An Evaluation of Sciaenid Growth in the Gulf of Mexico

Shane Flinn

Louisiana State University and Agricultural and Mechanical College

Follow this and additional works at: https://repository.lsu.edu/gradschool_theses

Part of the Aquaculture and Fisheries Commons, Marine Biology Commons, and the Population Biology Commons

Recommended Citation


This Thesis is brought to you for free and open access by the Graduate School at LSU Scholarly Repository. It has been accepted for inclusion in LSU Master's Theses by an authorized graduate school editor of LSU Scholarly Repository. For more information, please contact gradetd@lsu.edu.
AN EVALUATION OF SCIAENID GROWTH IN THE GULF OF MEXICO

A Thesis
Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Master of Science
in
The Department of Oceanography and Coastal Sciences

by
Shane Flinn
B.S., Michigan State University, 2016
December 2018
ACKNOWLEDGMENTS

First and foremost, I would like to thank my advisor Dr. Steve Midway for his advice and guidance throughout my time at LSU, for which I will forever be a better scientist. I also would like to thank my committee members, Dr. Richard Shaw and Dr. Robert Rohli for their advice and encouragement in my thesis research.

I would like to thank the Louisiana Department of Wildlife and Fisheries (LDWF), the Texas Park and Wildlife Department (TPWD), and the Florida Fish and Wildlife Conservation Commission (FWC), especially Joe West (LDWF), Mark Fisher, (TPWD) and Jessica Carrol (FWC), for their help in data acquisition and throughout this research.

I would also like to express thanks to Dr. James Cowan for letting me pick his brain for all things fish, be it for my research or just a good fishing spot. Also, thanks to my fellow lab mates Matt Robertson and Lucas Pensinger, and fellow graduate student Mario Hernandez for making work fun. Finally, thank you to my family, especially my wife for all the support you have given me.
# TABLE OF CONTENTS

ACKNOWLEDGMENTS ........................................................................................................... ii

LIST OF TABLES ..................................................................................................................... v

LIST OF FIGURES ................................................................................................................... vi

ABSTRACT ............................................................................................................................... viii

CHAPTER 1. GENERAL INTRODUCTION .............................................................................. 1
  1.1. Growth Modeling ........................................................................................................... 1
  1.2. Study Species ............................................................................................................... 2
  1.3. Study Outline .............................................................................................................. 3
  1.4. References ................................................................................................................ 3

CHAPTER 2. TRENDS IN GROWTH MODELING IN FISHERIES ........................................... 6
  2.1. Introduction ................................................................................................................ 6
  2.2. Methods ...................................................................................................................... 9
  2.3. Results ....................................................................................................................... 16
  2.4. Discussion .................................................................................................................. 23
  2.5. References ................................................................................................................ 28

CHAPTER 3. MULTI-MODEL EVALUATION OF SCIAENID GROWTH IN THE GULF OF MEXICO ................................................................. 34
  3.1. Introduction ................................................................................................................ 34
  3.2. Methods ...................................................................................................................... 38
  3.3. Results ....................................................................................................................... 45
  3.4. Discussion .................................................................................................................. 57
  3.5. References ................................................................................................................ 67

CHAPTER 4. SPATIAL VARIATION AND DRIVERS OF SCIAENID GROWTH IN THE GULF OF MEXICO ................................................................. 73
  4.1. Introduction ................................................................................................................ 73
  4.2. Methods ...................................................................................................................... 78
  4.3. Results ....................................................................................................................... 83
4.4. Discussion ................................................................................................................................................. 94
4.5. References .................................................................................................................................................. 98

CHAPTER 5. GENERAL CONCLUSIONS ............................................................................................................. 104
5.1. Thesis Summary ......................................................................................................................................... 104
5.2. References .................................................................................................................................................. 106

APPENDIX A. CHAPTER 3 SUPPLEMENTAL MATERIAL ................................................................. 108

APPENDIX B. CHAPTER 4 SUPPLEMENTAL MATERIAL ........................................................................ 111

APPENDIX C. GEAR SELECTIVITY HISTOGRAMS ............................................................................... 113

VITA .................................................................................................................................................................. 119
LIST OF TABLES

Table 2.1. Model equations, parameter descriptions, and references for the most commonly evaluated growth models .........................................................12

Table 2.2. Selection rate of various growth models from multi-model studies (2+ models evaluated) ..................................................................................................................15

Table 2.3. Best-fitting models by system type .................................................................................................................................20

Table 3.1. Candidate models for sciaenid growth modeling in Chapter 3 .................................................................42

Table 3.2. AIC and Akaike weight for models fit to black drum length-at-age data ...................................................46

Table 3.3. Black drum growth model parameter estimates (and SE) for all candidate models from Louisiana and Texas ........................................................................49

Table 3.4. AIC and Akaike weight for models fit to red drum length-at-age data ............................................51

Table 3.5. Red drum growth model parameter estimates (and SE) for all candidate models from Louisiana and Texas ........................................................................53

Table 3.6. AIC and Akaike weight for models fit to spotted seatrout length-at-age data .........55

Table 3.7. Spotted seatrout growth model parameter estimates (and SE) for all candidate models from Louisiana and Texas .............................................................................................56

Table 4.1. The untransformed mean and range for the environmental covariates ($x$) ........................................81

Table 4.2. Estuary-specific intercept ($\alpha_j$) and slope ($\beta_j$) estimates for black drum, red drum, and spotted seatrout .............................................................................87

Table 4.3. Posterior mean estimates and 95% credible intervals for population level intercept ($\gamma_0^a$), population level slope ($\gamma_0^b$), effect of drainage area ($\gamma_1^b$) ..........90

Table 4.4. Pearson correlation coefficient ($r$) of growth rates between black drum, red drum, and spotted seatrout females and males .................................................................94
LIST OF FIGURES

Figure 2.1. Four common growth functions used to model fish growth...........................................7

Figure 2.2. Trends in the total number of age and growth studies (solid line), multi-model (≥ 2 models) studies (dashed line), and multi-model studies not including VBGM to be best fitting model (dotted line) .................................................................17

Figure 2.3. Counts of the number of studies evaluating different numbers of growth models based on 196 peer-reviewed age and growth literature between 1988–2016.................18

Figure 2.4. Total number of times individual models were evaluated within 196 peer-reviewed studies from 1988–2016.................................................................19

Figure 2.5. Model selection procedure usage over time..........................................................22

Figure 3.1. Growth model parameter estimates ($L_\infty$ and $k$) and 95% confidence intervals for black drum female and male from Louisiana and Texas.................................47

Figure 3.2. Observed black drum length-at-age and best-fit growth curves for Louisiana (top panel) and Texas (bottom panel)..........................................................48

Figure 3.3. Growth model parameter estimates ($L_\infty$ and $k$) and 95% confidence intervals for red drum female and male from Louisiana and Texas...............................50

Figure 3.4. Observed red drum length-at-age and best-fit growth curves for Louisiana (top panel) and Texas (bottom panel).........................................................52

Figure 3.5. Observed spotted seatrout length-at-age and best-fit growth curves for Louisiana (top panel) and Texas (bottom panel)................................................54

Figure 4.1. Map of the US Gulf of Mexico region and the 18 estuaries (yellow dots) represented in the Chapter 4 analysis.................................................................78

Figure 4.2. Observed length (mm) at age (yr.) and fitted estuary-specific (gray) and population mean (red) linear growth models for black drum (A), red drum (B), and spotted seatrout females (C) and males (D).........................................................84

Figure 4.3. Estimated estuary-specific slope ($\beta_j$ [mm/yr.]; black dot), 95% CI (thin vertical line), 90% CI (thick vertical line) and population mean 95% CI (dark gray area) and 90% CI (light gray area) for black drum.............................85

Figure 4.4. Black drum relationship between estuary-specific slope (growth rate) and estuary drainage area, marsh edge, relative depth, and freshwater area.................86
Figure 4.5. Estimated estuary-specific slope ($\beta_j$ [mm/yr.]; black dot), 95% CI (thin vertical line), 90% CI (thick vertical line) and population mean 95% CI (dark gray area) and 90% CI (light gray area) for red drum.

Figure 4.6. Red drum relationship between estuary-specific slope (growth rate) and estuary drainage area, marsh edge, relative depth, and freshwater area.

Figure 4.7. Estimated estuary-specific slope ($\beta_j$ [mm/yr.]; black dot), 95% CI (thin vertical line), 90% CI (thick vertical line) and population mean 95% CI (dark gray area) and 90% CI (light gray area) for female (A) and male (B) spotted seatrout.

Figure 4.8. Female spotted seatrout relationship between estuary-specific slope (growth rate) and estuary drainage area, marsh edge, relative depth, and freshwater area.

Figure 4.9. Male spotted seatrout relationship between estuary-specific slope (growth rate) and estuary drainage area, marsh edge, relative depth, and freshwater area.
ABSTRACT

Growth models estimate life history parameters that are used in the management of fisheries stocks. The most commonly used growth model in fisheries is the von Bertalanffy growth model (VBGM), yet it has been shown to provide a poor fit for length-at-age data of some species and other models exist. I reviewed 196 peer-reviewed age and growth studies and 50 NOAA stock assessments to examine temporal trends in the use of growth models and model selection in fisheries. I found that the use of multi-model frameworks has increased since the year 2000 and information theoretic approaches are replacing goodness-of-fit and *a priori* model selection in fisheries studies. However, NOAA stock assessments rely almost exclusively on the von Bertalanffy growth model. Furthermore, factors such as the study location, and maximum age, usually did not contribute to the final model selected.

