods .................................................................................................................. 50
  Data Sources ......................................................................................................... 50
  Growth-Independent Parameter Estimations ....................................................... 51
Chapter 1: General Introduction

Problem Statement

Throughout human history, elasmobranchs have been subjected to artisanal, commercial, and recreational fishing (Walker 2005). Presently, numerous artisanal fisheries harvest shark meat for high protein sustenance. Commercially, meat and fins make up the majority of the shark trade (Walker 2005, Clarke et al. 2006). The production and sale of shark meat constitutes the largest quantity of international trade of shark products. Much of this meat is shipped to European markets (Clarke et al. 2006). Recently, the demand for shark fins as ingredients in foods, and in particular soups, has risen significantly. This increase is largely the result of the growing economic success of China and the increasing affluence of its citizens. As a result, the shark fin trade has become one of the most lucrative fishing industries (Clarke et al. 2006). Despite these markets for shark meat and fins, there are few fisheries targeting elasmobranchs. Nonetheless, sharks often experience high mortality as incidental catch or bycatch in teleost fisheries (Walker 2005). The increasing profile of the fin trade paired with the discarding of shark bycatch has generated heightened inquiry into the possible rates of overexploitation of shark populations.

Despite the long history and prevalence of elasmobranchs in world fisheries, scientific research pertaining to elasmobranch population dynamics and management did not emerge until the 1960s and 1970s (Bonfil 2005). Teleost fisheries, largely owing to their generally greater harvest levels and economic value, have received the bulk of the focus of fisheries science and management (Walker 2005). As a result, our understanding
of vital information regarding life histories, migratory patterns, and population size and structure of many elasmobranchs has only begun to receive serious attention. For many species, such information is still largely unknown (Walker 2005). However, it is widely agreed upon that the general life history of elasmobranchs (i.e., slow growth, late maturity, and low fecundity) makes this group of fishes particularly sensitive to changes in fishing pressure (Hoenig and Gruber 1990, Smith et al. 1998). As such, it is extremely important for fisheries scientists and managers to be able to accurately describe the life histories and population dynamics of elasmobranchs. Considerable effort has been invested into modeling the lifetime growth of elasmobranchs (and fishes in general) and the growth model parameters generated are required for assessing the size and health of stocks and most importantly, estimating the instantaneous rate of mortality ($M$). In the following sections of this chapter, I briefly review common techniques for describing lifetime growth and estimating mortality in elasmobranch literature (and fisheries in general). While direct estimates of $M$ are typically perceived as the ‘best’ estimates, they require extensive amounts of time and data (Simpfendorfer et al. 2005). As such, direct estimates of $M$ are often infeasible for elasmobranchs, and so, the use of indirect methods to estimate $M$ is typically used.

**Literature Review**

**Conventional Growth Models in the Elasmobranch Literature**

Numerous growth models have been used to describe the lifetime growth of fishes (e.g., the logistic and Gompertz growth models). But it is the von Bertalanffy growth model (VBGM; Beverton and Holt (1957)) that is perhaps the most common in the
elasmobranch literature (Cailliet et al. 2006). The VBGM is a single curve in which
growth steadily slows as it approaches an upper asymptote (von Bertalanffy 1938,
Beverton and Holt 1957). This curve is typically expressed as:

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

where \( L_t \) is length at age \( t \), \( L_\infty \) is asymptotic length, \( K \) is the coefficient of growth, and \( t_0 \) is the x-intercept. This model was originally developed to describe the anabolic and
catabolic changes that take place throughout the lifespan of an organism. It was
popularized by Beverton and Holt (1957) for studying fisheries population dynamics, and
has since dominated the fisheries literature. The popularity of the VBGM stems largely
from its overall utility and ability to estimate many commonly used life history correlates

The VBGM is popular but is also widely criticized. For example, Lipinski and
Roeleveld (1990) challenged the assumption that von Bertalanffy growth is indicative of
metabolism by showing a tight fit to the ‘lifetime’ growth of a plastic squid. However,
most critics argue that the VBGM should only be applied to adults (e.g., Ricker 1975,
Cubillos 2006, Quince et al. 2008a). The crux of this argument is that the VBGM is a
single curve that fails to account for changes in energy allocation upon reaching maturity,
and often results in poor fits to immature growth. Fitting the VBGM to all age classes can
also skew parameter estimates (Ricker 1975). Thus, immature and mature growth should
be described using separate models (Day and Taylor 1997, Lester et al. 2004).
Numerous authors have proposed the use of two-phase growth models for describing the lifetime growth of fishes (e.g., Soriano et al. 1992, Day and Taylor 1997, Lester et al. 2004, Araya and Cubillos 2006, Braccini et al. 2007, Aversa et al. 2011, Dale and Holland 2012). Changes in growth rate may be brought on by changes in habitat use and feeding, but there is also strong support for the energy-allocation hypothesis (Carlson and Baremore 2005, Araya and Cubillos 2006, Braccini et al. 2007, Dale and Holland 2012). Soriano et al. (1992) developed a two-phase growth model (TPGM) that incorporated a modifying factor to the traditional VBGM with the intention of identifying the change point in the growth curve:

\[ L_t = L_\infty (1 - e^{-KA_t(t-t_0)}) , \]

where \( A_t \) incorporates the age at which the transition between phases occurs (\( t_h \)) and the maximum difference between the VBGM and the TPGM (\( h \)).

The TPGM was adapted by Araya and Cubillos (2006) for 16 species of elasmobranchs; by Braccini et al. (2007) for the shortnose spurdog, *Squalus megalops*; by Tribuzio et al. (2010) for the spiny dogfish, *Squalus acanthias*; and Aversa et al. (2011) for the beaked skate, *Dipturus chilensis*. However, the TPGM often predicts negative growth unless constrained (Soriano et al. 1992), can create the appearance of post-maturation growth spurts, and parameter estimates can be sensitive to starting values (Tribuzio et al. 2010).

**The Lester Growth Model**

Lester et al. (2004) proposed a biphasic growth model (LGM) that describes immature growth as a straight line and mature growth as a von Bertalanffy curve. Prior to
maturity, surplus energy is allocated primarily toward somatic growth. Assuming that the ratio of energy gained from foraging and lost to maintenance remains constant, immature growth in the lead-up to maturity is well approximated by a linear model (Lester et al. 2004):

\[ L_t = h_1(t - t_1) , \]

where \( h_1 \) is the rate of immature growth and \( t_1 \) is the intercept on the x-axis for the regression. Linearity ‘in the lead-up to maturity’ is an important distinction that allows for ontogenetic shifts in juvenile diet, which have been observed in a number of elasmobranchs (e.g., Estrada et al. 2006, Farias et al. 2006, McElroy et al. 2006, Lucifora et al. 2009). Linear growth has been observed in immature dusky sharks, *Carcharhinus obscurus* (Simpfendorfer 2000).

Once an individual matures, some proportion of surplus energy is allocated to gonadal growth and reproductive behaviors (courtship, mating, migration, etc.). This reallocation results in a curved growth trajectory that is described by the VBGM. To account for the influence of \( h_1, t_1, \) age-at-maturity \( (T) \), and investment in reproduction \( (g) \) on mature growth, Lester et al. (2004) described the VBGM parameters as:

\[ L_\infty = 3h_1/g , \]

\[ K = \ln(1 + g/3) , \]

\[ t_0 = T + \ln\left(1 - \frac{g(T-t_1)}{3}\right)/\ln(1 + g/3) . \]

To date, the LGM has been applied to over a dozen freshwater and marine teleosts (see articles citing Lester et al. (2004)) and tends to outperform the VBGM as a method
for describing lifetime growth (Quince et al. 2008b). However, the LGM has yet to be applied to elasmobranchs.

**Indirect Mortality Estimation**

Indirect estimation of $M$ are typically based on observed relationships between direct $M$ estimates and various life-history parameters (e.g., Alverson and Carney 1975, Pauly 1980, Hoenig 1983, Jensen 1996, Charnov et al. 2013) or developed from life history theory (e.g., Roff 1984, Chen and Watanabe 1989, Lester et al. 2004). The life-history parameters are either directly observed or estimated using growth models. Herein, I refer to methods that use life-history parameters derived from growth models as growth-dependent, and those not reliant on growth models as growth-independent. All indirect mortality methods used in this study are summarized in Table 1 in Appendix A.

**Growth-Independent Methods**

The most popular indirect method in elasmobranch literature is that of Hoenig (1983). Hoenig (1983) used maximum observed age ($t_{\text{max}}$) to develop four relationships for estimating $M$. We collectively refer to these relationships as Hoenig’s Methods. Three of these relationships are prevalent in elasmobranch literature, while the fourth is based upon mollusks and therefore not applicable to elasmobranch stocks. The most widely used of the three relationships was developed from 84 fish stocks, 80 of which were teleosts (hereafter referred to as Hoenig’s First Method):

\[
\ln(M) = 1.46 - 1.01 \ln(t_{\text{max}})
\]
where \( t_{\text{max}} \) is the oldest observed age. Due to the overrepresentation of teleosts, this relationship may cause bias when applied to elasmobranchs. Hoenig’s Second Method is based on cetaceans:

\[
\ln(M) = 0.941 - 0.873 \ln(t_{\text{max}}).
\]

This method has been used for elasmobranchs (Tsai et al. 2010) because they are often described as having “mammal-like” life-histories. Hoenig’s Third Method was developed from the combined data of fish, cetaceans, and mollusks and is hereafter referred to as:

\[
\ln(M) = 1.44 - 0.982 \ln(t_{\text{max}}).
\]

Hoenig’s Methods were later reevaluated and updated by Hewitt and Hoenig (2005) and Then et al. (2014).

Although Hoenig’s Methods and their variations are common throughout the literature, they do have caveats. To accurately estimate maximum age, large sample sizes are needed to catch the largest (and oldest) individuals (Hoenig 1983). The collection of large sample sizes for many elasmobranchs is impractical, thus increasing the likelihood of inaccurate estimates of maximum age. It should also be recognized that there will be an observed lag in changes in maximum age resulting from changing fishing pressures (Hoenig 1983, Kenchington 2014). Lastly, errors resulting from inaccurate aging cause bias and can be a significant problem for elasmobranchs (Cailliet et al. 2006).

The last growth-independent method that I consider was developed by Jensen (1996) and is expressed as:

\[
M = \frac{1.65}{T_m},
\]
where $T_m$ the observed age-at-50%-maturity. Jensen (1985) observed that $T_m$ was closely approximated by the inflection point of the von Bertalanffy growth equation. This observation was further built upon to describe $M$ as a function of $T_m$ (Jensen 1996). I refer to this method as Jensen’s First Method. The derived relationship between $M$ and $T$ was based on observations of teleost populations and appears to generate upwardly bias estimates when applied to elasmobranchs (Simpfendorfer 1999, McAuley et al. 2005, Knip et al. 2012). Furthermore, when analyzing the VBGM, Jensen (1996) set $t_0$ to 0. This is unrealistic for elasmobranchs and may alter the point of inflection of the growth curve (Hisano et al. 2011). To account for this, Hisano et al. (2011) recommended a modified version to account for $t_0$:

$$M = \frac{1.65}{T-t_0} .$$

I refer to this method as Hisano’s Method.

**von Bertalanffy Growth-Dependent Methods**

Since the popularization of the VBGM by Beverton and Holt (1957), numerous investigators have sought to develop relationships between $M$ and the VBGM parameters. The most popular of these methods were developed by Pauly (1980) and Jensen (1996). Pauly (1980) developed two equations for estimating $M$ using length-at-age and weight-at-age VBGM parameters along with mean water temperatures ($C$):

$$\log M = -0.0066 - 0.279\log L_\infty + 0.6543\log K + 0.4634\log C$$

and

$$\log M = -0.2107 - 0.0824\log W_\infty + 0.6757\log K + 0.4627\log C$$ .
I refer to these relationships collectively as Pauly’s Method. Pauly’s Method was based on $M$ estimates for 175 fish populations (only two of which were elasmobranchs) and was derived from multiple linear regressions. However, Jensen (1996) reanalyzed the data from Pauly (1980) and found a simple linear regression between $M$ and the growth coefficient $K$ to be just as good as the multiple linear regression. In other words, temperature didn’t appear to be important for estimating $M$. I refer to this method as Jensen’s Third Method. Similarly, Then et al. (2014) reevaluated Pauly’s Method by comparing the full method against one excluding temperature (hereafter referred to as Then’s Method). They found that the variation that excluded temperature was a better estimate of $M$ than the original temperature dependent method (Then et al. 2014).