I then performed a multi-model evaluation of growth models to (1) determine the best-fitting growth model for black drum (*Pogonias cromis*), red drum (*Sciaenops ocellatus*), and spotted seatrout (*Cynoscion nebulosus*) length-at-age data from coastal Gulf of Mexico; and (2) to evaluate the variation among state-wide and sex-specific parameter estimates. I found that sex-specific models were better fitting than pooled models, black and red drum were fit best by biphasic models, and spotted seatrout by seasonal and sigmoidal models. Texas fish were estimated to grow to larger sizes and Louisiana fish grew at a faster rate. Lastly, I modeled estuary-specific growth rates of black drum, red drum, and spotted seatrout up to age-3 and incorporated static spatial drivers as covariates into hierarchical linear models to evaluate the (1) spatial variation of growth rate among estuaries and (2) effect of static spatial drivers on the spatial variation of growth rate among estuaries. I found significant variation among estuary-specific growth rates; furthermore, distance of marsh edge and estuary depth had a moderate
effect in driving the variation in growth rate of female spotted seatrout and black drum, respectively. Because of sciaenid’s significant importance in the Gulf of Mexico, a deep understanding of the dynamics of their growth is of critical value to fisheries managers.
CHAPTER 1. GENERAL INTRODUCTION

1.1. Growth Modeling

Growth is the fundamental biological process of increasing in physical size (e.g. length or weight). Growth of fishes has long been of interest to fisheries managers because outside of recruitment, the increase in biomass of fish populations comes about primarily through individuals increasing in size (Ricker 1975). Furthermore, fish growth is related to other life history metrics such as survival, reproduction (Beverton and Holt 1957; Beverton 1992), natural mortality, and fecundity (Pauly 1980; Gislason et al. 2010; Hixon et al. 2013). Fisheries managers use growth rates along with other population dynamics rates to inform management decisions and set harvest regulations (Ricker 1975). To estimate growth, fisheries managers have traditionally used growth models, the most common growth model being the von Bertalanffy growth model (VBGM; Bertalanffy 1938). The VBGM was introduced to fisheries by Beverton and Holt (1957) and has since received much attention, but also criticisms (Roff 1980; Day and Taylor 1997). The uncertainty surrounding the use of growth models and model parameter estimates has driven the introduction of new models, model selection procedures, and estimation methods.

The use of mathematical equations and growth parameters allows managers to compare growth between populations and assess the spatial variation of fish growth. Growth of fishes varies spatially based on the biotic and abiotic conditions of an environment (Sogard 1992; Robins et al. 2006; Smith et al. 2008). Understanding the variability in growth among fish populations may aid fisheries managers in setting regulations based on observed spatial patterns which better reflect the true nature of these populations, rather than aggregating them into one large population based on some arbitrary political boundary (e.g. states). Additionally, evaluating
the spatial variation of fish populations can inform managers how fish populations will respond to various management regimes, or in changing environments (e.g., Rypel 2012; Massie et al. 2018).

The ubiquity and tremendous variation in the methodologies employed to model fish growth serves as an example of the importance placed on growth modeling and reducing uncertainty with regard to parameter estimates. This is especially true for commercially and recreationally harvested fish populations. As computational power has increased so has the ability to evaluate complex models and utilize methods such as Bayesian estimation (Hansen et al. 2018; Massie et al. 2018). Today growth models that incorporate seasonal variation (Porch et al. 2002), energetic costs of reproduction (Lester et al. 2004; Ohnishi et al. 2012; Minte-Vera et al. 2016), and otolith ageing-error (Hatch and Jiao 2016) are being developed and evaluated to reduce uncertainty and estimate the growth of fishes more accurately.

1.2. Study Species

Sciaenids, specifically black drum (*Pogonias cromis*), red drum (*Sciaenops ocellatus*), and spotted seatrout (*Cynoscion nebulosus*) inhabit estuaries for all or part of their lives (i.e., estuarine-dependent). They are among the most targeted recreational and commercial fishes in the Gulf of Mexico (Nieland et al. 2002; Powers et al. 2012; LDWF 2015). Because of this recreational and commercial importance, the growth of these sciaenids has been studied heavily. In fact, Pearson (1929) was the first to report on the growth of sciaenids in the Gulf of Mexico and a consistent amount of research has continued since (see Chapter 3). Nevertheless, important research questions regarding sciaenid growth in the Gulf of Mexico remain today.
1.3. Study Outline

In this study, I sought to evaluate the trends in the methodological approach to length-at-age growth modeling in the peer-reviewed fisheries growth literature and to compare those trends with recent NOAA stock assessments to determine if new methods that are found to improve model fit to length-at-age data in peer-reviewed research are being used in the management of fisheries populations. I then conduct a multi-model evaluation of growth models to three recreationally and culturally important species in the Gulf of Mexico to determine whether the most commonly used growth model (VBGM) is in fact the best fit for sciaenids and whether that fit varies based on sex and location. Lastly, I fit estuarine-specific models to length-at-age data of sub-adult fishes and incorporate environmental covariates into Bayesian hierarchical models to evaluate whether or not abiotic static spatial drivers of estuaries (e.g. estuary drainage area) contribute to the growth of sciaenids in the Gulf of Mexico. Overall, this study is an in-depth look at the growth of sciaenids in the Gulf of Mexico, including how growth rate and model fit varies spatially across the Gulf of Mexico, and what drivers contribute to that spatial variation of growth.

1.4. References


CHAPTER 2. TRENDS IN GROWTH MODELING IN FISHERIES

2.1. Introduction

Growth—the change in organism size with age—is a basic yet critically important biological process that integrates numerous processes and shapes the life history of fishes. Growth can be directly linked to other life history traits such as natural mortality and fecundity (Pauly 1980; Gislason et al. 2010; Hixon et al. 2013). The ability to model fish growth accurately has a wide range of applications in population dynamics (Smart et al. 2016). Outside of recruitment, increases in the biomass of a (closed) stock come about by the growth of individuals. For population analyses (e.g., stock assessments), mathematical models relating the size (typically length) of a fish species to its age are necessary inputs to other models. Growth models estimate parameters that are inputs into larger stock assessment models, which are used to inform management decisions. Growth curves are also used to select length limits for harvest and make other regulatory and management decisions. Furthermore, growth data can be used to assess the status of a fishery and determine how fisheries have responded or will respond to exploitation (Zhu et al. 2009). For example, growth parameter estimates can be used to compare different populations (or stocks) over time as a tool to evaluate density-dependence or prey-availability (Lauerburg et al. 2018; Matthias et al. 2018). Growth of fishes often varies by species and within species along gradients (e.g., latitude, temperature), and the use of mathematical models to represent growth allows for comparison (DeVries and Grimes 1997; Helser and Lai 2004; Midway et al. 2015).

Growth modeling is typically achieved by relating the size of a species (e.g., length or weight) to its age. Traditionally in fisheries science, it was common to fit one growth model to size-at-age data. However, many model types have been proposed and evaluated to estimate the
growth of fishes. Most are asymptotic, sigmoidal, or biphasic (having two growth phases) in shape, but other model types such as linear (Nieland et al. 2002; Curtis and Shima 2005) and polynomial functions (Chen et al. 1992) have also been used to describe growth of some species (Figure 2.1). von Bertalanffy (1938) derived his well-known growth equation that balances the catabolic and anabolic processes of growth, to relate organism size based on its age. Beverton and Holt (1957) modified and introduced the von Bertalanffy growth model (VBGM) to fisheries

Figure 2.1. Four common growth functions used to model fish growth. The von Bertalanffy growth function (upper left), logistic growth function (upper right), Lester biphasic growth function (lower left) and power growth function (lower right) are shown to illustrate the differences among models. Data (black dots) were simulated from the same model parameterization that fit the individual growth functions (red lines). The shaded background areas correspond to parameter interpretations, although please reference specific growth equations for details.
and it has received much attention and use in the following decades. Prior to the introduction of the VBGM, growth parameters were not estimated in size-at-age studies; instead observed (or mean) size-at-age data were plotted to visualize the trajectory of growth and make inferences. However, size-at-age studies were very inaccurate prior to otolith aging; for example, Pearson (1929) estimated the maximum age of red drum (*Sciaenops ocellatus*) to be between 3 – 6 years, yet we now know it to be around 50 years (Ross et al. 1995). Since 1957, the VBGM has been the most widely used growth model in fisheries. However, other commonly used growth models now include the Gompertz growth model (Gompertz 1825), the logistic model (Ricker 1975), the generalized VBGM (Pauly 1979), and the Schnute-Richards model (Schnute and Richards 1990), to name a few.

The uncertainty around how well growth models predict growth has driven the introduction of new methods, models, and model selection procedures. Today, it is common for fisheries researchers to fit multiple growth models to size-at-age data and use information theoretic (IT) procedures to select the best fitting model. Model selection using IT is a relatively new practice in biological sciences that has emerged as one way to account for the uncertainty surrounding the *a priori* use of growth models (Katsanevakis 2006; Katsanevakis and Maravelias 2008). The most widely used IT for model selection is Akaike’s Information Criterion (AIC; Akaike 1973). Other IT criteria such as Bayesian Information Criterion (BIC; Schwarz 1978), small-sample bias-corrected form of AIC (AICc; Shono 2000), and Akaike weight (Burnham and Anderson 2002; Katsanevakis 2006; Katsanevakis and Maravelias 2008) have also been used in fisheries studies to select best fitting growth models.

I reviewed the peer-reviewed literature to examine how the use of growth models and model selection has changed over time, and whether any trends can be determined in the approach to
growth modeling. I also examined how the approach to growth modeling is influenced by various factors (e.g., marine vs. fresh, developed vs. undeveloped countries, maximum age of species). I also considered (i) whether certain models have been used more frequently or have been shown to be better fitting for certain species or families, and (ii) how the approach to growth modeling changes as a function of a species maximum age, system (e.g., marine or freshwater), or diet. Additionally, I reviewed recent stock assessments from NOAA regional fisheries management councils (FMC) to analyze whether or not the trends in growth modeling in the peer-reviewed literature is reflected in stock assessments.

2.2. Methods

2.2.1. Peer-Reviewed Literature

I used Web of Science to conduct two peer-reviewed literature searches. First, I used the search terms, Title: ‘growth’ AND Topic: ‘models’ AND Topic: ‘fish’ NOT Publication Name: ‘aquaculture’. For the second search I used, Topic: ‘growth’ AND Topic: ‘models’ AND Topic: ‘fish’ NOT Publication Name: ‘aquaculture’. The results of both searches were refined by Web of Science Categories ‘fisheries’. The first search was conducted on October 17, 2016, and produced 769 results. The second search was conducted on January 25, 2017, and produced 2,666 results. In my first search, ‘growth’ was included in the title, whereas in my second search, ‘growth’ was included as the topic. This change in the search terms resulted in a larger sample size, after the first search produced what I thought to be a low sample size.

To evaluate trends in the use of growth models, model fit, and model selection, a dataset was compiled from the individual studies of my search. I chose to only include studies that were estimating growth of a group (e.g., stock or population) of wild fishes using length-at-age data.
Therefore, mark-recapture, aquaculture, larval, and juvenile growth studies were excluded. From the studies matching my criteria, I recorded information for the lead author, year of publication, species name, species family, location of the study population, the number and type of candidate growth models evaluated in the study, the best fit model, the model selection process used, what estimation process was used (if reported; e.g., least squares, maximum likelihood, Bayesian), whether or not the model took into account effects on growth (defined by the addition of model parameters), and whether or not separate growth models were ultimately fit for males and females. From FishBase (Froese et al. 2017) I also collected any available diet (e.g., benthivorous, piscivorous), system (freshwater or marine), and maximum age information for species from each study.

While collecting these data, I had 16 categories for models; 2-parameter VBGM, 3-parameter VBGM, 2-parameter Gompertz, 3-parameter Gompertz, 2-parameter logistic, 3-parameter logistic, Schnute, Richards, Schnute-Richards, double VBGM, generalized VBGM, linear VBGM, seasonal VBGM, power, linear regression, and other (Table 2.1). Some models that were evaluated by individual studies were obscure, having low usage in the literature and, therefore, could not be placed into one of my discrete categories, thus I classified these models as other. Most of these models were fixed-parameter, specialized, or modified variations of more common growth models, such as the VBGM. Likewise, there was a large amount of variation among individual studies and my other variables of interest (e.g., best fitting model \[n=40\] unique entries) and model selection procedure \[n=26\] unique entries), thus I aggregated certain variables based on the following criteria. For best fitting model, I included a second variable (best fit 2) that more broadly grouped the models into one of six groups, either the Gompertz, logistic, VBGM, double VBGM, seasonal VBGM, or Richards-Schnute. These aggregated
groups included 2-parameter, 3-parameter, seasonal, and other variations of the five parent model types. The seasonal and double VBGM were kept separate from the VBGM group because they each had high selection as best-fit (50 and 75% of the time evaluated, respectively) relative to other variations of traditional models (Table 2.2). I also aggregated model selection (model select 2) such that only IT (Information theoretic), GOF (goodness-of-fit), and a priori were considered as model selection types. Information theoretic consisted of AIC, AICc, Akaike weight, BIC, and DIC. Goodness-of-fit consisted of R², log-likelihood, residual sum of squares, GOF, mean squared error, likelihood ratio tests, and principal components analysis, while a priori consisted of those studies that only evaluated and used one growth model in their respective study. Lastly, I grouped locations broadly by continent.

These data were divided into two classes based on the number of models evaluated: (i) those studies that only used one growth model (a priori) and (ii) those that evaluated multiple models. I further divided those studies that evaluated multiple growth models, based on what model was found to be best fit: (i) those that found the VBGM (or variation of VBGM) to be best-fit and (ii) those that found a model other than the VBGM to be best-fit.

I summarized the data and analyzed spatial and temporal trends in the use of growth models and model selection criterion in the peer-reviewed literature. I also consider whether the evaluation of multiple growth models and model selection has been especially beneficial in finding better fitting growth models for certain families (or species), and how the approach to growth modeling changes as a function of a species maximum age, system (marine or fresh), or diet, by subsetting and summarizing the data.
Table 2.1. Model equations, parameter descriptions, and references for the most commonly evaluated growth models. References in bold refer to original usage or formulation of the model and subsequent references serve as examples of its use.

<table>
<thead>
<tr>
<th>Model name</th>
<th>Model equation</th>
<th>Parameter description</th>
<th>Reference(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-parameter VBGM</td>
<td>(L(t) = L_\infty \left(1 - e^{-k_1(t)}\right))</td>
<td>(L_\infty = ) asymptotic length; (t = ) age; (L_{00} = ) length-at-age, (t); (k_1 = ) Brody growth parameter</td>
<td>Fischer et al. (2004)</td>
</tr>
<tr>
<td>3-parameter VBGM</td>
<td>(L(t) = L_\infty \left(1 - e^{-k_1(t-t_0)}\right))</td>
<td>(t_0 = ) age at zero length</td>
<td>Beeverton and Holt (1957)</td>
</tr>
<tr>
<td>2-parameter Gompertz</td>
<td>(L(t) = L_0 e^{G \left(1-e^{-k_2 t}\right)}), (G = \ln \frac{L_\infty}{L_0})</td>
<td>(k_2 = ) rate of exponential decrease of relative growth with age</td>
<td>Mollet et al. (2002); Tribuzio et al. (2010)</td>
</tr>
<tr>
<td>3-parameter Gompertz</td>
<td>(L(t) = L_\infty e^{-k_2(t-\alpha)})</td>
<td>(\alpha = ) inflection point of the sigmoid curve</td>
<td>Gompertz (1825); Tribuzio et al. (2010)</td>
</tr>
<tr>
<td>3-parameter Gompertz</td>
<td>(L(t) = L_\infty e^{-k_3(t-\alpha)})</td>
<td>(k_3 = ) relative growth rate parameter</td>
<td>Ricker (1975); Tribuzio et al. (2010)</td>
</tr>
<tr>
<td>3-parameter Logistic</td>
<td>(L(t) = \frac{L_\infty}{1 + e^{-k_3(t-\alpha)}})</td>
<td></td>
<td>Ricker (1979); Tribuzio et al. (2010)</td>
</tr>
<tr>
<td>Linear VBGM</td>
<td>(L(t) = (b_0 + b_1 t)\left(1 - e^{-k_1(t-t_0)}\right))</td>
<td>(b_0, b_1 = ) linear coefficients; (b_0) (intercept), (b_1) (slope)</td>
<td>Hoese et al. (1991); Vaughan (1996); Porch et al. (2002)</td>
</tr>
<tr>
<td>Double VBGM</td>
<td>(L(t) = \begin{cases} L_\infty \left(1 - e^{-k_4(t-t_1)}\right) &amp; \text{if } t &lt; t_p \ L_\infty \left(1 - e^{-k_5(t-t_2)}\right) &amp; \text{if } t &gt; t_p \end{cases})</td>
<td>(k_4, k_5 = ) instantaneous growth rate coefficients; (t_p = ) ‘pivotal age’; (t_1, t_2 = ) age intercept parameters</td>
<td>Condrey et al. (1988); Vaughan and Helser (1990); Porch et al. (2002)</td>
</tr>
</tbody>
</table>

(table cont’d.)
<table>
<thead>
<tr>
<th>Model name</th>
<th>Model equation</th>
<th>Parameter description</th>
<th>Reference(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lester Model</td>
<td>[ t_p = \frac{(k_5 t_2 - k_4 t_1)}{(k_5 - k_4)} ]</td>
<td>( h ) = juvenile growth rate ( t_1 ) (Lester) = immature) hypothetical age at length-0</td>
<td>Lester et al. (2004)</td>
</tr>
<tr>
<td></td>
<td>[ L(t) = \begin{cases} h(t - t_1) &amp; \text{if } t \leq T \ L_{\infty}(1 - e^{-k_1(t-t_0)}) &amp; \text{if } t \geq T \end{cases} ]</td>
<td>( T ) = last immature age ( t_0 ) (Lester) = VBGM (adult) hypothetical age at length-0</td>
<td></td>
</tr>
<tr>
<td>Generalized VBGM</td>
<td>[ L(t) = L_{\infty}(1 - e^{-k_1(t-t_0)})^p ]</td>
<td>( p ) = dimensionless factor</td>
<td>Pauly (1979)</td>
</tr>
<tr>
<td></td>
<td>( L(t) = L_{\infty} \left{ 1 - e^{-k_1(t-t_0)} - \frac{e^{ck}}{2\pi} \left[ \sin 2\pi(t-t_5) \sin 2\pi(t_0-t_5) \right] \right} )</td>
<td>( c ) = amplitude of oscillations ranging between 0 and 1</td>
<td>Gayanilo and Pauly (1997); Stewart et al. (2013)</td>
</tr>
<tr>
<td>Seasonal VBGM</td>
<td>[ L(t) = \left[ t^\rho + \delta^\rho - t^\rho \frac{1 - e^{-\lambda(t-t_1)}}{1 - e^{-\lambda(t_2-t_1)}} \right]^\frac{1}{\rho} ]</td>
<td>( \rho ) = an incremental relative growth rate ( \lambda ) = relative growth rate ( \tau_1 ) = lowest age in the data set ( \tau_2 ) = highest age in the data set</td>
<td>Schnute (1981); Aragon-Noriega (2014)</td>
</tr>
<tr>
<td>Schnute</td>
<td>[ L_{\infty} = \left[ \frac{e^{\lambda \tau_2 \delta^\rho} - e^{\lambda \tau_1 \delta^\rho}}{e^{\lambda \tau_2} - e^{\lambda \tau_1}} \right] ] ( 1 )</td>
<td>( \delta ) (Schnute) = size at age ( \tau_1 ) ( \delta ) (Richards) = a shape parameter, and the sigmoidal Gompertz function</td>
<td>Richards (1959); Porch et al. (2002); Balazik et al. (2012)</td>
</tr>
<tr>
<td>Richards</td>
<td>[ L(t) = L_{\infty}(1 - \delta e^{-k_6(t-t_4)})^\frac{1}{\delta} ] where ( \delta \neq 0 ]</td>
<td>( k_6 ) = relative growth parameter</td>
<td></td>
</tr>
</tbody>
</table>