Jensen (1996) also derived a method for estimating $M$ from $K$ based again on the observation that $T$ was closely approximated by the inflection point of the VBGM:

$$M = 1.5K$$

I refer to this method as Jensen’s Second Method. However, multiple authors have found Jensen’s Second Method to overestimate elasmobranch $M$ (Simpfendorfer 1999, McAuley et al. 2005, Knip et al. 2012), suggesting bias when applied to elasmobranchs.

Roff (1984) developed an equation for estimating $M$ from VBGM parameters based on life history theory (hereafter referred to as Roff’s Method):

$$M = \frac{3K}{(e^{K T} - 1)}.$$
However, this method was derived from life history theory as it applies to teleosts and assumes $t_0$ to be roughly equal to 0. Because $t_0$ is rarely 0 in elasmobranchs, this method likely generates bias when applied to elasmobranchs.

Alverson and Carney (1975) developed a method for estimating $M$ based VBGM parameters via analyses of growth and decay curves. I refer to this method as Alverson and Carney’s Method:

$$M = \frac{3K}{(e^{0.38Kt_{\text{max}}}-1)}.$$

However, like Roff’s Method, Alverson and Carney’s Method assumes $t_0$ is roughly equivalent to 0 and is, therefore, likely to generate bias estimates of $M$ in elasmobranchs.

The remaining two VBGM-dependent methods included in this study provide age or length specific estimates of $M$. Chen and Watanabe (1989) sought to estimate age-specific $M$ from the VBGM parameters using life-history theory:

$$M(t) = \begin{cases} \frac{K}{1-e^{-K(t-t_0)}}, & t < T \\ \frac{K}{a_0+a_1(t-T)+a_2(t-T)^2}, & t \geq T \end{cases},$$

where:

$$a_0 = 1 - e^{-K(T-t_0)},$$

$$a_1 = Ke^{-K(T-t_0)},$$

$$a_2 = -\frac{1}{2}K^2e^{-K(T-t_0)}.$$

I refer to this method as Chen and Watanabe’s Method. This method was built on the concept that $M$ cannot be assumed to be constant throughout life and can be described
using the bathtub curve. This curve describes $M$ during three distinct phases: initially high mortality, a prolonged period of low mortality, and high mortality due to senescence (Chen and Watanabe 1989). Chen and Watanabe’s Method is most commonly used in stock assessments, though single constant $M$ estimates may generate equally valuable results (Deroba and Schueller 2013, Then et al. 2014).

Gislason et al. (2010) developed relationship to estimate length-specific $M$ based on relationships between observed direct estimates of $M$ from marine and brackish water fishes and VBGM parameters and temperature. They found the VBGM parameters $K$ and $L_\infty$ to be significantly correlated to $M$, but not temperature. This relationship was later revised by Charnov et al. (2013) and is expressed as:

$$M = K \left( \frac{L}{L_\infty} \right)^{-1.5},$$

where $L$ is length of the fish. I refer to this method as Charnov’s Method. However, like other methods, the direct estimates of $M$ were composed almost entirely of teleosts, so this model may not be appropriate for elasmobranchs.

An additional VBGM-dependent method common in fisheries literature was developed by Peterson and Wroblewski (1984):

$$M_w = 1.92w^{-0.25},$$

where $w$ is dry weight. This relationship is typically used to estimate age-specific $M$ from weight based VBGM parameters. Cortés (2002) suggested using a conversion factor of one fifth to estimate dry weight from wet weight in sharks. In this study I did not analyze weight-at-age data, and so I do not consider this method further.
Lester Growth-Dependent Methods

Lester et al. (2004) developed two methods for estimating $M$ from LGM parameters. The first method that I consider is dependent on the LGM parameter $g$, the reproductive investment:

$$M = - \ln \left( 1 - \frac{g}{1.18} \right).$$

I refer to this method as Lester’s First Method. The second relationship is dependent on the parameters $T$ and the slope of the juvenile growth curve ($t_1$). This relationship was later revised by Lester et al. (2014) and is hereafter referred to as Lester’s Second Method:

$$M = \frac{2}{(T - t_1 + 1)}.$$

Life history trade-offs in fishes have been extensively studied (Roff 1984, Stearns 1989, Reznick et al. 1990, Charnov and Berrigan 1991, Gunderson 1997, Cortés 2000). Trade-offs between reproduction and $M$ are also well documented. Reznick et al. (1990) experimentally induced increased adult mortality in natural populations of guppies, *Poecilia reticulata*, in an effort to document trade-offs between reproduction, growth, and mortality. This increase in mortality resulted in earlier ages of maturation and a higher reproductive effort. Furthermore, Reznick et al. (1990) demonstrated that these changes in reproductive traits were hereditary, indicating these life history trade-offs have a genetic basis. Therefore, Lester’s First and Second Methods in theory harbor extremely high biological significance. These methods have yet to be applied to elasmobranch species.
Conclusion

There have been many attempts to accurately describe growth and indirectly estimate mortality in fishes. Although the VBGM is outdated and heavily criticized, it remains popular due to its overwhelming prevalence in the literature and its utility for describing important life history parameters, particularly $M$. In chapter 2, I assess the effectiveness of the VBGM and three other conventional growth models (Gompertz, logistic, and TPGM) for describing the lifetime growth of elasmobranchs. I then compare the performance of these models to the LGM. The LGM model has previously been applied to a host of teleost fishes (see articles citing Lester et al. (2004)) and regularly outcompetes the VBGM (Quince et al. 2008b). However, this model has yet to be applied to elasmobranchs.

The VBGM and LGM allow for the indirect estimation of $M$. While direct estimates of $M$ are preferred, they are often impractical for elasmobranchs. In their lieu, indirect methods based on easily estimated life history parameters are used (Simpfendorfer et al. 2005). In Chapters 3 and 4 I assess existing and emerging techniques for indirectly estimating $M$ by comparing the performance of the LGM (Lester et al. 2004) to conventional methods for estimating $M$ (e.g., (Hoenig 1983, Jensen 1996, Charnov et al. 2013). In Chapter 3, I assess the ability of methods common in fisheries literature (including LGM methods) for estimating observed direct $M$. This chapter is presented as a case study of three species of elasmobranch ($Heterodontus portusjacksoni$, $Rhizoprionodon taylori$, and $Carcharhinus limbatus$) and is intended to provide recommendations for the most accurate $M$ methods. Using the recommendations of
Chapter 3, in Chapter 4 I assess the accuracy of the most common methods for estimating $M$ in the elasmobranch literature. This analysis is applied to 29 species of sharks, skates, and rays. The purpose of this study is to guide future research aimed at improving our understanding of the life history and population dynamics of elasmobranchs which will in turn aid in the proper management of elasmobranchs as a whole.
Chapter 2: Lifetime Growth of 29 Species of Elasmobranch

Introduction

Accurately describing the lifetime growth of fishes (including elasmobranchs) is required for the estimating of a suite of life history traits and is central to the proper understanding the dynamics of a population. A number of different models have been developed to describe growth (e.g., von Bertalanffy, Gompertz, logistic), but no single model routinely provides the best fit. Despite the lack of consensus on the best fitting growth model, the von Bertalanffy growth model (VBGM) is the most prevalent in the elasmobranch literature and in many cases is the only growth model considered in a given study (Cailliet et al. 2006).

The default status of the VBGM may be due to the fact that model parameters can be used to predict a variety of life history traits. First used by Beverton and Holt (1957) to simplify yield calculations, the VBGM has since dominated the fisheries literature. The VBGM parameters are typically used to derive additional life history traits, often as part of a stock assessment. However, the VBGM has been heavily criticized for lacking biological realism. Much of the criticism centers on the inability of the VBGM to address changes in energy allocation (and therefore growth) at the onset of maturity (Ricker 1975, Roff 1980, Day and Taylor 1997, Lester et al. 2004).

When elasmobranchs (and fishes in general) mature, they begin to invest surplus energy previously directed towards somatic growth into reproductive growth (i.e., gonadal growth) and behaviors associated with reproduction (e.g., migration or mating).
(Lester et al. 2004). The result of this re-allocation is a decrease in the rate of somatic growth. Because the VBGM is monophasic, it is incapable of describing this change in growth rate (Roff 1980, Day and Taylor 1997, Lester et al. 2004). In an attempt to address this issue, Soriano et al. (1992) developed a two-phase growth model (TPGM) that uses a modifying factor to identify the time and magnitude of the phase change. However, like the VBGM, the TPGM parameters are largely descriptive parameters and are difficult to interpret biologically.

Lester et al. (2004) proposed a growth model that accounts for the change in somatic growth associated with reproduction (Lester et al. 2004). In this model, immature growth is described linearly and adult growth is approximated by a variation of the VBGM. Using life history theory, Lester et al. (2004) modified the typical VBGM to describe the original parameters using reproductive characteristics (i.e., reproductive energy investment and age-at-maturity) and characteristics of immature growth. As a result, the LGM has a much higher degree of biological relevance than traditional growth models. The LGM has been found to describe teleost growth better than traditional growth models (Lester et al. 2004, Quince et al. 2008b), but has yet to be applied to elasmobranchs.

In this chapter, I evaluate the ability of the LGM and four traditional methods (the VBGM, Gompertz, logistic, and TPGM) to effectively describe elasmobranch lifetime growth by analyzing 30 populations comprising 29 species of sharks, rays, and skates. Parameters derived from growth models are used to estimate important life history traits. These estimates can be used to estimate biological reference points intended to guide
further stock assessments (Smith et al. 1998). Thus, it is extremely important to be able to accurately and appropriately describe elasmobranch lifetime growth.

Methods

Data

I collected readily available, sex specific growth and age-at-maturity data from 29 elasmobranch species (Table 2 in Appendix A). I obtained raw length-at-age data directly from authors for 12 species, by digitizing figures for 10 species, and from tabulated means for 7 species. I only included digitized data if I was able to closely approximate the growth model parameters that were reported in the original study. I analyzed two populations of *Carcharhinus limbatus* separately due to between-population differences in growth rate and age-at-maturity (Carlson et al. 2006).

Growth Models

I used five growth models to describe the lifetime growth of males and females of each species. The first model was the typical 3-parameter VBGM, (Beverton and Holt 1957), which takes the form:

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

(eq. 2.1)

where \(L_t\) is length at age \(t\), \(L_\infty\) is asymptotic length, \(K\) is the coefficient of growth, and \(t_0\) is the x-intercept.

I also fit a version of the Gompertz growth model (Ricker 1975):

\[
L_t = L_0 e^{\ln(L_\infty/L_0)(1-e^{-Kg^t})} \quad ,
\]

(eq. 2.2)
where \( L_0 \) is the length at age 0 (the y-intercept) and \( K_g \) is the Gompertz coefficient of growth. The third model was the logistic model (Ricker 1975):

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

(eq. 2.3)

where \( K_L \) is the logistic growth coefficient. The remaining two growth models assumed two distinct phases of lifetime growth. The first of these models was the two-phase model (TPGM) proposed by Soriano et al. (1992). This model includes an age-dependent modifier of \( K \):

\[
L_t = L_\infty (1 - e^{-K_A(t-t_0)}) ,
\]

(eq. 2.4)

where \( A_t \) incorporates the age at which the transition between growth phases occurs \( (t_h) \) and \( h \), the maximum difference between the new two-phase curve and the original von Bertalanffy curve, and takes the form:

\[
A_t = 1 - h/((t - t_h)^2 + 1)
\]

(eq. 2.5)

Lastly, I fit a LGM (Lester et al. 2004), which required independent estimates of the mean age at which individuals begin to invest in reproduction \( (T) \). Because maturity in sharks is determined by gonadal inspection rather than observed reproductive behavior, I set values of \( T \) to age-at-50%-maturity estimates reported in the same studies from which I obtained length-at-age data. I then used \( T \) to categorize each length-at-age measure as either immature or mature. Age-at-50%-maturity was not estimated for \( H. \) portusjacksoni, \( A. \) superciliosus, or \( S. \) zygaena. For \( H. \) portusjacksoni I derived our own \( T \) estimate by assigning maturity status based on length-at-50%-maturity from a parallel study (Powter and Gladstone 2008a), and then fitting a logistic curve. For
A. superciliosus and S. zygaena I estimated $T$ from oldest observed age ($t_{max}$) as described by Frisk et al. (2001):

$$T = 7.20 \ln(t_{max}) - 12.68 \quad (eq. \ 2.6)$$

For each species, I then fit a linear model to immature ages:

$$L_t = h_1(t - t_1) , \quad (eq. \ 2.7)$$

where $h_1$ is the rate of immature growth and $t_1$ is the intercept on the x-axis for the regression (Lester et al. 2004). For this fit, I excluded influential outliers as indicated by a combination of high leverage and Cook’s Distances >1. I then fit the biphasic version of the VBGM to adults. This version describes the influence of $h_1$, $T$, $t_1$, and investment in reproduction ($g$) on the von Bertalanffy parameters as described by Lester et al. (2004):

$$L_\infty = 3h_1/g , \quad (eq. \ 2.8)$$

$$K = \ln(1 + g/3) , \quad (eq. \ 2.9)$$

$$t_0 = T + \ln \left(1 - \frac{g(T-t_1)}{3}\right) / \ln(1 + \frac{g}{3}) . \quad (eq. \ 2.10)$$