(table cont’d.)
<table>
<thead>
<tr>
<th>Model name</th>
<th>Model equation</th>
<th>Parameter description</th>
<th>Reference(s)</th>
</tr>
</thead>
</table>
| Schnute-Richards | $L(t) = L_\infty (1 + \delta e^{-k \gamma^\nu})^{\frac{1}{\gamma}}$ | $\nu, \delta, \gamma$ = dimensionless parameters  
$\kappa$ = units yr$^{-\nu}$ | Schnute and Richards (1990);  
Katsanevakis (2006) |
| Power            | $L(t) = a_0 + a_1 t^b$                 | $a_0$ = y-intercept or the mean length at age 0  
$a_1, b$ = parameters that describe the shape of the curve but have no biological interpretation | Katsanevakis (2006);  
Katsanevakis and Maravelias (2008); Williams et al. (2012) |

¹ Many variations and reparameterizations have been excluded for brevity.
Table 2.2. Selection rate of various growth models from multi-model studies (2+ models evaluated).

<table>
<thead>
<tr>
<th>Model</th>
<th>Evaluated</th>
<th>Selected</th>
<th>Selection rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Schnute-Richards</td>
<td>2</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Double VBGM</td>
<td>4</td>
<td>3</td>
<td>0.75</td>
</tr>
<tr>
<td>Seasonal VBGM</td>
<td>10</td>
<td>5</td>
<td>0.50</td>
</tr>
<tr>
<td>3-parameter VBGM</td>
<td>79</td>
<td>31</td>
<td>0.39</td>
</tr>
<tr>
<td>Other</td>
<td>32</td>
<td>12</td>
<td>0.38</td>
</tr>
<tr>
<td>Power</td>
<td>6</td>
<td>2</td>
<td>0.33</td>
</tr>
<tr>
<td>Richards</td>
<td>8</td>
<td>1</td>
<td>0.13</td>
</tr>
<tr>
<td>2-parameter VBGM</td>
<td>17</td>
<td>2</td>
<td>0.12</td>
</tr>
<tr>
<td>3-parameter Gompertz</td>
<td>40</td>
<td>4</td>
<td>0.10</td>
</tr>
<tr>
<td>Schnute</td>
<td>14</td>
<td>1</td>
<td>0.07</td>
</tr>
<tr>
<td>3-parameter Logistic</td>
<td>31</td>
<td>2</td>
<td>0.06</td>
</tr>
<tr>
<td>Generalized VBGM</td>
<td>10</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2-parameter Gompertz</td>
<td>6</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2-parameter Logistic</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Linear VBGM</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

2.2.2. Stock Assessments

In addition to my search of peer-reviewed literature and in order to evaluate trends in the use of growth models, model fit, and model selection among stock assessments in the United States, I searched the most recent stock assessments and compiled a dataset for species managed by NOAA regional fisheries management councils (FMC). I recorded information from the following FMC: Gulf of Mexico, Pacific, North Pacific, South Atlantic, and the Mid-Atlantic. I recorded the regional FMC, the year of the assessment, the species being assessed, the location of the stock assessment, the growth model(s) evaluated, and whether or not the assessment fit separate models for male and females. Once again from FishBase (Froese et al. 2017) I added the following information to the data, the adult diet of the species, the maximum age of the species, the system (e.g., fresh or marine), and the species’ family. I searched for stock assessments that have been conducted in freshwater systems but were unable to find any, although I recognize that
they have been done. All data and statistical analyses were performed in the open-source software R (R Core Team 2016).

2.3. Results

2.3.1. Peer-Reviewed Studies

I reviewed 196 peer-reviewed studies reporting use of a fish growth model published between 1988 and 2016 that met my criteria for inclusion. Only 14% of the studies I reviewed occurred before 2000. The most represented families were Scombridae and Sciaenidae (n=16 studies each), and the most represented species was albacore (*Thunnus alalunga*; n=4). About 60% of the studies were of piscivorous fish and nearly 75% were of marine species. The longest-lived species studied was orange roughy (*Hoplostethus atlanticus*) with a reported maximum age of 149 years. The mean maximum age of all fish studied was 31, and the median was 22.5. I performed a Poisson ANOVA and found no significant patterns of best-fit model as a function of maximum age (from FishBase). The geographic location with the most studies was North America (n=66), followed by Australia (n=36), and Europe (n=35). The most common estimation method was least squares (34%), while 32% of studies did not explicitly report their estimation method. Maximum likelihood and Bayesian estimation were explicitly reported in 15% and 2% of studies, respectively. Only 14% of studies added parameters to growth equations to model effects on growth, and 58% separated sexes for growth modeling.

2.3.1.1. Growth Modeling

The use of multi-model frameworks has been increasing, especially after the year 2000 (Figure 2.2). Aside from one outlier in 1992 (one study that evaluated 6 growth models), the annual
average inclusion of growth models increased from about 1 throughout the 1990s to 2.45 in 2016. Despite this increase in multi-model frameworks, only 42% of studies considered more than one candidate growth model (Figure 2.3). The largest number of models evaluated by one study was 7, and the mean number of models evaluated among all studies was 2 (median = 1).

Figure 2.2. Trends in the total number of age and growth studies (solid line), multi-model (≥ 2 models) studies (dashed line), and multi-model studies not including VBGM to be best fitting model (dotted line), based on peer-reviewed literature between 1988–2016.

Among all peer-reviewed studies, the most common models to be considered as candidate models were the 3-parameter VBGM (95% of studies), followed by the 3-parameter Gompertz model (21%), and the 3-parameter logistic model (16%). Some studies (22%) evaluated one or more candidate models that did not fall into my discrete categories (because of extremely low usage) and were thus classified as “other” (Figure 2.4).
Figure 2.3. Counts of the number of studies evaluating different numbers of growth models based on 196 peer-reviewed age and growth literature between 1988–2016.

2.3.1.2. Multi-Model Framework Studies

The 3-parameter VBGM was evaluated as a candidate model in 95% of multi-model framework studies \((n=83)\), compared to the 3-parameter Gompertz model (48%), the 3-parameter logistic model (37%), the Schnute model (17%), and the generalized VBGM and linear VBGM (12% each).

When multiple models were evaluated, the 3-parameter VBGM was selected as best-fit 37% of the time. The mean number of models evaluated for studies evaluating multiple models was 3.4 (median = 3). The families with the most multi-model framework studies were Sciaenidae \((n=9)\), Carcharhinidae \((n=6)\), Serranidae \((n=6)\), Scombridae \((n=5)\), and Rajidae \((n=4)\). The
species with the most multi-model framework studies was spotted seatrout (*Cynoscion nebulosus; n=3*).

Figure 2.4. Total number of times individual models were evaluated within 196 peer-reviewed studies from 1988–2016. Model types are clustered within a model family (e.g., Gompertz, Logistic), in which models are further described and where numbers correspond to parameters in a specific version of that model. *Other* (within the Other category) refers to models or model variations that had low usage and were, therefore, grouped together. Details of specific models can be found in Table 2.1.

Studies of species in marine systems tended to evaluate multiple models more frequently, with 48% (*n=71*) of studies in marine systems using a multi-model framework, compared to 20% (*n=8*) in freshwater systems. Marine studies also tended to evaluate a wider range of candidate models (Table 2.3). The number of models evaluated ranged from 1 to 7 in marine
systems (mean = 2.17, median = 1) and ranged from 1 to 6 in freshwater systems (mean = 1.52, median = 1).

Table 2.3. Best-fitting models by system type. Migratory refers to species living in both marine and freshwater systems in a single life cycle (e.g., catadromous and anadromous fishes). Specific refers to studies that found multiple models to be best-fitting based on sex, species, location, or some other factor.

<table>
<thead>
<tr>
<th></th>
<th>Fresh</th>
<th>Marine</th>
<th>Migratory</th>
</tr>
</thead>
<tbody>
<tr>
<td>Double VBGM</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Gompertz</td>
<td>1</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Linear Regression</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Logistic</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Power</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Schnute-Richards</td>
<td>0</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Seasonal VBGM</td>
<td>1</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Specific</td>
<td>1</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>VBGM</td>
<td>35</td>
<td>107</td>
<td>8</td>
</tr>
</tbody>
</table>

2.3.1.3. Multi-Model non-VBGM Studies

When multiple models were evaluated and the 3-parameter VBGM, or a variation of the VBGM was not selected as the best fitting model (n=19), the seasonal VBGM (n=5), Gompertz (n=4), and Schnute-Richards (n=4) models tended to be selected, while the logistic (n=2) and power (n=2) models, along with linear regression (n=2) tended to be selected for less (Table 2.2). Of the 3 spotted seatrout multi-model framework studies, 2 studies found that the VBGM was not the best fit model; this was the highest number of studies to find models other than the VBGM to be best fit for any one species. One spotted seatrout study found the Gompertz and linear regression to best fit females and males, respectively, and another study found the logistic growth model to be the best fit. The families demonstrating non-VBGM selected as best fit are Sciaenidae (n=5), Carcharhinidae (n=2), and Scombridae (n=2). Of the studies that found a model other than the VBGM (or variation) to be best fitting, 89% were in marine systems.
2.3.1.4. Model Selection

Among all peer-reviewed studies, 55% chose growth models \textit{a priori}. The 3-parameter VBGM (or variation) was used \textit{a priori} in 103 of 106 studies compared to one time each for linear regression, the seasonal VBGM, and a sinusoidal Schnute model. The family with the most \textit{a priori} use of growth models was Scombridae \((n=10)\); however, the \textit{a priori} use of growth models was also common for studies modeling the growth of multiple species (or families). In freshwater systems, 72% of studies used growth models \textit{a priori}, compared to just under 50% in marine environments. Of those studies using \textit{a priori} model selection, 42% did not report their estimation method.

Among peer-reviewed studies, 11% used GOF to select the best model. The most common GOF method was \(R^2\), followed by log-likelihood. The use of GOF has decreased over time, especially after 2008 (Figure 2.5). The \textit{a priori} use of growth models and GOF for model selection were common throughout the 1990s, but since then GOF methods of model selection have seen a sharp decline.

Some form of IT criteria was used for model selection by 28% of studies. AIC was the most common IT criteria for model selection, followed by AIC\(_c\). The first uses of IT criteria in my dataset occurred in 2002 (Imai et al. 2002; Porch et al. 2002). After that point, a marked increase in use of IT criteria is apparent (Figure 2.5). The first use of IT in my dataset was AIC, and since that time more complex IT methods such as AIC\(_c\), and Akaike weight have become more common in fisheries research. The two most common model selection methods today are \textit{a priori} and IT, although the use of \textit{a priori} model selection seems to be declining in recent years.
2.3.2. Stock Assessments

I also reviewed a total of 50 stock assessments that were the most up-to-date for each species. The results of this search were less variable than my search of peer-reviewed studies, with only three stock assessments using a model other than the traditional 3-parameter VBGM. The Pacific FMC used a Schnute parameterized version of the VBGM to model the growth of three species: kelp greenling (*Hexagrammos decagrammhus*), blue rockfish (*Sebastes mystinus*), and starry flounder (*Platichthys stellatus*), although it was not explicitly stated why that model was used. The most assessed family was Pleuronectidae (*n*=10, or 20% of total stock assessments). The regional FMC with the most stock assessments was by far the Pacific (*n*=20, or 40% of total stock assessments).
stock assessments), followed by the North Pacific (n=10, or 20% of total stock assessments). Sexes were separated for growth modeling in 66% of stock assessments I reviewed. Model selection was never mentioned in any of the stock assessments, thus all were assumed to be selected a priori.

2.4. Discussion

2.4.1. Growth Modeling

The use of multi-model frameworks in peer-reviewed fisheries studies has been increasing, especially since 2000. Marine systems have more multi-model framework studies, and also tend to evaluate a wider range of models. The maximum age, system, and diet of fish species appear to be only secondary (at best) factors in determining the best-fit model. However, species biology and growth are often specific and tends toward a specific growth function; therefore, it could be that within these grouping factors a sufficient diversity of growth forms prevents the emergence of strong patterns. Location also appears to not be a factor, although my results suggest that countries with more developed management infrastructure will have more complex modeling methods; however, I realize the bias toward North American studies in my sample which arises from my limitation to studies published in English. In many cases, studies in developing regions are more concerned in providing a baseline for fisheries in some given area and the VBGM is used due to ease of fitting and comparability to other studies. However, many studies have used the VBGM without any consideration of whether or not it is the best model to describe growth of a given species. In some cases, it may be because the VBGM is relatively easy to use, yields biologically meaningful parameters, and includes parameters that can be used in comparative studies. However, this is only true if the VBGM is a good fit, otherwise these
estimates will be unreliable. Therefore, I strongly suggest that unless the VBGM has previously been found to be the best fitting model for a species, multiple models should be considered. Furthermore, multi-model studies are becoming common in fisheries, which indicates that best fitting models for species are still being examined. If, in the future, we were to see the number of multi-model studies begin to decrease we may hypothesize that it is due to finding best fitting models for species rendering multi-model approaches less informative.

The families Sciaenidae, Scombridae, and Carcharhinidae appear to benefit most from the use of multi-model frameworks and model selection, meaning they are more frequently found to have models besides the VBGM selected as best fit. However, this may be because they were evaluated with more models than other families, and furthermore, it is unclear whether these studies resulted in more accurate size-at-age estimates, and ultimately better management. Smart et al. (2016) found that although multi-model framework studies are now common in elasmobranch studies, length-at-age estimates of 74 elasmobranch studies were only marginally affected by the approach, and the VBGM was equally likely to be best-fit as other candidate models. Furthermore, fixed-parameter models (categorized as ‘other’ in this study) are a common candidate model choice in chondrichthyan age and growth studies and varying degrees of support for this practice exist in the literature (Cailliet et al. 2006; Pardo et al. 2013).

There have been criticisms of how well growth models capture the plasticity of growth in nature (Lorenzen 2016). Because growth is variable by species and within species along gradients such as temperature, it seems logical to conclude that no one model—the VBGM—could accurately describe the growth of all fish species. However, I found it surprising that nearly half of the time the VBGM (or variation thereof) was selected as the best fitting model when multiple growth models were considered. Furthermore, despite the increase in multi-model
framework studies, there was no increase with time in non-VBGM models being determined to be better fit. This study excluded larval and juvenile studies, but a major criticism of the VBGM is that it does not model the first year of growth well, and the Gompertz model has been used to model the growth of young fish (Gamito 1998).

Although this study has found that the VBGM performs quite well in model selection routines, ample evidence still exists in support of multi-model approaches for modeling growth of fishes. When models are not considered, they cannot be selected (Katsanevakis 2006; Katsanevakis and Maravelias 2008), and it cannot be known if there is a better model to describe growth for a given stock or species. The seasonal VBGM tends to be selected for most among all growth models when the VBGM is not the best fitting, therefore the ability to improve growth modeling in fisheries may lie in incorporating seasonal variation in growth into commonly used growth models. The seasonal VBGM was suggested as being a strong candidate model for long-lived fish (Gamito 1998) and it has since been used to model the growth of economically important fish species such as red drum in Louisiana (Porch et al. 2002), sardine (Sardina pilchardus) in the Mediterranean and northeast Atlantic (Silva et al. 2008), and bonito (Sarda australis) in Australia (Stewart et al. 2013). Not only has the seasonal VBGM been shown to perform well on a variety of fish species, it is rooted in ecological and biological theory whereby fish grow faster in warmer conditions and slower in colder conditions.

2.4.2 Model Selection

Between 1988 and 2016, IT criteria emerged as the most common process by which to select growth models. Similar to the use of multi-model frameworks, the use of IT criteria increased beginning around 2000—corresponding to the publishing of Burnham and Anderson (1998)—
which advocated and popularized methods for the use of this IT approach. The use of IT criteria in fisheries also follows the general trend of other ecological fields (Guthery et al. 2005; Symonds and Moussalli 2011). With the increase in IT approaches, the most rapid decline was seen in GOF methods. This is likely due to advances in statistical programming packages that made it relatively easy to obtain AIC values for model comparison.

Statistical model selection in fisheries appears to have two dominant paradigms, GOF and IT. Despite this recent movement toward the use of IT criteria, there have been criticisms that the IT approach only amounts to a substitution of one statistical ritual for another and that ecology, not statistics should be at the forefront of all ecological studies (Guthery et al. 2005). Furthermore, the IT approach (specifically AIC) has been criticized because it considers model parsimony, such that models with fewer parameters will be preferentially selected (Pardo et al. 2013). However, others have argued for AIC biases in the opposite direction—such that more complex models (i.e., models with more parameters) are too often selected (see Ye et al. 2008). Zhu et al. (2009) compared six model selection approaches of fish growth models and found that AICc and BIC performed best for small and large data sets, respectively. Brewer et al. (2016) also found AICc and BIC to be the best model selection methods when unobserved heterogeneity was small and large, respectively, and suggested the use of multiple model selection methods.

2.4.3. Stock Assessments

Even though many growth models are available, it is rare for stock assessments to test multiple candidate models (Lorenzen 2016). This may be due in part to the software that is used to perform stock assessments. However, I found it surprising that NOAA regional FMC tended to use the VBGM almost exclusively a priori in stock assessments. Furthermore, the only
noticeable similarity between peer-reviewed studies and stock assessments regarding their approach to growth modeling, are that they both seem to separate sexes for growth modeling at a similar proportion (58% of peer-reviewed studies compared to 66% of stock assessments). Because growth can be stock-specific (widely distributed species’ life histories may vary), it seems unreasonable to expect that one growth model could accurately describe growth for all stocks. There may be unintended consequences if growth parameters are being estimated using the VBGM *a priori* and used to inform management decisions if there are better models to describe growth of a given species. I found three stock assessments for species that have peer-reviewed studies which showed a model other than the traditional VBGM to be best fit, gag grouper (*Mycteroperca microlepis*; Matthias et al. 2016), spiny dogfish (*Squalus acantbias*; Tribuzio et al. 2010), and red snapper (*Lutjanus campechanus*; Fischer et al. 2004), and would be interested in knowing if they have been evaluated or considered by fisheries managers. Those performing future stock assessments should consider evaluating additional candidate growth models to ensure that their estimates are as accurate as possible, and integrating various growth models, or environmental variation into stock assessment models may be an area of future research.