Substituting these equations into eq. 2.1 results in:

$$L_t = 3h_1/g \left(1 - e^{-\ln(1+g/3)(t-(T+\ln(1-g(T-t_1)/3)/\ln(1+g/3)))}\right) , \quad (eq. \ 2.11)$$

where $g$ is the only estimable parameter. Preliminary analysis indicated that the two curves of the LGM were unable to converge at $T$ for some data sets with limited points near $T$ in relation to other ages. Those datasets were therefore not included in this study.
Model Selection

I used Akaike’s information criterion corrected for a small sample size (AICc) (Burnham and Anderson 2002) to determine the best fitting model:

\[ AICc = n \log(\hat{\sigma}) + 2P + \frac{2P(P+1)}{n-P-1} , \] (eq. 2.12)

Where \( P \) = number of parameters, \( n \) = sample size, and \( \hat{\sigma} \) is the residual sum of squares divided by the sample size. To compare models, I calculated the \( \Delta AICc \) and the AICc weights of each model. \( \Delta AICc \) allows the direct comparison of each model relative to the best (i.e. the lowest AICc) and is calculated as follows:

\[ \Delta AICc = AICc_i - \min AICc , \] (eq. 2.13)

where \( \min AICc \) is the best fit model and \( AICc_i \) is the model being compared. I concluded there was strong support for a model if \( \Delta AICc \) was < 2. The Akaike weight \( (w_i) \) shows the relative probability that a given model is the optimal model and is calculated using the equation:

\[ w_i = e^{(-0.5\Delta AICc)}/\sum_{r=1}^{R} e^{(-0.5\Delta AICc)} , \] (eq. 2.14)

where \( R \) is the number of models. All analyses were conducted using R Statistical Software (R 3.0.3, R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org/).

Results

When the LGM is not included, the best model varied by species and sex (Table 2.1, Figure 2.1). Overall, the VBGM was the best fitting model (\( \Delta AICc = 0 \)) for 18
(34.6%) datasets, the logistic for 17 (32.7%) datasets, the TPGM for 10 (19.2%) datasets, and the Gompertz for seven (13.5%) datasets. There was also strong support (0 < ΔAICc < 2) for the Gompertz model (21 datasets), the VBGM and TPGM (11 datasets each), and the logistic model (seven datasets).

Table 2.1. Species and sex specific ΔAICc and w_i results for species analyzed in this study independent of the LGM. Model results with strong support (ΔAICc < 2) are in bold.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>ΔAICc</th>
<th>Logistic</th>
<th>Gompertz</th>
<th>TPGM</th>
<th>wi</th>
<th>VBGM</th>
<th>Logistic</th>
<th>Gompertz</th>
<th>TPGM</th>
</tr>
</thead>
<tbody>
<tr>
<td>B. parnifera</td>
<td>M</td>
<td>20.07</td>
<td>3.89</td>
<td>0.00</td>
<td>19.92</td>
<td>0.00</td>
<td>0.13</td>
<td>0.87</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>27.80</td>
<td>6.24</td>
<td>0.00</td>
<td>17.18</td>
<td>0.00</td>
<td>0.04</td>
<td>0.96</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td>A. radiata</td>
<td>M</td>
<td>8.40</td>
<td>1.60</td>
<td>0.00</td>
<td>10.13</td>
<td>0.01</td>
<td>0.31</td>
<td>0.68</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>7.71</td>
<td>2.53</td>
<td>0.00</td>
<td>5.14</td>
<td>0.02</td>
<td>0.20</td>
<td>0.72</td>
<td>0.06</td>
<td></td>
</tr>
<tr>
<td>L. ocellata</td>
<td>F</td>
<td>2.34</td>
<td>0.09</td>
<td>0.00</td>
<td>1.50</td>
<td>0.13</td>
<td>0.25</td>
<td>0.42</td>
<td>0.20</td>
<td></td>
</tr>
<tr>
<td>R. clavata</td>
<td>M</td>
<td>1.27</td>
<td>0.55</td>
<td>0.00</td>
<td>12.15</td>
<td>0.23</td>
<td>0.33</td>
<td>0.44</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>6.86</td>
<td>0.79</td>
<td>0.15</td>
<td>0.04</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>R. radula</td>
<td>M</td>
<td>2.38</td>
<td>4.36</td>
<td>0.00</td>
<td>7.67</td>
<td>0.14</td>
<td>0.77</td>
<td>0.07</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>5.15</td>
<td>0.71</td>
<td>0.21</td>
<td>0.02</td>
<td>0.05</td>
<td></td>
</tr>
<tr>
<td>D. chilensis</td>
<td>M</td>
<td>1.53</td>
<td>0.00</td>
<td>0.40</td>
<td>4.55</td>
<td>0.20</td>
<td>0.42</td>
<td>0.34</td>
<td>0.04</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>8.12</td>
<td>2.24</td>
<td>0.00</td>
<td>10.31</td>
<td>0.01</td>
<td>0.24</td>
<td>0.74</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td>D. lata</td>
<td>M</td>
<td>20.33</td>
<td>7.03</td>
<td>0.00</td>
<td>10.10</td>
<td>0.00</td>
<td>0.03</td>
<td>0.97</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>14.59</td>
<td>4.80</td>
<td>0.00</td>
<td>16.66</td>
<td>0.00</td>
<td>0.08</td>
<td>0.92</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td>S. mitsukarii</td>
<td>M</td>
<td>2.31</td>
<td>0.93</td>
<td>0.00</td>
<td>4.84</td>
<td>0.16</td>
<td>0.31</td>
<td>0.49</td>
<td>0.04</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>3.28</td>
<td>0.00</td>
<td>0.52</td>
<td>3.81</td>
<td>0.46</td>
<td>0.36</td>
<td>0.07</td>
<td>0.11</td>
<td></td>
</tr>
<tr>
<td>E. pusillus</td>
<td>M</td>
<td>0.00</td>
<td>0.00</td>
<td>0.52</td>
<td>2.92</td>
<td>0.81</td>
<td>0.04</td>
<td>0.15</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.00</td>
<td>0.00</td>
<td>6.14</td>
<td>17.49</td>
<td>0.00</td>
<td>0.00</td>
<td>0.15</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td>H. portusjacksoni</td>
<td>M</td>
<td>4.10</td>
<td>0.99</td>
<td>0.89</td>
<td>0.00</td>
<td>0.05</td>
<td>0.26</td>
<td>0.27</td>
<td>0.42</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>3.65</td>
<td>0.12</td>
<td>0.00</td>
<td>2.52</td>
<td>0.07</td>
<td>0.39</td>
<td>0.42</td>
<td>0.12</td>
<td></td>
</tr>
<tr>
<td>A. superciliosus</td>
<td>M</td>
<td>0.00</td>
<td>0.00</td>
<td>0.58</td>
<td>1.17</td>
<td>0.38</td>
<td>0.29</td>
<td>0.21</td>
<td>0.12</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.00</td>
<td>0.00</td>
<td>0.84</td>
<td>0.61</td>
<td>0.31</td>
<td>0.26</td>
<td>0.20</td>
<td>0.23</td>
<td></td>
</tr>
<tr>
<td>A. valpinus</td>
<td>M</td>
<td>0.00</td>
<td>1.84</td>
<td>0.92</td>
<td>4.13</td>
<td>0.46</td>
<td>0.18</td>
<td>0.06</td>
<td>0.29</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>1.51</td>
<td>5.49</td>
<td>10.11</td>
<td>0.00</td>
<td>0.31</td>
<td>0.04</td>
<td>0.00</td>
<td>0.65</td>
<td></td>
</tr>
<tr>
<td>C. taurus</td>
<td>M</td>
<td>3.68</td>
<td>1.26</td>
<td>0.00</td>
<td>5.48</td>
<td>0.09</td>
<td>0.30</td>
<td>0.57</td>
<td>0.04</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>4.58</td>
<td>1.91</td>
<td>0.00</td>
<td>2.28</td>
<td>0.06</td>
<td>0.21</td>
<td>0.55</td>
<td>0.18</td>
<td></td>
</tr>
<tr>
<td>T. megalopterus</td>
<td>M</td>
<td>0.00</td>
<td>1.98</td>
<td>0.00</td>
<td>4.28</td>
<td>0.55</td>
<td>0.21</td>
<td>0.07</td>
<td>0.18</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>1.67</td>
<td>0.00</td>
<td>1.60</td>
<td>3.50</td>
<td>0.21</td>
<td>0.49</td>
<td>0.22</td>
<td>0.08</td>
<td></td>
</tr>
<tr>
<td>M. canis</td>
<td>M</td>
<td>1.33</td>
<td>0.00</td>
<td>14.01</td>
<td>3.30</td>
<td>0.30</td>
<td>0.59</td>
<td>0.00</td>
<td>0.11</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>8.04</td>
<td>3.84</td>
<td>0.00</td>
<td>2.22</td>
<td>0.01</td>
<td>0.10</td>
<td>0.67</td>
<td>0.22</td>
<td></td>
</tr>
<tr>
<td>G. sauteri</td>
<td>M</td>
<td>12.61</td>
<td>5.93</td>
<td>0.00</td>
<td>2.12</td>
<td>0.00</td>
<td>0.04</td>
<td>0.71</td>
<td>0.25</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>4.79</td>
<td>2.54</td>
<td>0.72</td>
<td>0.00</td>
<td>0.04</td>
<td>0.14</td>
<td>0.34</td>
<td>0.48</td>
<td></td>
</tr>
<tr>
<td>C. acronotus</td>
<td>M</td>
<td>8.86</td>
<td>5.61</td>
<td>2.90</td>
<td>0.00</td>
<td>0.01</td>
<td>0.05</td>
<td>0.18</td>
<td>0.77</td>
<td></td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>3.72</td>
<td>1.59</td>
<td>0.68</td>
<td>0.00</td>
<td>0.10</td>
<td>0.28</td>
<td>0.61</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>Sex</td>
<td>Atlantic Bight</td>
<td>Gulf of Mex.</td>
<td>C. plumbeus</td>
<td>C. sorrah</td>
<td>N. brevirostris</td>
<td>P. glauca</td>
<td>R. taylori</td>
<td>S. lewini</td>
<td>S. mokarran</td>
</tr>
<tr>
<td>---------------</td>
<td>-----</td>
<td>----------------</td>
<td>--------------</td>
<td>-------------</td>
<td>-----------</td>
<td>----------------</td>
<td>----------</td>
<td>------------</td>
<td>----------</td>
<td>-------------</td>
</tr>
<tr>
<td>C. limbatis</td>
<td>M</td>
<td>0.00</td>
<td>1.39</td>
<td>0.00</td>
<td>0.37</td>
<td>1.45</td>
<td>14.44</td>
<td>0.00</td>
<td>1.08</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.00</td>
<td>1.99</td>
<td>0.00</td>
<td>0.37</td>
<td>0.00</td>
<td>2.93</td>
<td>0.00</td>
<td>0.69</td>
<td>0.00</td>
</tr>
<tr>
<td>Atlantic Bight</td>
<td>F</td>
<td>1.61</td>
<td>3.71</td>
<td>1.26</td>
<td>1.78</td>
<td>0.00</td>
<td>48.88</td>
<td>7.00</td>
<td>2.71</td>
<td>2.40</td>
</tr>
<tr>
<td>C. limbatis</td>
<td>M</td>
<td>0.00</td>
<td>2.66</td>
<td>0.00</td>
<td>0.00</td>
<td>1.99</td>
<td>14.89</td>
<td>7.21</td>
<td>7.57</td>
<td>12.40</td>
</tr>
<tr>
<td>Gulf of Mex.</td>
<td>F</td>
<td>3.42</td>
<td>2.58</td>
<td>0.17</td>
<td>3.12</td>
<td>4.35</td>
<td>84.17</td>
<td>18.97</td>
<td>5.02</td>
<td>23.35</td>
</tr>
<tr>
<td>C. plumbeus</td>
<td>M</td>
<td>0.54</td>
<td>0.00</td>
<td>0.17</td>
<td>0.00</td>
<td>0.29</td>
<td>84.17</td>
<td>0.00</td>
<td>0.60</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.24</td>
<td>1.00</td>
<td>0.37</td>
<td>0.00</td>
<td>0.20</td>
<td>0.00</td>
<td>0.19</td>
<td>0.69</td>
<td>0.00</td>
</tr>
<tr>
<td>C. sorrah</td>
<td>M</td>
<td>0.50</td>
<td>0.00</td>
<td>0.00</td>
<td>0.17</td>
<td>0.49</td>
<td>0.00</td>
<td>0.19</td>
<td>0.74</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.25</td>
<td>1.00</td>
<td>0.19</td>
<td>0.09</td>
<td>0.49</td>
<td>0.00</td>
<td>0.19</td>
<td>0.74</td>
<td>0.00</td>
</tr>
<tr>
<td>N. brevirostris</td>
<td>M</td>
<td>0.00</td>
<td>0.00</td>
<td>1.90</td>
<td>0.00</td>
<td>0.20</td>
<td>0.00</td>
<td>0.00</td>
<td>0.61</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.00</td>
<td>0.00</td>
<td>0.71</td>
<td>0.19</td>
<td>0.41</td>
<td>0.00</td>
<td>0.00</td>
<td>0.61</td>
<td>0.00</td>
</tr>
<tr>
<td>P. glauca</td>
<td>M</td>
<td>0.00</td>
<td>1.22</td>
<td>1.00</td>
<td>0.00</td>
<td>0.20</td>
<td>0.00</td>
<td>0.00</td>
<td>0.61</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.00</td>
<td>0.00</td>
<td>0.71</td>
<td>0.19</td>
<td>0.41</td>
<td>0.00</td>
<td>0.00</td>
<td>0.61</td>
<td>0.00</td>
</tr>
<tr>
<td>R. taylori</td>
<td>M</td>
<td>0.00</td>
<td>1.00</td>
<td>1.22</td>
<td>0.00</td>
<td>0.20</td>
<td>0.00</td>
<td>0.00</td>
<td>0.61</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.00</td>
<td>0.00</td>
<td>0.71</td>
<td>0.19</td>
<td>0.41</td>
<td>0.00</td>
<td>0.00</td>
<td>0.61</td>
<td>0.00</td>
</tr>
<tr>
<td>S. lewini</td>
<td>M</td>
<td>0.00</td>
<td>0.00</td>
<td>1.00</td>
<td>0.00</td>
<td>0.20</td>
<td>0.00</td>
<td>0.00</td>
<td>0.61</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.00</td>
<td>0.00</td>
<td>0.71</td>
<td>0.19</td>
<td>0.41</td>
<td>0.00</td>
<td>0.00</td>
<td>0.61</td>
<td>0.00</td>
</tr>
<tr>
<td>S. mokarran</td>
<td>M</td>
<td>0.00</td>
<td>1.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.20</td>
<td>0.00</td>
<td>0.00</td>
<td>0.61</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.00</td>
<td>0.00</td>
<td>0.71</td>
<td>0.19</td>
<td>0.41</td>
<td>0.00</td>
<td>0.00</td>
<td>0.61</td>
<td>0.00</td>
</tr>
<tr>
<td>S. tiburo</td>
<td>F</td>
<td>0.00</td>
<td>0.00</td>
<td>2.20</td>
<td>2.62</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.61</td>
<td>0.00</td>
</tr>
<tr>
<td>S. zygaena</td>
<td>F</td>
<td>0.00</td>
<td>0.00</td>
<td>2.20</td>
<td>2.62</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.61</td>
<td>0.00</td>
</tr>
</tbody>
</table>
**Figure 2.1** Frequency of the four conventional growth models as having strong support \((\Delta\text{AIC}_c < 2)\) independent of the LGM. Grey bars represent the number of times a given model was the ‘best’ model \((\Delta\text{AIC}_c = 0)\), and white bars represent the number of times that \(0 < \Delta\text{AIC}_c < 2\) for a model.