### 2.4.4. Conclusion

In studying historic and recent trends to fish growth modeling it was apparent that while some approaches remained constant over time (*a priori* use of VBGM), there is still a large amount of variability in how fisheries scientists evaluate growth. The current state of growth modeling in fisheries is dynamic, and is increasingly becoming more complex and statistically demanding as models are created that account for variability in growth due to a variety of factors (environment,
maturity, etc.; Kimura 2008; Ohnishi et al. 2012; Minte-Vera et al. 2016). It is likely that the next phase of fish growth modeling will move past multi-model approaches and focus on making the species-specific, best-fitting models more advanced. For example, hierarchical Bayesian models have recently appeared in the literature and have made advancements in growth comparisons (Helser and Lai 2004), changes in growth over time (He and Bence 2007), and accounting for spatial variability (Midway et al. 2015). Measurement-error models also show promise as a way to explicitly include observer (aging) error into growth models (Hatch and Jiao 2016).

Despite these statistical advances on the horizon, relatively little advancement has been made to incorporate growth models other than the VBGM into stock assessment models. Despite an increase in attempts to find better fitting models, the VBGM is often chosen as best fit and thus, this lack of advancement may be inconsequential to stock status. Additionally, from the perspective of long-term assessment, the benefit of the consistency of one model (VBGM) over time may outweigh the cost of not using the best fitting model for a shorter time. More accurate estimates of growth improve management and protection of stocks for the future, and thus, we should always be evaluating new models, regardless of whether or not these new models will ultimately be used in stock assessments and the decision-making process of fisheries managers.

2.5. References


CHAPTER 3. MULTI-MODEL EVALUATION OF SCIAENID GROWTH 
IN THE GULF OF MEXICO

3.1. Introduction

Many members of the family Sciaenidae are economically and culturally important across their range, and as a result their age and growth has been heavily studied. Sciaenids, specifically black drum (Pogonias cromis), red drum (Sciaenops ocellatus), and spotted seatrout (Cynoscion nebulosus), are estuarine dependent species that inhabit estuaries and nearshore coastal environments along the Gulf of Mexico (GoM) and Atlantic coasts. They are among the most popular recreationally targeted species throughout their range and are primarily managed individually by states. Pearson (1929) was the first to describe the age and growth of sciaenids in Texas and since then they have been the subject of many age and growth studies (see Appendix A). Additionally, because of heavy exploitation in the commercial and recreational fisheries, many sciaenid species have a long history of regulation and management.

In the GoM, red drum was one of the first species to be designated as overfished, a designation that occurred in 1987. Since that designation, the harvest of red drum in federal waters of the GoM has been prohibited and the majority of red drum landings take place in state waters by the recreational sector (Murphy and Crabtree 2001). Of the three species considered here, black drum receives the least targeted recreational fishing pressure; however, black drum harvest (commercial and recreational) did increase in the mid-1980s as a response to the red drum harvest reductions (Beckman et al. 1990). Black drum currently supports important commercial fisheries in the GoM, with the majority of commercial landings occurring in Louisiana and Texas state waters (LDWF 2015), although black drum is also available for commercial harvest in federal waters. Commercial harvest of spotted seatrout is permitted in Louisiana, although landings fell sharply in 1997 after gear restrictions banning nets designated
the fishery as rod-and-reel only (West et al. 2014). In Texas, commercial harvest of spotted seatrout is not permitted and currently the majority of spotted seatrout landings in Louisiana and Texas occur in the recreational fishery.

Age and growth data and growth modeling are important to fisheries stock assessment and regulation; outside of recruitment, growth of individuals (increase in length or weight) is the major source of gains to biomass of populations (Haddon 2001). Age and growth data are typically estimated using calcified-structures (e.g. otoliths, spines, etc.) and length and/or weight measurements. Growth models are fit to these data and estimates of size-at-age are obtained, which are used by fisheries managers to create size limits, creel limits, and other regulatory decisions. Typically, because fishes have indeterminate growth, non-linear models are used to model the growth of fish in size with age; however, linear models have also been used (Nieland et al. 2002; Curtis and Shima 2005). The von Bertalanffy growth model (VBGM; Beverton and Holt 1957) has historically been the most widely used growth model since its introduction to fisheries, yet other growth models exist that have been shown to fit length-at-age better than the VBGM for some species. Because estimates of growth are used to manage fisheries populations, reducing uncertainty and improving model fit is of critical importance to fisheries managers.

Growth models must be a good fit statistically but also must make biological and ecological sense given the species of interest. Life histories are an important factor that shapes the trajectory of growth; therefore, the selection of candidate growth models should represent not just a best fit to the data, but an interpretable fit to a species’ life history. Black and red drum life histories are similar in that they spend their juvenile phase in estuaries before leaving for the open ocean (Richards 1973; Murphy and Taylor 1990). Both black and red drum are estimated to have a maximum age around 50–60 years (Murphy and Taylor 1989; Ross et al. 1995). Black
and red drum are unique species in that they grow and mature quickly (usually within 2–6 years) and are long-lived (Murphy and Taylor 1990; Jones and Wells 1998). Of the three species considered in this study, spotted seatrout are the shortest lived, with an estimated maximum age of 18 years (Froese et al. 2017). Spotted seatrout live their entire lives within their natal estuaries and adjacent coast lines, and do not travel far in their lifetime (Iversen and Tabb 1962; Walters et al. 2009). Spotted seatrout mature by the first summer after hatching and females are known to grow faster and be larger-at-age than males (Nieland et al. 2002).

Despite the VBGM being the most widely used growth model in fisheries, previous studies have shown that the VBGM is a poor fit for red drum (Ross et al. 1995; Porch et al. 2002) and spotted seatrout (Murphy and Taylor 1994; Nieland et al. 2002; Dippold et al. 2016) length-at-age data as well as other sciaenids (Gulf corvina Cynoscion othonopterus; Aragon-Noriega 2014). Although previous black drum length-at-age studies have not extensively evaluated multiple growth models for fit, no growth model has been shown to be a better-fit for black drum than the traditional VBGM. Because black and red drum are similar in their life history—which includes a distinct juvenile phase in estuaries and a distinct adult phase offshore—a seasonal or biphasic variation of the VBGM may be appropriate to model length-at-age of black drum, as has been shown with red drum.

Spotted seatrout length-at-age data are often fit best by sigmoidal or linear models, and of the three species considered here, spotted seatrout has perhaps the most variable growth across the GoM. For example, the logistic model was found to be better fitting than the two parameter VBGM, three parameter VBGM, and Gompertz model in Mississippi (Dippold et al. 2016), a linear model was used to model growth in Barataria Bay, Louisiana (Nieland et al. 2002), and sex-specific growth models were best-fitting in Florida, in which females were best modeled by
the Gompertz model, and males by linear regression from a suite of candidate models including the Schnute model (Schnute 1981), generalized VBGM, Gompertz, VBGM, and linear regression (Murphy and Taylor 1994). Because spotted seatrout are limited in their lifetime movements and are comprised of many different stocks across GoM estuaries (Iversen and Tabb 1962; Baker and Matlock 1993), the trajectory of growth and best-fitting growth model may differ even between nearby estuaries (Bortone 2003).

At least 15 or more commonly used growth models (and countless parameterizations) can be found in the literature (see Chapter 2), necessitating a need for some type of model selection criteria when evaluating multiple growth models. To aid in choosing the best-fit growth model, model selection using Information Theoretic Criterion has emerged as one way to choose the best-fitting model and today is the dominant practice in fisheries science (see Chapter 2). Information theoretic criteria such as Akaike Information Criterion (AIC; Akaike 1973), and Bayesian Information Criterion (BIC; Schwarz 1978) have become common in fisheries age and growth studies for choosing the best-fitting growth model. Additional fitting practices such as multi-model inference (MMI) and model-averaging using Akaike weights have shown promise with sciaenid species (Aragon-Noriega 2014; Aragon-Noriega et al. 2015) and have been suggested as a way to make robust parameter estimates and reduce uncertainty (Katsanevakis 2006; Katsanevakis and Maravelias 2008).

Growth modeling is an integral part of stock management and errors in growth estimates can cause problems when included in stock assessments and other models. Therefore, multiple models should be evaluated for fit, rather than relying on one model (e.g. the traditional VBGM). Age and growth studies that use multiple models and model selection make robust parameter estimates and reduce the uncertainty surrounding the estimates of growth models (Katsanevakis
Due to the significant economic, recreational, and cultural importance of sciaenids in the GoM, reducing the uncertainty surrounding the use of growth models and resulting estimates of growth is of critical value to fisheries managers. The objectives of this study are: (1) to determine the best-fitting growth model(s) for black drum, red drum, and spotted seatrout length-at-age data from the western GoM (Louisiana and Texas); and (2) to evaluate the spatial and sex-specific variation among growth parameter estimates.

3.2. Methods

3.2.1. Data

In order to evaluate the variation in goodness-of-fit of growth models among sciaenids across the western GoM, I used data collected from fisheries-independent sampling programs led by the Louisiana Department of Wildlife and Fisheries (LDWF) and the Texas Parks and Wildlife Department (TPWD). Data were available from a variety of gears; however, to reduce the effect of gear selectivity I only used fish collected from fishery-independent experimental gill net surveys (see Appendix C). In Louisiana, a 228.6-m long experimental monofilament gill net is used to sample finfish. The net is 2.4 m in depth and composed of five 45.7 m long panels of 51, 64, 76, 89, and 102 mm stretch mesh (LDWF 2002). In Texas, a 183-m long experimental monofilament gill net is used to sample finfish. The net is 1.2 m in depth and composed of four 45.7 m panels of 76, 102, 127, and 152 cm stretch mesh (Matich et al. 2017). Sample sizes of fish varied by species and state as well as differed in the years collected (see Appendix A).

At the time of capture, all fish were measured to total length (TL in mm) or fork length (FL in mm) and sexed by macroscopic examination of gonads. Otoliths were extracted and processed, and ages were estimated (for full details see GSMFC, 2009). Multiple readers were
used (to reduce reader bias and improve accuracy of age estimates) to estimate age classes by counting otolith annuli using one of the sagittal otoliths (GSMFC, 2009). Biological ages were then calculated based on the completed month prior to capture and assumed birthdates. In both states, black drum are assumed to have a April 1 birthdate, red drum a October 1 birthdate, and spotted seatrout a July 1 birthdate. Biological ages could not be calculated for Texas red drum or Texas spotted seatrout because these fish have stocking programs in Texas; thus an individual fish of the same age class may be significantly larger or smaller based on whether or not it was a hatchery-raised fish. For these two datasets, the whole age was used to model growth.

The three variables of interest were length, age, and sex. Weight was not available in the Texas data and was recorded inconsistently in the Louisiana data. Therefore, it was not analyzed. Although most lengths were recorded as total length (TL), some were recorded as fork length (FL). Regulations for these three species are set in TL; therefore, I converted FL to TL with the following equations.

Spotted Seatrout: TL (in.) = 1.0008 * FL (in.) + 0.6306 (Joe West, LDWF, personal comm.)
Black Drum: TL (mm) = 1.03 * FL (mm) – 3.8 (Murphy and Taylor 1989)
Red Drum: TL (in.) = 1.092 * FL (in.) – 1.01 (Goodyear 1996)

Furthermore, from my data, outliers that exceeded three times the standard deviation of the mean length-at-age (biological age and whole age when biological age was not available) were excluded. Removal of these data excluded observations that seemed biologically unreasonable; i.e., fish that appeared too large or too small for their age class. Because otolith aging is not always 100% accurate, it is not unreasonable to assume that some aging error has
occurred. Thus, by removing these extreme data points we can be more confident in the aging process that has generated these data. The percentage of outliers removed from the original data represented \( n < 1\% \) for all data sets.

Because Texas does not sacrifice any old, large black or red drum, length-at-age data for Texas does not exist beyond a certain size (approximately 630 mm TL for black drum and approximately 780 mm TL for red drum). Attempts were made to determine if any length-at-age data existed for older fishes in Texas—including inquiries to agency personnel and university researchers—but no data were found. Lack of older, larger fish may affect model fitting and therefore, the resulting parameter estimates. As a solution to minimize any potential model fitting effects, I subset very large, old fish from the Louisiana data to add to the Texas data, in order to inform maximum asymptotic size. Data were added to TX for age classes that had reached 98\% of the \( L_\infty \) estimates from my Louisiana VBGM estimates.

Although borrowing data from another region is not ideal, it can be justified because these fish all come from the same GoM stock (Jones and Wells 1998; Seyoum et al. 2000). In other words, older black and red drum are known to move throughout the GoM (Gold and Turner 2002), which may be obscuring local influences on maximum average size. Little is known about the adult black and red drum stocks and this is especially true in regard to natal homing; however, adult red drum are thought to be highly mobile because tagged fish have been recaptured more than 700 km from their original tagging location (Powers et al. 2012). Thus, to improve the contrast in the data, I included old, large black and red drum from Louisiana in the Texas data. The addition of Louisiana black drum female data accounted for 10\% of the total data used to estimate growth of Texas black drum females, while the addition of Louisiana black drum male data accounted for 6\% of the total data used to estimate growth of Texas black drum
males. The addition of Louisiana red drum female data accounted for 2% of the total data used to estimate growth of Texas red drum females and the addition of Louisiana red drum male data also accounted for 2% of the total data used to estimate growth of Texas red drum males. In recognition of the fact that old, large fish can influence the fit of a model, the proportion of borrowed sample was limited to \( \leq 10\% \) for any given data set.

3.2.2. Models and model justification

All growth models were fitted to observed length-at-age data in \( R \) (R Core Team 2016) using the \textit{nls} function, which estimates parameters by least squares. Dimorphic growth between sexes of each species and state was assessed by comparing the pooled sex AIC score with the sum of the sex-specific AIC scores. Additionally, model parameters were evaluated by comparing the \( L_\infty \) parameter estimates and 95% confidence intervals (\( \pm 1.96 \times \) standard error) for the best-fit models.

Candidate growth models and the parameter explanations are given in Table 3.1. The VBGM (Beverton and Holt 1957), Gompertz (Ricker 1975), and logistic (Ricker 1979) models were fit to all three species because they represent the three most commonly used growth models in fisheries (see Chapter 2). Thus, they estimate parameters that are the most comparable with previous studies. Generally, the VBGM represents growth as asymptotic, while the Gompertz and logistic models represent growth as sigmoidal.

For black and red drum the double VBGM (Vaughan and Helser 1990; Ross et al. 1995; Porch et al. 2002) was fit to observed length-at-age data. Unlike the VBGM which estimates a single growth rate parameter (\( k \)), the double VBGM allows the rate at which an organism approaches the asymptotic length to change after some pivotal age, \( t_p \). The double VBGM
accommodates the possibility that older, larger fish might grow more slowly in proportion to their length than younger, smaller fish (Porch et al. 2002). The double VBGM, and other

Table 3.1. Candidate models for sciaenid growth modeling in Chapter 3. Model 1= 3-parameter VBGM; 2= 3-parameter Gompertz, 3= 3-parameter logistic, 4= double VBGM, 5= seasonal VBGM, and 6= power model.

<table>
<thead>
<tr>
<th>Model</th>
<th>Model equation</th>
<th>Parameter description</th>
</tr>
</thead>
</table>
| 1     | \( L(t) = L_\infty (1 - e^{-k_1(t-t_0)}) \) | \( L_\infty = \text{asymptotic length} \)
|       |                | \( t = \text{age} \)
|       |                | \( L_{t0} = \text{length-at-age, \( t \)} \)
|       |                | \( k_1 = \text{Brody growth parameter} \)
|       |                | \( t_0 = \text{age at zero length} \)
|       |                | \( k_2 = \text{rate of exponential decrease of relative growth with age} \)
|       |                | \( t_1 = \text{parameter produced during deduction of model} \)
| 2     | \( L(t) = L_\infty e^{-e^{-k_2(t-t_1)}} \) | \( k_3 = \text{relative growth rate parameter} \)
| 3     | \( L(t) = \frac{L_\infty}{1 + e^{-k_3(t-a)}} \) | \( \alpha = \text{inflection point of the sigmoid curve} \)
|       | \( L(t) = \begin{cases} 
L_\infty (1 - e^{-k_4(t-t_2)}) & \text{if } t < t_p \\
L_\infty (1 - e^{-k_5(t-t_3)}) & \text{if } t > t_p 
\end{cases} \) | \( k_4, k_5 = \text{instantaneous growth rate coefficients} \)
| 4     | \( t_p = \frac{(k_5 t_3 - k_4 t_2)}{(k_5 - k_4)} \) | \( t_p = \text{‘pivotal age’} \)
|       | \( t_2, t_3 = \text{age intercept parameters} \)
|       | \( c = \text{amplitude of oscillations ranging between 0 and 1} \)
| 5     | \( L(t) = L_\infty \left\{ 1 - e^{-k_1(t-t_0)-\frac{c}{2\pi}[\sin 2\pi(t-t_5)-\sin 2\pi(t_0-t_5)]} \right\} \) | \( t_s = \text{the summer point or when growth rate is maximized ranging between 0 and 1} \)
|       |                | \( t_5 = \text{the summer point or when growth rate is maximized ranging between 0 and 1} \)
|       |                | \( a_0 = y\text{-intercept or the mean length at age 0} \)
| 6     | \( L(t) = a_0 + a_1 t^b \) | \( a_0, b = \text{parameters that describe the shape of the curve but have no biological interpretation} \)
biphasic growth models have been shown to be a good fit for species that experience a change in growth rate due to maturation, habitat shift, or ontogenetic shift (Wilson et al. 2018). The inclusion of this model as a candidate model is biologically justified because black and red drum experience rapid growth up to about age 3–6 (prior to maturation; Murphy and Taylor 1990; Jones and Wells 1998), after which their growth rate decreases substantially. Furthermore, after black and red drum mature within their natal estuaries, they change their habitat from estuaries to open ocean; this substantial change in habitat may also influence their growth by changing energetic demands and prey sources. The double VBGM was not evaluated for fit with spotted seatrout. It is unlikely that spotted seatrout experience a sudden shift in growth rate because they mature quickly, usually within their first year (Nieland et al. 2002) and do not change their habitat preference with age. Furthermore, spotted seatrout have previously been modeled with linear models (e.g., constant growth rate with age); thus, a double VBGM was not hypothesized to provide a better fit to length-at-age data for this species.