Akaike weights \(w_i\) were asymmetrically distributed for all four models with high frequencies in low-ranged values (Figure 2.2). For all models except the Gompertz, the highest frequency occurred at \(w_i\) values of 0-0.09. Peak frequency for the Gompertz model occurred at \(w_i\) values of 0-0.09 and 0.20-0.29 with 15 occurrences each.
**Figure 2.2** Distribution of Akaike weights $w_i$ (%) for each of the four conventional growth models without the influence of the LGM applied to all datasets in this study.

After including the LGM, none of the conventional models performed well relative to the LGM (Table 2.2, Figure 2.3). The LGM was the best fitting model for 42 (80.8%) of the 52 datasets. The remaining data sets were best described by the VBGM (five datasets or 9.6%), the Gompertz model (three sets or 5.8%), and the logistic model.
(two sets or 3.8%). Additionally, there was strong support ($0 < \Delta AICc < 2$) for the Gompertz model (five datasets), the LGM, VBGM, and logistic models (two datasets each) and the TPGM (one dataset).

**Table 2.2.** Species and sex specific $\Delta AICc$ and $w_i$ results for species analyzed in this study. Model results with strong support ($\Delta AICc < 2$) are in bold.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>$\Delta AICc$</th>
<th>Gompert</th>
<th>Logistic</th>
<th>TPG</th>
<th>LG</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>VBG M</td>
<td>Gompert</td>
<td>Logistic</td>
<td>TPG</td>
<td>LG</td>
<td>VBG M</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>z</td>
<td>M</td>
<td>M</td>
<td>M</td>
<td>F</td>
</tr>
<tr>
<td>B. parmi fer a</td>
<td>M</td>
<td>227.89</td>
<td>211.71</td>
<td>207.82</td>
<td>4</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>155.91</td>
<td>134.35</td>
<td>128.11</td>
<td>9</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>A. radiata</td>
<td>M</td>
<td>25.83</td>
<td>19.04</td>
<td>17.43</td>
<td>27.56</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>37.52</td>
<td>32.34</td>
<td>29.81</td>
<td>34.95</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>L. ocellata</td>
<td>F</td>
<td>276.73</td>
<td>275.41</td>
<td>274.39</td>
<td>9</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>R. clavata</td>
<td>M</td>
<td>151.00</td>
<td>0.80</td>
<td>0.25</td>
<td>12.40</td>
<td>0.00</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.00</td>
<td>3.27</td>
<td>6.08</td>
<td>7.11</td>
<td>5.34</td>
<td>0.75</td>
</tr>
<tr>
<td>R. radula</td>
<td>M</td>
<td>14.40</td>
<td>16.83</td>
<td>21.26</td>
<td>19.55</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>3.38</td>
<td>0.00</td>
<td>4.71</td>
<td>7.67</td>
<td>0.10</td>
<td>0.08</td>
</tr>
<tr>
<td>D. chilensis</td>
<td>M</td>
<td>153.00</td>
<td>0.00</td>
<td>0.40</td>
<td>4.55</td>
<td>2.24</td>
<td>0.17</td>
</tr>
<tr>
<td>D. lata</td>
<td>M</td>
<td>38.07</td>
<td>32.19</td>
<td>29.95</td>
<td>40.26</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>225.42</td>
<td>212.12</td>
<td>205.09</td>
<td>9</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>S. acanthias</td>
<td>M</td>
<td>65.60</td>
<td>63.34</td>
<td>61.80</td>
<td>64.92</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>86.54</td>
<td>76.75</td>
<td>71.95</td>
<td>88.61</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>S. mit su karit</td>
<td>M</td>
<td>2.31</td>
<td>0.93</td>
<td>0.00</td>
<td>4.84</td>
<td>7</td>
<td>0.16</td>
</tr>
<tr>
<td>E. pusillus</td>
<td>M</td>
<td>0.00</td>
<td>0.52</td>
<td>3.81</td>
<td>2.92</td>
<td>3.70</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0.00</td>
<td>6.14</td>
<td>17.49</td>
<td>3.42</td>
<td>3</td>
<td>0.81</td>
</tr>
<tr>
<td>H. portus jacksoni</td>
<td>M</td>
<td>187.22</td>
<td>184.10</td>
<td>184.01</td>
<td>1</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>352.70</td>
<td>349.17</td>
<td>349.05</td>
<td>7</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>A. superciliosus</td>
<td>M</td>
<td>57.40</td>
<td>57.98</td>
<td>58.58</td>
<td>59.81</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>127.44</td>
<td>127.84</td>
<td>128.28</td>
<td>5</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>A. vulpinus</td>
<td>M</td>
<td>21.59</td>
<td>23.43</td>
<td>25.72</td>
<td>22.51</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>145.59</td>
<td>149.57</td>
<td>154.19</td>
<td>8</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>C. taurus</td>
<td>M</td>
<td>31.13</td>
<td>28.71</td>
<td>27.45</td>
<td>32.93</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>T. megalo pterus</td>
<td>M</td>
<td>38.46</td>
<td>35.78</td>
<td>33.88</td>
<td>36.15</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>83.39</td>
<td>85.38</td>
<td>87.67</td>
<td>85.69</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>M. canis</td>
<td>M</td>
<td>331.87</td>
<td>330.20</td>
<td>331.80</td>
<td>0</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>288.10</td>
<td>286.77</td>
<td>300.78</td>
<td>7</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>G. sauteri</td>
<td>M</td>
<td>8.04</td>
<td>3.84</td>
<td>0.00</td>
<td>2.22</td>
<td>0.45</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>37.15</td>
<td>30.47</td>
<td>24.54</td>
<td>26.67</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Fish Species</td>
<td>Sex</td>
<td>Location</td>
<td>Weight (g)</td>
<td>Length (cm)</td>
<td>Width (cm)</td>
<td>Height (cm)</td>
<td>%</td>
</tr>
<tr>
<td>-------------------</td>
<td>------</td>
<td>----------------</td>
<td>------------</td>
<td>-------------</td>
<td>------------</td>
<td>-------------</td>
<td>---</td>
</tr>
<tr>
<td>C. acronotus</td>
<td>M</td>
<td>Atlantic Bight</td>
<td>102.95</td>
<td>100.71</td>
<td>98.88</td>
<td>98.16</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td></td>
<td>172.02</td>
<td>168.77</td>
<td>165.06</td>
<td>9.30</td>
<td>0.00</td>
</tr>
<tr>
<td>C. brevipinna</td>
<td>F</td>
<td></td>
<td>3.72</td>
<td>1.59</td>
<td>0.00</td>
<td>6.00</td>
<td>0.00</td>
</tr>
<tr>
<td>C. limbatus</td>
<td>M</td>
<td>Atlantic Bight</td>
<td>15.31</td>
<td>19.60</td>
<td>22.89</td>
<td>17.86</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td></td>
<td>11.58</td>
<td>13.20</td>
<td>14.64</td>
<td>15.00</td>
<td>0.00</td>
</tr>
<tr>
<td>C. limbatus</td>
<td>M</td>
<td>Gulf of Mex.</td>
<td>8.42</td>
<td>9.81</td>
<td>11.08</td>
<td>11.33</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td></td>
<td>0.00</td>
<td>1.99</td>
<td>3.71</td>
<td>2.58</td>
<td>0.00</td>
</tr>
<tr>
<td>C. plumbeus</td>
<td>M</td>
<td></td>
<td>55.45</td>
<td>56.71</td>
<td>58.52</td>
<td>55.62</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td></td>
<td>70.08</td>
<td>68.99</td>
<td>69.18</td>
<td>69.99</td>
<td>0.00</td>
</tr>
<tr>
<td>C. sorrah</td>
<td>M</td>
<td>Atlantic Bight</td>
<td>69.74</td>
<td>71.15</td>
<td>72.49</td>
<td>69.37</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td></td>
<td>6.05</td>
<td>7.97</td>
<td>9.97</td>
<td>7.42</td>
<td>0.00</td>
</tr>
<tr>
<td>N. brevirostris</td>
<td>M</td>
<td></td>
<td>147.21</td>
<td>145.75</td>
<td>150.10</td>
<td>146.0</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td></td>
<td>144.36</td>
<td>151.44</td>
<td>163.33</td>
<td>146.2</td>
<td>0.00</td>
</tr>
<tr>
<td>P. glauca</td>
<td>M</td>
<td></td>
<td>110.39</td>
<td>144.84</td>
<td>180.12</td>
<td>95.95</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td></td>
<td>59.43</td>
<td>71.39</td>
<td>82.24</td>
<td>56.50</td>
<td>0.00</td>
</tr>
<tr>
<td>R. taylori</td>
<td>M</td>
<td>Gulf of Mex.</td>
<td>13.22</td>
<td>20.53</td>
<td>26.75</td>
<td>14.44</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td></td>
<td>0.00</td>
<td>7.04</td>
<td>13.09</td>
<td>14.44</td>
<td>0.00</td>
</tr>
<tr>
<td>S. lewini</td>
<td>M</td>
<td></td>
<td>121.69</td>
<td>120.61</td>
<td>125.63</td>
<td>1</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td></td>
<td>13.64</td>
<td>26.04</td>
<td>36.99</td>
<td>15.73</td>
<td>0.00</td>
</tr>
<tr>
<td>S. mokarran</td>
<td>M</td>
<td></td>
<td>56.37</td>
<td>57.74</td>
<td>60.12</td>
<td>40.09</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td></td>
<td>13.47</td>
<td>15.49</td>
<td>17.56</td>
<td>12.78</td>
<td>0.00</td>
</tr>
<tr>
<td>S. tiburo</td>
<td>F</td>
<td></td>
<td>64.12</td>
<td>64.58</td>
<td>65.01</td>
<td>62.38</td>
<td>0.00</td>
</tr>
<tr>
<td>S. zygaena</td>
<td>F</td>
<td></td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>
Figure 2.3 Frequency of the five growth models used in this study as having strong support (ΔAICc < 2). Grey bars represent the number of times a given model was the ‘best’ model (ΔAICc = 0), and white bars represent the number of times that 0 < ΔAICc < 2 for a model.

Akaike weights were asymmetrically skewed for all models so that the highest frequencies occurred at $w_i$ values of 0-0.09 for all four conventional models and at $w_i$ values of 0.90-1.00 for the LGM (Figure 2.4)
Figure 2.4 Distribution of Akaike weights $w_i$ (%) for the 52 datasets of this study and each of the five growth models.
Discussion

In this chapter, I found that the best fitting conventional model for describing lifetime growth (i.e., VBGM, logistic, Gompertz, and TPGM) varied among species. A lack of consensus among growth models is consistent with the literature: different VBGMs have provided the best fit for the common thresher shark, *Alopius vulpinus* (Gervelis and Natanson 2013) and sandbar shark, *C. plumbeus* (Romine et al. 2006), the logistic model has provided best fit for the spinner shark, *C. brevipinna* (Carlson and Baremore 2005) and brown stingray, *Dasyatis lata* (Dale and Holland 2012), and the Gompertz model has provided the best fit for male smooth lantern sharks, *Etmopterus pusillus* (Coelho and Erzini 2007). See also Araya and Cubillos (2006). The LGM growth model has not been previously assessed for elasmobranchs. My results show that the LGM has a tendency to outcompete traditional models (providing the best fit for ~81% of the data sets).

Model selection should not rely entirely on statistics, but also consider the biological relevance of the model and its parameters (Cailliet et al. 2006). Although the VBGM parameters $L_\infty$ and $K$ can be interpreted biologically (albeit with some difficulty at times) (Cailliet et al. 2006), the parameter $t_0$ was originally developed to simplify yield calculations and is largely artificial (Beverton and Holt 1957). Because $t_0$ can distort estimates of $L_\infty$ and $K$, Cailliet et al. (2006) recommended use of the VBGM incorporating $L_0$. However, this study demonstrated that replacing the parameter $L_0$ with observed size at birth may skew other VBGM parameters and reduce statistical support for the model. Additionally, the VBGM as a whole has little biological relevance when applied to the lifetime growth of fishes: Lipinski and Roeleveld (1990) showed that a
good fit using VBGM is not necessarily indicative of metabolic change, and Day and Taylor (1997) expressed concern that multiple biological characteristics (i.e., pre-maturity growth, age-at-maturity, post-maturity growth) were combined into a single, overarching descriptor. The TPGM is similar to the VBGM, but incorporates the parameters \( h \) and \( t_h \) to account for changing growth phases. The parameter \( h \) describes the magnitude of the difference between the original and new curves (Soriano et al. 1992), and while \( t_h \) can agree with the observed age-at-50\%-maturity (Czarnoleśki and Kozłowski 1998, Braccini et al. 2007), this is not always the case (e.g., Tribuzio et al. 2010). As such, \( h \) and \( t_h \) are descriptive parameters that have limited biological relevance.

The Lester growth model, on the other hand, is deeply rooted in life history tradeoffs between reproduction and adult survival. Lester et al. (2004) described the traditional VBGM parameters using key reproductive characteristics (i.e., age-at-maturity, reproductive investment), thus giving this model a high degree of biological relevance.

This study has shown that the LGM is a reasonable approach to describing lifetime growth in sharks and tends to outcompete traditional models. There is, however, one major caveat: ages must be validated in order to accurately describe lifetime growth. Many, if not most, studies over the past decades have neglected to validate ages in elasmobranchs (Cailliet et al. 2006). This causes serious concern for fisheries biologists and managers. Without validating ages, the reliability of growth parameters cannot be reasonably assumed and increases the potential for inaccurate estimates of crucial life history parameters (including the rate of mortality). In this study, I applied the LGM to 29 species representing ca. 3\% of elasmobranch diversity. My results suggest that the LGM regularly outcompetes conventional growth models in elasmobranchs, although
more research is needed to determine if the results of this study can be generalized across a wider range of species.
Chapter 3: Accurately Estimating Indirect Mortality: A Case Study of Three Species of Shark

Introduction

Instantaneous natural mortality rate ($M$) is one of the most important parameters used in elasmobranch (and fish) population dynamics, yet it is notoriously difficult to reliably estimate (Simpfendorfer et al. 2005). Ideally, $M$ is estimated via direct methods such as tagging studies (Grant et al. 1979, Xiao et al. 1999, Swinsburg 2013), telemetry (Heupel and Simpfendorfer 2002), or catch curve analysis (Simpfendorfer 1999).

harvest rates; all of which aid in developing proper conservation and management strategies for elasmobranch populations (Simpfendorfer 2005).

In this chapter, I assess the ability of traditional and emerging techniques for indirectly estimating \( M \) by comparing the performance of traditional indirect methods (e.g., Alverson and Carney 1975, Hoenig 1983, Roff 1984, Chen and Watanabe 1989, Jensen 1996, Charnov et al. 2013) and methods dependent on the LGM (Lester et al. 2004, Lester et al. 2014) to published direct estimates of \( M \). For this case study, I used published length-at-age, maturity, and direct mortality estimates from three shark species for which these data were available for both sexes and from the same population and time frame: the Port Jackson shark, *Heterodontus portusjacksoni* (family: Heterodontidae); Australian sharpnose shark, *Rhizoprionodon taylori* (family: Carcharhinidae); and blacktip shark, *C. limbatus* (family: Carcharhinidae).

**Methods**

**Data**

I analyzed published data from four shark populations: *H. portusjacksoni* from New South Wales, Aus., *R. taylori* off the coast of Queensland, Aus., and two populations of *C. limbatus* from the eastern Gulf of Mexico and North America’s South Atlantic Bight between Florida and North Carolina. I obtained raw length-at-age data directly from Ramos (2007) for *H. portusjacksoni*, by digitizing Figures 5 and 6 in Simpfendorfer (1993) for *R. taylori*, and from tabulated means in Carlson et al. (2006) for both populations of *C. limbatus*. I analyzed the *C. limbatus*
populations independently because of between-population differences in growth rates and age of maturity (Carlson et al. 2006).

Direct estimates of $M$ were derived from visual surveys and tagging (Powter and Gladstone 2008b), catch curve analysis (Simpfendorfer 1999), and long-term tag-recovery data (Swinsburg 2013) for *H. portusjacksoni*, *R. taylori*, and *C. limbatus* respectively. Powter and Gladstone (2008b) reported estimates of $M$ separately for immature and mature populations of *H. portusjacksoni*. Because most indirect $M$ methods estimate mature $M$, only the mature $M$ estimate was used in this study. Each population in this study is subject to fishing or bycatch mortality of varying degrees. The *H. portusjacksoni* population is subject to light recreational and commercial fishing (Powter and Gladstone 2008b), *R. taylori* is caught as bycatch in commercial gillnet and prawn trawl fisheries (Simpfendorfer 1999), and *C. limbatus* was until recently the target species of one of the largest shark fisheries in the United States (Swinsburg 2013). Because each population is subjected to fishing pressures, all estimates of $M$ derived from indirect methods represent total mortality as opposed to natural mortality.

**Indirect Mortality Methods**

I used nine conventional methods (or their variants) found in fisheries literature (Alverson and Carney 1975, Roff 1983, Chen and Watanabe 1989, Jensen 1996, Hewitt and Hoenig 2005, Hisano et al. 2011, Charnov et al. 2013, Then et al. 2014) and two methods relatively new to fisheries literature (Lester et al. 2004, Lester et al. 2014) to indirectly estimate mortality (Table 2). Two of these methods, Hewitt and Hoenig’s Method and Jensen’s First Method, do not rely on growth parameters and were therefore independent of the choice of growth model. Hewitt and Hoenig (2005) recommended
using their updated version of Hoenig’s Methods over the originals. Although Then et al. (2014) revised Hewitt and Hoenig’s Method, preliminary analyses indicated Hewitt and Hoenig’s Method gave more accurate estimates of $M$ for the species in this study. Hewitt and Hoenig’s Method is described as:

$$M = \frac{4.22}{t_{max}}$$ \hspace{1cm} \text{(method 3.1)}

where $t_{max}$ is maximum age and was set to the age of the oldest observed individual for each species and sex. For Jensen’s First Method, I used published (Simpfendorfer 1993, Carlson et al. 2006) and calculated (Powter and Gladstone 2008a) estimates of age-at-50%-maturity ($T$). Jensen’s First Method takes the form:

$$M = \frac{1.65}{T}$$ \hspace{1cm} \text{(method 3.2)}

The remaining seven conventional indirect methods used estimate $M$ from one or more VBGM parameters ($K$, $L_\infty$, and $t_0$). Alverson and Carney’s Method took the form:

$$M = \frac{3K}{(e^{0.38Kt_{max}}) - 1}$$ \hspace{1cm} \text{(method 3.4)}

Roff’s Method is describes as:

$$M = \frac{3K}{(e^{KT}) - 1}$$ \hspace{1cm} \text{(method 3.5)}

A VBGM dependent method described by Jensen (1996) was used (Jensen’s Second Method) and takes the form:

$$M = 1.5K$$ \hspace{1cm} \text{(method 3.6)}
Although Jensen (1996) indicated that Pauly’s Method could be approximated from a simple linear regression between $M$ and $K$, this relationship was not formally presented as a method for estimating $M$ and is not included in this analysis. However, Then et al. (2014) reevaluated Pauly’s Method concluding that temperature is not an important parameter when estimating $M$ and presented a revised method. Then’s Method is described as:

$$M = 4.118K^{0.73}L_{\infty}^{-0.33}.$$  \hspace{1cm} \text{(method 3.7)}

Hisano et al. (2011) suggested a modification of Jensen’s First Method so as to incorporate non-zero values of $t_0$:

$$M = \frac{1.65}{T-t_0}.$$  \hspace{1cm} \text{(method 3.8)}

Chen and Watanabe’s Method and Charnov’s Method estimate $M$ for specific ages ($t$) or lengths ($L$) respectively. Charnov’s Method was empirically derived and takes the form:

$$M = K\left(\frac{L}{L_{\infty}}\right)^{-1.5}.$$  \hspace{1cm} \text{(method 3.9)}

Chen and Watanabe’s Method is based on life history theory and is described as:

$$M(t) = \begin{cases} 
\frac{K}{1-e^{-K(t-t_0)}}, & t < T \\
\frac{K}{a_0+a_1(t-T)+a_2(t-T)^2}, & t \geq T 
\end{cases}.$$  \hspace{1cm} \text{(method 3.10)}

where:

$$a_0 = 1 - e^{-K(T-t_0)},$$  \hspace{1cm} \text{(eq. 3.2)}

$$a_1 = Ke^{-K(T-t_0)},$$  \hspace{1cm} \text{(eq. 3.3)}
\[ a_2 = -\frac{1}{2} K^2 e^{-K(T-t_0)} \]  \hspace{1cm} \text{(eq. 3.4)}

To generate a single overall \( M \) estimate in which to compare to the corresponding direct estimate of \( M \) for a given dataset, I calculated \( M \) for a range of lengths or ages and then averaged. This range corresponded to the range of lengths or ages that were used to directly estimate mortality (Simpfendorfer 1999, Powter and Gladstone 2008b, Swinsburg 2013). To identify a single overall estimate for each method, I estimated mortality at each half-year age increments and the corresponding length, and then calculated the mean across the entire age range.

The two methods relatively new to the fisheries literature were derived from biphasic growth theory. Parameters used for these methods were estimated using the LGM (see Chapter 2). I estimated mortality from \( g \) using Lester’s First Method (Lester et al. 2004):

\[ M = -\ln(1 - \frac{g}{1.18}) \]  \hspace{1cm} \text{(method 3.11)}

Lester’s Second Method relies on \( T \) and aspects of the immature regression:

\[ M = \frac{2}{(T-t_1+1)} \]  \hspace{1cm} \text{(method 3.12)}

Because VBGM parameters can be estimated from the LGM (see Chapter 2, eqs. 2.8 – 2.10) methods 3.4 – 3.10 were applied to both the VBGM and the LGM. Methods 3.4 – 3.10 were given a subscript of ‘vb’ when applied to the VBGM and a subscript of ‘bp’ when applied to the LGM.
Mortality Comparison

I compared derived indirect estimates of $M$ to published direct estimates of $M$ (Simpfendorfer 1999, Powter and Gladstone 2008b, Swinsburg 2013). To compare direct and indirect estimates across all species and sexes, I expressed each indirect estimate of $M$ as the log$_{10}$-ratio of the indirect estimate to the corresponding direct estimate and then averaged ratios across species, populations, and sexes. When multiple direct estimates of $M$ were available (i.e., (Powter and Gladstone 2008b), I used the average value. I then used one-sample t-tests to test the hypothesis that the mean, log$_{10}$-ratio $M$ estimate associated with each indirect approach was different from 0. If the p-value of a test was $\geq$ 0.05, I concluded that indirect and direct methods were in agreement. All analyses were conducted using R Statistical Software (R 3.0.3, R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org/).

Results

Overall, indirect methods tended to overestimate $M$ (Table 3.1, 3.2; Figure 3.1). Both growth-independent methods (methods 3.1 and 3.2) and four growth-dependent methods (3.4$_{bp}$; 3.5$_{vb, bp}$; 3.6$_{vb}$; and 3.9$_{vb}$) generated estimates significantly greater than direct estimates. Five methods (3.6$_{bp}$, 3.7$_{bp}$, 3.8$_{bp}$, 3.9$_{bp}$, and 3.10$_{bp}$) significantly underestimated $M$. The remaining methods (3.4$_{vb}$, 3.7$_{vb}$, 3.8$_{vb}$, 3.10$_{vb}$, 3.11, and 3.12) estimated values of $M$ that were not significantly different from direct estimates. Five of these methods were relatively accurate and (or) precise: Lester’s First and Second Methods (methods 3.11 and 3.12), which relied on the LGM; and Then’s Method,
Hisano’s Method, and Chen and Watanabe’s Method (methods 3.7_vb, 3.8_vb, and 3.10_vb respectively), which relied on the VBGM.

**Table 3.1.** Life history traits and associated indirect $M$ estimates obtained from growth-independent methods and growth-dependent methods assuming von Bertalanffy growth parameters. Direct $M$ for *H. portusjacksoni* represents the average of published estimates.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>$T$</th>
<th>$t_0$</th>
<th>$t_{max}$</th>
<th>VB</th>
<th>$K$</th>
<th>Direct $M$</th>
<th>3.1</th>
<th>3.2</th>
<th>3.4_v0</th>
<th>3.5_v0</th>
<th>3.6_v0</th>
<th>3.7_v0</th>
<th>3.8_v0</th>
<th>3.9_v0</th>
<th>3.10_v0</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. portusjacksoni</em></td>
<td>F</td>
<td>17.5</td>
<td>-4.20</td>
<td>32.25</td>
<td>0.060</td>
<td>0.069</td>
<td>0.131</td>
<td>0.092</td>
<td>0.166</td>
<td>0.097</td>
<td>0.090</td>
<td>0.050</td>
<td>0.076</td>
<td>0.082</td>
<td>0.074</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>11.2</td>
<td>-3.51</td>
<td>27.91</td>
<td>0.079</td>
<td>0.069</td>
<td>0.151</td>
<td>0.138</td>
<td>0.181</td>
<td>0.167</td>
<td>0.118</td>
<td>0.064</td>
<td>0.112</td>
<td>0.107</td>
<td>0.099</td>
<td></td>
</tr>
<tr>
<td><em>R. taylori</em></td>
<td>F</td>
<td>1</td>
<td>-0.47</td>
<td>7.01</td>
<td>1.002</td>
<td>0.560</td>
<td>0.602</td>
<td>1.650</td>
<td>0.224</td>
<td>1.744</td>
<td>1.502</td>
<td>1.000</td>
<td>1.124</td>
<td>1.372</td>
<td>0.818</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>1</td>
<td>-0.42</td>
<td>5.77</td>
<td>1.317</td>
<td>0.700</td>
<td>0.731</td>
<td>1.650</td>
<td>0.233</td>
<td>1.446</td>
<td>1.975</td>
<td>1.267</td>
<td>1.164</td>
<td>1.726</td>
<td>0.243</td>
<td></td>
</tr>
<tr>
<td><em>C. limbatus</em></td>
<td>F</td>
<td>5.7</td>
<td>-2.90</td>
<td>12.50</td>
<td>0.182</td>
<td>0.178</td>
<td>0.338</td>
<td>0.289</td>
<td>0.398</td>
<td>0.300</td>
<td>0.273</td>
<td>0.227</td>
<td>0.192</td>
<td>0.286</td>
<td>0.245</td>
<td></td>
</tr>
<tr>
<td>Gulf of Mexico</td>
<td>M</td>
<td>4.5</td>
<td>-3.50</td>
<td>11.50</td>
<td>0.149</td>
<td>0.259</td>
<td>0.367</td>
<td>0.487</td>
<td>0.468</td>
<td>0.223</td>
<td>0.196</td>
<td>0.206</td>
<td>0.259</td>
<td>0.215</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>C. limbatus</em></td>
<td>F</td>
<td>6.7</td>
<td>-5.01</td>
<td>15.50</td>
<td>0.109</td>
<td>0.178</td>
<td>0.272</td>
<td>0.246</td>
<td>0.363</td>
<td>0.304</td>
<td>0.164</td>
<td>0.150</td>
<td>0.141</td>
<td>0.189</td>
<td>0.157</td>
<td></td>
</tr>
<tr>
<td>S. Atlantic Bight</td>
<td>M</td>
<td>5</td>
<td>-2.48</td>
<td>13.50</td>
<td>0.206</td>
<td>0.259</td>
<td>0.313</td>
<td>0.330</td>
<td>0.344</td>
<td>0.308</td>
<td>0.249</td>
<td>0.221</td>
<td>0.307</td>
<td>0.272</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table 3.2.** Life history traits and associated $M$ estimates obtained from growth-based methods assuming biphasic growth parameters. Direct $M$ for *H. portusjacksoni* represents the average of published estimates.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>$T$</th>
<th>$t_1$</th>
<th>$g$</th>
<th>BP</th>
<th>$K$</th>
<th>Direct $M$</th>
<th>3.11</th>
<th>3.12</th>
<th>3.4_v0</th>
<th>3.5_v0</th>
<th>3.6_v0</th>
<th>3.7_v0</th>
<th>3.8_v0</th>
<th>3.9_v0</th>
<th>3.10_v0</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. portusjacksoni</em></td>
<td>F</td>
<td>17.5</td>
<td>-6.63</td>
<td>0.09</td>
<td>0.029</td>
<td>0.069</td>
<td>0.077</td>
<td>0.074</td>
<td>0.204</td>
<td>0.132</td>
<td>0.043</td>
<td>0.029</td>
<td>0.033</td>
<td>0.040</td>
<td>0.036</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>11.2</td>
<td>-9.13</td>
<td>0.05</td>
<td>0.018</td>
<td>0.069</td>
<td>0.048</td>
<td>0.094</td>
<td>0.237</td>
<td>0.242</td>
<td>0.027</td>
<td>0.018</td>
<td>0.045</td>
<td>0.060</td>
<td>0.033</td>
<td></td>
</tr>
<tr>
<td><em>R. taylori</em></td>
<td>F</td>
<td>1</td>
<td>-1.47</td>
<td>0.84</td>
<td>0.247</td>
<td>0.560</td>
<td>1.247</td>
<td>0.577</td>
<td>0.796</td>
<td>2.645</td>
<td>0.371</td>
<td>0.342</td>
<td>0.347</td>
<td>0.392</td>
<td>0.321</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M</td>
<td>1</td>
<td>-1.55</td>
<td>0.93</td>
<td>0.269</td>
<td>0.700</td>
<td>1.542</td>
<td>0.564</td>
<td>1.003</td>
<td>2.614</td>
<td>0.404</td>
<td>0.383</td>
<td>0.288</td>
<td>0.387</td>
<td>0.322</td>
<td></td>
</tr>
<tr>
<td><em>C. limbatus</em></td>
<td>F</td>
<td>5.7</td>
<td>-4.65</td>
<td>0.29</td>
<td>0.092</td>
<td>0.178</td>
<td>0.279</td>
<td>0.176</td>
<td>0.504</td>
<td>0.401</td>
<td>0.137</td>
<td>0.141</td>
<td>0.032</td>
<td>0.122</td>
<td>0.092</td>
<td></td>
</tr>
<tr>
<td>Gulf of Mexico</td>
<td>M</td>
<td>4.5</td>
<td>-6.59</td>
<td>0.13</td>
<td>0.043</td>
<td>0.259</td>
<td>0.118</td>
<td>0.165</td>
<td>0.624</td>
<td>0.604</td>
<td>0.064</td>
<td>0.070</td>
<td>0.106</td>
<td>0.132</td>
<td>0.085</td>
<td></td>
</tr>
<tr>
<td><em>C. limbatus</em></td>
<td>F</td>
<td>6.7</td>
<td>-9.95</td>
<td>0.10</td>
<td>0.031</td>
<td>0.178</td>
<td>0.084</td>
<td>0.113</td>
<td>0.464</td>
<td>0.402</td>
<td>0.047</td>
<td>0.054</td>
<td>0.069</td>
<td>0.089</td>
<td>0.058</td>
<td></td>
</tr>
<tr>
<td>S. Atlantic Bight</td>
<td>M</td>
<td>5</td>
<td>-5.33</td>
<td>0.20</td>
<td>0.066</td>
<td>0.259</td>
<td>0.189</td>
<td>0.177</td>
<td>0.492</td>
<td>0.507</td>
<td>0.098</td>
<td>0.103</td>
<td>0.090</td>
<td>0.125</td>
<td>0.091</td>
<td></td>
</tr>
</tbody>
</table>
**Figure 3.1** Mean mortality estimates of *H. portusjacksoni, C. limbatus*, and *R. taylori* as log\(_{10}\) -ratios of species- and sex-specific direct estimates of *M* (horizontal dashed lined) with 95% confidence intervals. P-values are given for mean *M* estimates that did not differ significantly from direct *M* estimates according to independent *t*-tests.

**Discussion**

Instantaneous mortality is one of the most difficult yet important parameters to estimate in fisheries. In this study, I found five methods that consistently estimated observed direct *M*. Three of these methods are revisions of traditional methods dependent on the VBGM while the remaining two are relatively new to fisheries and dependent on the LGM. The LGM incorporates well-known life history trade-offs between reproduction, survival, and growth, suggesting a higher likelihood for accurately
estimating \( M \) (Lester et al. 2004). For example, the LGM parameter \( g \) is investment in reproduction, and provided relatively accurate estimates of \( M \) (method 3.11 in Figure 3.1). However, the extent to which a life history parameter is rooted in life history theory does not guarantee reliable estimates of \( M \): LGM methods 3.4_{bp} and 3.5_{bp} overestimated \( M \); LGM methods 3.6_{bp}, 3.7_{bp}, 3.8_{bp}, 3.9_{bp}, and 3.10_{bp}, underestimated \( M \); and the VBGM methods 3.4_{vb}, 3.7_{vb}, 3.8_{vb}, and 3.10_{vb} predicted \( M \) with relative accuracy (though 3.4_{vb} did not show high precision). Similarly, it may be unreasonable to expect methods 3.6_{bp}, 3.7_{bp}, 3.8_{bp}, 3.9_{bp}, and 3.10_{bp} to provide reasonable estimates of \( M \) given that they were derived empirically from VBGM parameters.

Another advantage of the LGM is that indirect estimates of \( M \) based on Lester’s First and Second Methods appear to be robust to harvest-induced density-dependent life history changes. Obtaining data from unfished stocks is often difficult or impossible. Although there is strong evidence for density-dependent life history changes in teleosts (Rose et al. 2001), relatively few studies have reported density-dependent changes in elasmobranchs. Nonetheless, density-dependent changes have been observed in elasmobranch immature growth (Sminkey and Musick 1995, Stevens and West 1997), age and size at maturity (Walker et al. 1998, Carlson and Baremore 2003, Sosebee 2005, Cassoff et al. 2007, Coutré et al. 2013), and fecundity (Coutré et al. 2013). If, however, investment in reproduction (i.e., gonadal mass/somatic mass expressed in equivalent energetic units) is density-independent (Lester et al. 2014), then \( M \) estimates based on this parameter or some LGM correlate (e.g., \( K, T, t_o \)) would be expected to be robust to exploitation. The relative accuracy of methods based on \( g \) and its correlates lends support to this hypothesis (methods 3.7_{vb}, 3.8_{vb}, and 3.10_{vb} notwithstanding). Further work is
needed to determine the extent to which i) elasmobranch investment in reproduction is density-independent; and ii) the LGM parameters used in methods Lester’s First and Second Methods (3.11 and 3.12) are robust to fisheries-related exploitation.

This study has shown that LGM parameters can be used to reliably estimate $M$ through indirect methods. There is, however, one major caveat to consider; it is assumed that direct estimates of $M$ are themselves accurate. Direct estimates of $M$ can be biased by numerous factors including gear selectivity towards particular age or size classes and small sample sizes. Therefore, our results do not suggest that Then’s (3.7vb), Hisano’s (3.8vb), Chen and Watanabe’s (3.10vb), and Lester’s First and Second Methods (3.11 and 3.12) estimate true $M$, but that they estimate $M$ with as much accuracy as direct methods. With this in mind, more research is needed to determine if these results can be generalized to other species of elasmobranch (and fishes in general). Until more research is conducted, I recommend estimating $M$ in elasmobranchs by averaging across these five methods.
Chapter 4: Indirect Mortality of 29 Species of Elasmobranchs

Introduction

Instantaneous natural mortality rate ($M$) is one of the most important and most difficult parameters to estimate in elasmobranchs (Simpfendorfer et al. 2005). Direct methods for estimating $M$ are based on observations of the actual stock and are thought to be the most accurate. Common methods for directly estimating $M$ are tagging, telemetry, visual surveys, and catch curve analysis (Simpfendorfer 1999, Xiao et al. 1999, Campana et al. 2002, Heupel and Simpfendorfer 2002, Simpfendorfer et al. 2005, Powter and Gladstone 2008b, Swinsburg 2013). However, these methods are very data intensive. This is particularly problematic for many elasmobranch species in which extensive data collection is infeasible. Because of the difficulty of directly estimating $M$, considerable effort has been invested in indirect methods reliant on easily obtained growth and life-history information. In Chapters 1 and 3, I discussed a number of methods (and updated variations) found throughout the fisheries literature. However, many of these methods have been rarely (if ever) applied to elasmobranchs. In the elasmobranch literature, the most commonly used indirect methods are those of Hoenig (1983), Jensen (1996), Pauly (1980), Chen and Watanabe (1989), and Peterson and Wroblewski (1984). Of these methods, I previously found Chen and Watanabe’s Method to be the only reasonable predictor of direct $M$ (see Chapter 3). This suggests the most common methods in elasmobranch literature may be generating biased estimates of $M$. 

49
In this chapter, I compare \( M \) estimates derived using the most popular indirect methods (and some variations) in elasmobranch literature to \( M \) estimates derived from the five methods recommended in Chapter 3. In Chapter 3, I found that Then’s Method, Hisano’s Method, Chen and Watanabe’s Method, and Lester’s First and Second Methods were able to reliably and accurately estimate \( M \) in four shark populations. I recommended averaging across these five methods to generate a single \( M \) estimate. Using this recommendation, I examine the relative accuracy of Hoenig’s Methods (excluding that based on mollusks), Hewit and Hoenig’s Method (a variation of Hoenig (1983)), and Jensen’s First, Second, and Third Methods (the latter being an informal variation of Pauly (1980)), and determine the magnitude by which each method may be over- or under-estimating \( M \) in elasmobranchs. Although Pauly’s Methods and Peterson and Wroblewski’s Method are common in elasmobranch litterature, they require temperature and weight data, respectively, which were not collected for this study.

**Methods**

**Data Sources**

Readily available data from which to indirectly estimate \( M \) was collected as described in the methods section of Chapter 2. I analyzed published sex specific growth and maturity data from 29 elasmobranch species (30 populations) representing six orders, 11 families, and 19 genera (Table 2.1).
Growth-Independent Parameter Estimations

Two growth-independent parameters, longevity \((t_{\text{max}})\) and age at which individuals begin investing in reproduction \((T)\), are required for estimating \(M\). For each sex and population, I defined \(T_{\text{max}}\) as the oldest individual in the sample. I set values of \(T\) equal to published age-at-50%-maturity reported for each sex and population. Age-at-50%-maturity for *Alopias superciliosus* and *Sphyrna zygaena* were unavailable, and so I estimated \(T\) from longevity following Frisk et al. (2001):

\[
T = 7.20 \ln(t_{\text{max}}) - 12.68 .
\]  

(eq. 4.1)

Growth-Dependent Parameter Estimation

I used the VBGM and the LGM (see Chapter 2) to generate the growth-dependent parameters that were required for indirectly estimating \(M\). In short, the LGM parameters were used to estimate \(M\) from Lester’s first and second methods, and the VBGM parameters were used in conjunction with all other growth-dependent \(M\) methods.

Indirect Mortality Methods

I used ten indirect \(M\) estimators commonly found in elasmobranch literature (or variations), and two emerging methods to indirectly estimate \(M\) across all species and sexes. Of these methods, five are growth-independent and six are growth-dependent. Four variations of (Hoenig 1983) were used which estimate \(M\) from longevity \(T_{\text{max}}\) (Hoenig 1983, Hewitt and Hoenig 2005). The first variation developed from fish stocks takes the form:

\[
\ln(M) = 1.46 - 1.01 \ln(t_{\text{max}}) .
\]  

(method 4.1)

The second variation was developed from cetaceans and is described as:
\[
\ln(M) = 0.941 - 0.873 \ln(t_{max}) .
\]  
(method 4.2)

Elasmobranch life history has been described as “mammal like,” prompting the use of this relationship. The third of Hoenig’s Methods I consider is the relationship derived from all fish, cetacean, and mollusk stocks analyzed (Hoenig 1983):

\[
\ln(M) = 1.44 - 0.982 \ln(t_{max}) .
\]  
(method 4.3)

Though not prevalent in elasmobranch literature, Hewitt and Hoenig (2005) developed a revision of Hoenig’s Methods and recommended its use in place of the original relationships:

\[
M = \frac{4.22}{t_{max}} .
\]  
(method 4.4)

I used three methods described by Jensen (1996). The first relies of the growth-independent parameter \( T \):

\[
M = \frac{1.65}{T} .
\]  
(method 4.5)

The second and third methods rely on the VBGM parameter \( K \). Jensen’s Second Method is described as:

\[
M = 1.5K .
\]  
(method 4.6)

Jensen’s Third Method was presented informally as a revision of Pauly’s Method:

\[
M = 1.6K .
\]  
(method 4.7)

Hisano et al. (2011) revised Jensen’s First Method to account for non-zero values of the VBGM parameter \( t_0 \) commonly observed in elasmobranchs:
\[
M = \frac{1.65}{T - t_0}.
\]  
(method 4.8)

Then et al. (2014) also revised the classic method described by Pauly (1980) so that it is independent of temperature:

\[
M = 4.118K^{0.73}L_\infty^{-0.33}.
\]  
(method 4.9)

Chen and Watanabe (1989) developed an age specific method reliant on \(T\) and the VBGM parameters \(K\) and \(t_0\):

\[
M(t) = \begin{cases} 
\frac{K}{1 - e^{-K(t-t_0)}}, & t < T \\
\frac{K}{a_0 + a_1(t-T) + a_2(t-T)^2}, & t \geq T 
\end{cases}
\]  
(method 4.10)

where:

\[
a_0 = 1 - e^{-K(T-t_0)}, \quad (eq. 4.5)
\]

\[
a_1 = Ke^{-K(T-t_0)}, \quad (eq. 4.6)
\]

\[
a_2 = -\frac{1}{2}K^2 e^{-K(T-t_0)}. \quad (eq. 4.7)
\]

To generate a single estimate for comparison to other methods, I estimated \(M\) at every half-year age increment within the observed age range and averaged. Lastly, the methods described by Lester et al. (2004) and Lester et al. (2014) depend on the LGM parameters \(g\) (Lester’s First Method) and \(T\) and \(t_1\) (Lester’s Second Method) respectively. Lester’s First Method takes the form:

\[
M = -\ln(1 - \frac{g}{1.18^g}).
\]  
(method 4.11)

Lester’s Second Method is described as:
\[ M = \frac{2}{(T - t_1 + 1)} \quad \text{(method 4.12)} \]

**Method Comparison**

To evaluate the effectiveness of commonly used indirect methods for estimating \( M \), I first generated species, population, and sex specific averages of methods 4.8-4.12 \((M_A)\). These methods were found to accurately and reliably estimate \( M \) for four populations of sharks (Chapter 3). I then expressed species, population, and sex specific estimates of \( M \) from methods 4.1-4.7 as ratios \((M_R)\) of their corresponding \( M_A \) estimates with 95% confidence intervals.

**Results**

Across both sexes and all 29 species in this study, methods 4.1-4.7 tended to overestimate \( M \) by factors of 1.34-1.91 (Figure 4.1). Method 4.7, Jensen’s Third Method, provided the lowest overestimate of \( M \) with an \( M_R \) of 1.34 ± 0.13 times \( M_A \). Hoenig’s Third Method (method 4.3), provided the highest estimates of \( M \) with a \( M_R \) of 1.91 ± 0.23 times \( M_A \). Jensen’s Second and Third methods (methods 4.6 and 4.7) were dependent on VBGM parameters and provided better results than all growth-independent methods (methods 4.1-4.5). Of Hoenig’s Methods, method 4.2 (developed from cetaceans) gave the lowest results while method 4.3 (developed from fish, cetaceans, and mollusks combined) gave the highest results.
Discussion

In Chapter 3, five indirect methods were found to reliably predict direct \( M \) (methods 4.8-4.12) and advised averaging across these methods to generate a reasonable estimate of \( M \). In this chapter, I applied that recommendation to 29 species of elasmobranchs and compared those estimates to the most popular indirect methods in elasmobranch literature (methods 4.1-4.7). The results of this analysis were consistent with Chapter 3, in that the most common methods appear to be generating values of \( M \) that are much higher than values generated by the methods recommended in Chapter 3.

The tendency of traditional indirect methods to overestimate observed adult \( M \) has been noted for a number of elasmobranchs (Simpfendorfer 1999, McAuley et al. 2005,
Powter and Gladstone 2008b). Given that indirect $M$ estimates are commonly used in place of direct estimates in elasmobranchs, studies using these estimates to assess population growth rates and biological reference points (Smith et al. 1998) may likely be generating inaccurate results. Because population growth rates, rebound potentials, and other biological reference points are commonly used to assess the health of populations, any estimates of these parameters derived from inaccurate estimates of $M$ may result in the development of improper management strategies.

Traditional methods have also been applied to immature individuals and show a tendency to underestimate immature $M$ (Manire and Gruber 1993, Heupel and Simpfendorfer 2002). However, it is not surprising that traditional methods tend to underestimate immature $M$; with the exception of Chen and Watanabe’s Method, all methods were developed using data from mature fish and are therefore only applicable to mature individuals. As such, it is improper to apply these methods to immature individuals.

Despite Chen and Watanabe’s Method providing reasonable estimates of direct $M$ (Chapter 3), this method generated negative values of $M$ for three data sets; female *Shyrna mokarran*, *S. tiburo*, and *S. zygaena*. Similar results have been observed in other species as well (Kenchington 2014). Kenchington (2014) analyzed 13 fish stocks (two of which were sharks) and observed that Chen and Watanabe’s Method has a tendency to generate negative estimates in the oldest observed ages. This is concerning given that this method is routinely used to generate age-specific $M$ estimates in elasmobranch stock assessments.
This chapter indicated that the most common indirect $M$ methods (save Chen and Watanabe’s Method) tend to generate estimates much higher than the methods I recommended in Chapter 3. However, observed direct $M$ was unavailable for those species not considered in Chapter 3, and so it is difficult to derive any definitive conclusions of the performance of the traditional methods used in this study. Although it appears that the indirect methods common to elasmobranch literature generally overestimate $M$, more research is needed to verify these conclusions across multiple species. Unfortunately, this requires comparing these methods against direct $M$. Until more research is conducted, I recommend averaging across Lester’s First and Second Method, Hisano’s Method, Then’s Method, and Chen and Watanabe’s Method when indirectly estimating elasmobranch $M$. These updated estimates of $M$ can further be used to derive biological reference points (e.g., rebound potentials) that can help to gauge whether stocks are being properly managed (Smith et al. 1998).
Chapter 5: General Conclusion

Introduction

The ability to accurately describe elasmobranch lifetime growth and indirectly estimate mortality is crucial for the proper assessment of the size and health of stocks (Simpfendorfer 2005). Due to their unique life histories (slow growth, late maturity, low fecundity, and longevity) elasmobranchs are highly susceptible to overfishing, habitat destruction, and other anthropogenic stressors (Hoenig and Gruber 1990, Smith et al. 1998). To further compound this issue, many species of elasmobranch are still relatively poorly studied. Any inaccuracies in describing growth and estimating mortality could easily result in mismanagement of stocks. Thus, great care and effort must be put into the appropriate analysis the growth and life history of these stocks (Cailliet et al. 2006).

Modeling Elasmobranch Lifetime Growth

Modeling the lifetime growth of elasmobranchs is by no means a straight-forward process. The literature indicates that no single growth model will continuously provide the best fit. The result of this study, though strongly supportive of the LGM, are consistent with the literature. Although the LGM provided the best fitting model for ca. 81% of the data sets, in its absence all conventional models appear to describe lifetime growth reasonably well. Thus, it is important to consider the biological relevance of the growth model in addition to its statistical fit.
The VBGM is the most commonly used model in elasmobranch growth studies. However, this model has very little biological relevance. Though its parameters can be interpreted biologically, many are purely descriptive parameters. The most popular variation of the VBGM was introduced by Beverton and Holt (1957) to simplify yield calculations. The parameter $t_0$ was incorporated in place of $L_0$ (what most interpret as the length at age-0). However, Beverton and Holt (1957) indicated that the parameter $t_0$ has no biological significance and is simply a parameter to describe the intercept along the x-axis. However, because the VBGM was founded on metabolic principles (von Bertalanffy 1938) and many mistakenly interpret $t_0$ to be the age at length 0 (Cailliet et al. 2006), the typical VBGM is mistakenly viewed to have a reasonably high degree of biologically relevance.

Like the VBGM, the remaining traditional models (including the TPGM) suffer from a similar lack of biological relevance. The TPGM is perhaps the most biologically relevant of the remaining three traditional models (the others being the Gompertz and logistic models). Soriano et al. (1992) developed a modifying factor for the VBGM to address an apparent change in growth rate of fishes. This modifying factor could be interpreted biologically as the age-of-maturity or a shift in diet and feeding, but in reality it is largely an artificial parameter intended to describe the change in trajectory of the growth curve Soriano et al. (1992).

The LGM, on the other hand, uses life history theory to describe growth. Lester et al. (2004) developed a modified version of the VBGM so as the traditional parameters were described using reproductive characteristics. The trade-off between reproduction and growth is well known in life history theory, suggesting this growth model contains a
high degree of biological relevance. The biological relevance of the LGM is well
demonstrated by its ability to predict investment in reproduction in teleosts (Lester et al.
2004) and \( M \) in both teleosts (Lester et al. 2004, Quince et al. 2008b, Lester et al. 2014)
and elasmobranchs (methods 3.11 and 3.12 in Figure 3.1). Given the high support for the
LGM in describing lifetime growth (Chapter 2) and the relative accuracy of its
parameters in estimating \( M \) (Chapter 3), the LGM may provide a better alternative to
describing elasmobranch lifetime growth than traditional growth methods.

**Indirectly Estimating Elasmobranch Mortality**

Indirect methods for estimating mortality are very common in the elasmobranch
literature (Simpfendorfer 1999, Frisk et al. 2001, McAuley et al. 2005, Tsai et al. 2010,
Hisano et al. 2011, Knip et al. 2012). This is largely due to the relative difficulty in
directly estimating \( M \) in many (if not most) species (Simpfendorfer et al. 2005).
However, many of these methods were developed almost entirely from teleost stocks
2013). Because of the unique life history of elasmobranchs (i.e., slow growth, late
maturity, low fecundity, and long lived) as compared to teleosts, it stands to reason that
many of these indirect mortality methods may generate skewed estimates of \( M \). The
results of this study indicate that the most popular methods for estimating \( M \) for
elasmobranchs likely have a tendency to generate upwardly bias estimates (Chapter 4).
Chen and Watanabe’s Method was the only method common to elasmobranch literature
that generated reasonable results (see Chapter 3). However, this method tends to generate
negative values of \( M \) for some populations, particularly in older individuals (Chapter 4,
(Kenchington 2014). As such, when generating age-specific $M$ estimates, this method should be used with caution.

**Future Research**

Although the LGM provided the best fit for the vast majority of data sets and is more biologically realistic than traditional methods (Chapter 2), more research is needed to verify these results. In this study, I used published estimates of $T$ rather than allowing the model to generate its own estimate. To verify the biological relevance, research should be conducted to determine how accurately the LGM can predict observed age-at-50%-maturity derived from traditional methods. However, low sample sizes or a lack of individuals near the true age-at-maturity may skew estimates of observed age-at-50%-maturity, making it more difficult to assess the biological relevance of the LGM. Thus, an abundance of data points near the observed age-at-maturity is required to accurately assess the biological relevance of the LGM in elasmobranchs.

It is also very difficult to draw any reasonable conclusions about the most appropriate indirect $M$ methods based on this study. Of the species analyzed, only three had published direct estimates of $M$. Further research is need to determine if the trends seen in Chapter 3 can be generalized across more species. However, until further research is conducted, I recommend averaging across Lester’s First and Second Methods, Hisano’s Method, Then’s Method, and Chen and Watanabe’s Method to gain a reasonable estimate of indirect $M$ in elasmobranchs.
References


Frisk, M.G., Miller, T.J. (2006) Age, growth, and latitudinal patterns of two Rajidae species in the northwestern Atlantic: little skate (Leucoraja erinacea) and winter skate (Leucoraja ocellata). Canadian Journal of Fisheries and Aquatic Sciences 63, 1078-1091.


### Appendix A

**Table 1:** Indirect, life-history-based methods for estimating $M$ used in this study.

<table>
<thead>
<tr>
<th>Source</th>
<th>Method Name</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hoenig 1983</td>
<td>Hoenig’s First Method</td>
<td>$\ln(M) = 0.941 - 0.873\ln(t_{max})$</td>
</tr>
<tr>
<td></td>
<td>Hoenig’s Second Method</td>
<td>$\ln(M) = 1.46 - 1.01\ln(t_{max})$</td>
</tr>
<tr>
<td></td>
<td>Hoenig’s Third Method</td>
<td>$\ln(M) = 1.44 - 0.982\ln(t_{max})$</td>
</tr>
<tr>
<td>Hewitt and Hoenig (2005)</td>
<td>Hewitt and Hoenig’s Method</td>
<td>$M = e^{1.44 - 0.982\ln(t_{max})}$</td>
</tr>
<tr>
<td>Jensen (1996)</td>
<td>Jensen’s First Method</td>
<td>$M = \frac{1.65}{T}$</td>
</tr>
<tr>
<td></td>
<td>Jensen’s Second Method</td>
<td>$M = 1.5K$</td>
</tr>
<tr>
<td></td>
<td>Jensen’s Third Method</td>
<td>$M = 1.5K$</td>
</tr>
<tr>
<td>Hisano et al. (2011)</td>
<td>Hisano’s Method</td>
<td>$M = \frac{1.65}{T - t_0}$</td>
</tr>
<tr>
<td>Then et al. (2014)</td>
<td>Then’s Method</td>
<td>$M = 4.118K^{0.73}L_{\infty}^{-0.33}$</td>
</tr>
<tr>
<td>Alverson and Carney (1975)</td>
<td>Alverson and Carney’s Method</td>
<td>$M = \frac{3K}{(e^{0.38Kt_{max}} - 1)}$</td>
</tr>
<tr>
<td>Roff (1984)</td>
<td>Roff’s Method</td>
<td>$M = \frac{3K}{(e^{KT} - 1)}$</td>
</tr>
<tr>
<td>Charnov et al. (2012)</td>
<td>Charnov’s Method</td>
<td>$M = K\left(\frac{L}{L_{\infty}}\right)^{-1.5}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$M(t) = \begin{cases} \frac{K}{1 - e^{-K(T-t_0)}}, &amp; t &lt; T \ \frac{K}{a_0 + a_1(t - T) + a_2(t - T)^2}, &amp; t \geq T \end{cases}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>where $\begin{cases} a_0 = 1 - e^{-K(T-t_0)} \ a_1 = Ke^{-K(T-t_0)} \ a_2 = -\frac{1}{2}Ke^{-K(T-t_0)} \end{cases}$</td>
</tr>
<tr>
<td>Lester et al. (2004)</td>
<td>Lester’s First Method</td>
<td>$M = -\ln(1 - \frac{g}{1.18})$</td>
</tr>
<tr>
<td>Lester et al. (2014)</td>
<td>Lester’s Second Method</td>
<td>$M = \frac{2}{(T - t_1 + 1)}$</td>
</tr>
</tbody>
</table>

---

1. $t_{max} =$ maximum observed age; $T =$ age-at-50%-maturity; $g =$ reproductive investment; $T_1 =$ the BPGM x-intercept; $K =$ the growth coefficient; $L =$ length; $L_{\infty} =$ asymptotic length; $t =$ age; and $t_0 =$ the VBGM x-intercept
Table 2. Growth and maturity sources for species used in this study.

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Species</th>
<th>Growth Data Source</th>
<th>Growth Data Type</th>
<th>Maturity Source</th>
<th>Maturity Data Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rajidae</td>
<td></td>
<td>Amblyraja radiata</td>
<td>Sulikowski et al. (2005a)</td>
<td>Digitized</td>
<td>Sulikowski et al. (2005b)</td>
<td>Age-at-50%-Maturity</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Leucoraja ocellata</td>
<td>Frisk and Miller (2006)</td>
<td>Digitized</td>
<td>Sulikowski et al. (2005c)</td>
<td>Age-at-50%-Maturity</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Raja radula</td>
<td>Kadri et al. (2013)</td>
<td>Tabulated Means</td>
<td>Kadri et al. (2013)</td>
<td>Age-at-50%-Maturity</td>
</tr>
<tr>
<td>Myliobatiformes</td>
<td>Dasyatidae</td>
<td>Squalus acanthias</td>
<td>Bubley et al. (2011)</td>
<td>Raw</td>
<td>Bubley et al. (2013)</td>
<td>Age-at-50%-Maturity</td>
</tr>
<tr>
<td>Squaliformes</td>
<td>Squalidae</td>
<td>Squalus mitsukurii</td>
<td>Cotton et al. (2011)</td>
<td>Raw</td>
<td>Cotion et al. (2011)</td>
<td>Individual Maturity</td>
</tr>
<tr>
<td>Lamiiformes</td>
<td>Alopidae</td>
<td>Alopias superciliosus</td>
<td>Fernandez-Carvalho et al. (2011)</td>
<td>Digitized</td>
<td>Frisk et al. (2001)</td>
<td>Age-at-50%-Maturity</td>
</tr>
<tr>
<td>Carcharhiniformes</td>
<td>Triakidae</td>
<td>Triakis megalopterus</td>
<td>Booth et al. (2011)</td>
<td>Raw</td>
<td>Booth et al. (2011)</td>
<td>Age-at-50%-Maturity</td>
</tr>
<tr>
<td>Carcharhinidae</td>
<td></td>
<td>Galeus sauteri</td>
<td>Liu et al. (2011)</td>
<td>Digitized</td>
<td>Liu et al. (2011)</td>
<td>Age-at-50%-Maturity</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Carcharhinus brevipinna</td>
<td>Jung et al. (2005)</td>
<td>Raw</td>
<td>Jung et al. (2005)</td>
<td>Age-at-50%-Maturity</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sphyrna zygaena</td>
<td>Coelho et al. (2011)</td>
<td>Raw</td>
<td>Frisk et al. (2001)</td>
<td>Age-at-50%-Maturity</td>
</tr>
</tbody>
</table>