To accommodate the possibility that fish grow at different rates seasonally, a seasonal VBGM equation (Gayanilo and Pauly 1997; Haddon 2001; Stewart et al. 2013) was evaluated for all three species. Porch et al. (2002) developed a seasonal growth model similar to the VBGM that, according to AIC, fit red drum length-at-age data better than the traditional VBGM and suggested it may be appropriate to describe growth for species that change habitat preference with age or are subject to strong seasonal environmental fluctuations. Because black drum are similar in their life history and habitat preference to red drum (they live as juveniles in estuaries before maturing and moving offshore to join the adult population), a seasonal VBGM may also be appropriate and improve model fit. Likewise, spotted seatrout generally live their entire lives within estuaries and adjacent coast lines (Iversen and Tabb 1962); thus, they are likely to exhibit
seasonal variation in growth due to changing environmental conditions within estuaries. Additionally, considering spotted seatrout are shorter-lived than black or red drum, a given year or season may be more influential than for a long-lived species like black and red drum.

Lastly, I evaluated the power model (Katsanevakis and Maravelias 2008) for fit with spotted seatrout length-at-age data. This model was chosen because a wide range of models have been shown to be of good fit for spotted seatrout (see Appendix A), and the power model is a flexible growth model that can accommodate both linear and non-linear growth trajectories. Considering that spotted seatrout growth has been represented previously with both linear and non-linear models, the power model is a good candidate model. To the best of my knowledge, the power model has not been evaluated by any spotted seatrout age and growth study to date. However, power models have been shown to be a good fit for juvenile black drum (Beckman et al. 1990), as well as other sciaenids, such as Spotfin Croaker *Roncador stearnsii* (Williams et al. 2012).

### 3.2.3. Model selection

Two methods of model selection were used to select the best-fitting model. The first method is to choose one single best-fitting model based on AIC. Models that have the lowest AIC values are considered to be the best-fit to the data. Models that have a score difference (Δ AIC) of Δ > 10 have virtually no support and can be removed from further consideration (Burnham and Anderson 2002). Models with Δ < 2 have substantial support, and those models with 4 < Δ < 7 have marginal support (Burnham and Anderson 2002).

The second model selection method is to perform a MMI by model-averaging the parameter estimates based on Akaike weight (Burnham and Anderson 2002; Katsanevakis 2006;
Katsanevakis and Maravelias 2008). Akaike weights are interpreted as the weight of evidence in favor of a model being the actual best model from a set of candidate models (Burnham and Anderson 2002; Katsanevakis 2006; Katsanevakis and Maravelias 2008). Akaike weights are normalized across the set of candidate models to sum to one and are interpreted as probabilities, such that when a model has an Akaike weight equal to one it is completely supported by the data, whereas models with approximately equal weights have a similar level of support (Johnson and Omland 2004). Akaike weights are used for model averaging by weighting the model-specific estimates by the Akaike weight given to each model. Because the interpretation of \( k \) (growth coefficient) is relative to the growth model, it cannot be model-averaged accurately. Therefore, in the current study I can only model-average the \( L_\infty \) estimates. The \texttt{MuMI} package (Bartoń 2016) in R was used to calculate Akaike weights, based on AIC.

3.3. Results

My data included 1,251 black drum, 3,874 red drum, and 14,414 spotted seatrout from Louisiana and Texas that were sampled between 1989 and 2015. Age of black drum ranged from 0.5–41.6 years (mean = 4.8 years), red drum from 0–37.4 years (mean = 1.9), and spotted seatrout from 0–10 years (mean = 2.1). Sample sizes of fish varied by species and state and differed in the years collected. For a detailed sample description see Appendix A.

3.3.1. Black Drum

3.3.1.1 Louisiana Data

The growth of Louisiana black drum was sexually dimorphic (Figure 3.1). AIC indicated a better fit to sex-specific models than the pooled sex data (Table 3.2). The best-fit model for females
Table 3.2. AIC and Akaike weight for models fit to black drum length-at-age data. Best-fit model is in bold.

<table>
<thead>
<tr>
<th>State</th>
<th>Sex</th>
<th>Model name</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>LA</td>
<td>Combined</td>
<td>VBGM</td>
<td>9009.08</td>
<td>66.26</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>9057.48</td>
<td>114.66</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>9100.50</td>
<td>157.68</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>8998.24</td>
<td>55.42</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Double VBGM</td>
<td>8942.83</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>LA</td>
<td>Female</td>
<td>VBGM</td>
<td>5042.89</td>
<td>32.04</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>5062.98</td>
<td>52.12</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>5081.03</td>
<td>70.18</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>5024.32</td>
<td>13.46</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Double VBGM</td>
<td>5010.85</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>LA</td>
<td>Male</td>
<td>VBGM</td>
<td>3075.13</td>
<td>19.14</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>3091.31</td>
<td>35.32</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>3105.68</td>
<td>49.69</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>3077.39</td>
<td>21.40</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Double VBGM</td>
<td>3055.99</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>TX</td>
<td>Combined</td>
<td>VBGM</td>
<td>6129.04</td>
<td>44.70</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>6166.78</td>
<td>82.44</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>6196.85</td>
<td>112.51</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>6129.83</td>
<td>45.49</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Double VBGM</td>
<td>6084.34</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>TX</td>
<td>Female</td>
<td>VBGM</td>
<td>3277.26</td>
<td>59.59</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>3288.67</td>
<td>71.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>3298.85</td>
<td>81.18</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>3277.72</td>
<td>60.05</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Double VBGM</td>
<td>3217.67</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>TX</td>
<td>Male</td>
<td>VBGM</td>
<td>2850.73</td>
<td>112.31</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>2874.11</td>
<td>135.69</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>2891.05</td>
<td>152.63</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>2853.91</td>
<td>115.49</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Double VBGM</td>
<td>2738.42</td>
<td>0.00</td>
<td>1.00</td>
</tr>
</tbody>
</table>

was the double VBGM and parameter estimates (standard error, SE) were $L_\infty$ (mm) = 903.3 (13.40), $k_1 = 0.23$ (0.03), $k_2 = 0.13$ (0.01), $t_1 = -0.34$ (0.24), $t_2 = -2.57$ (0.34). The best-fit model for males was also the double VBGM and parameter estimates (SE) were $L_\infty$ (mm) = 1087.5.
(115.80), $k_1 = 0.11 (0.02), k_2 = 0.04 (0.02), t_1 = -1.94 (0.30), t_2 = -20.39 (9.90)$. Observed length-at-age and fitted growth curves are shown in Figure 3.2. Females attained a smaller asymptotic size and grew at a faster rate than males. Females reached 68% of $L_\infty$ at age-6 and

Figure 3.1. Growth model parameter estimates ($L_\infty$ and $k$) and 95% confidence intervals for black drum female and male from Louisiana and Texas. The $k_1$ estimate represents the juvenile growth phase and the $k_2$ estimate represents the adult phase growth coefficient.

95% of $L_\infty$ at age-20. Males reached 59% of $L_\infty$ by age-6 and 79% of $L_\infty$ by age-20. Parameter estimates for all candidate models are given in Table 3.3. The two best-fit models had 100% support by Akaike weight. For females, the second ranked model was the seasonal VBGM and for males, the second ranked model was the traditional VBGM. For both sexes, the VBGM outperformed the Gompertz and logistic models.
Figure 3.2. Observed black drum length-at-age and best-fit growth curves for Louisiana (top panel) and Texas (bottom panel). Female = red circle points and solid line, Male = blue triangle points and dotted line. All fitted growth curves are the double VBGM. Texas data borrowed from LA are data points > age-20.

3.3.1.2. Texas Data

The addition of Louisiana black drum female data accounted for 10% of the total data used to estimate growth of Texas black drum females, while the addition of Louisiana black drum male data accounted for 6% of the total data used to estimate growth of Texas black drum males.

Growth of Texas black drum was also sexually-dimorphic (Figure 3.1). AIC also indicated a better fit to sex-specific models than the pooled sex data (Table 3.2). Of the five candidate growth models, the best-fitting model for both the female and male data was also the double VBGM and parameter estimates (SE) were $L_\infty$ (mm) = 1252 (92.10), $k_1 = 0.076$ (0.01), $k_2 = 0.033$ (0.006), $t_1 = -1.72$ (0.01), $t_2 = -8.21$ (1.00) for females, and were $L_\infty$ (mm) = 1117
(55.80), $k_1 = 0.099 (0.008)$, $k_2 = 0.054 (0.010)$, $t_1 = -1.25 (0.16)$, $t_2 = -3.29 (1.31)$ for males.

Observed length-at-age and fitted growth curves are shown in Figure 3.2. Females reached 38% of $L_\infty$ at age-6 and 61% of $L_\infty$ at age-20, while males reached 39% of $L_\infty$ at age-6 and 72% of $L_\infty$ at age-20. The double VBGM also had 100% support by Akaike weight for both sexes. The traditional VBGM was ranked second among the candidate growth models and the logistic model was ranked last. The seasonal VBGM did not reach convergence for the female or male data.

Table 3.3. Black drum growth model parameter estimates (and SE) for all candidate models from Louisiana and Texas. Bold text indicates the best-fit model as determined by AIC. Model 1= VBGM, 2= Gompertz, 3= logistic, 4= double VBGM, and 5= seasonal VBGM.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>LA female</th>
<th>LA male</th>
<th>TX female</th>
<th>TX male</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$L_\infty$</td>
<td>876.5 (10.7)</td>
<td>929.0 (14.1)</td>
<td>1039 (30.1)</td>
<td>1051 (27.1)</td>
</tr>
<tr>
<td></td>
<td>$k$</td>
<td>0.18 (0.01)</td>
<td>0.15 (0.01)</td>
<td>0.06 (0.01)</td>
<td>0.07 (0.01)</td>
</tr>
<tr>
<td>2</td>
<td>$L_\infty$</td>
<td>860.0 (9.7)</td>
<td>906.1 (12.5)</td>
<td>971.2 (19.3)</td>
<td>999.6 (19.4)</td>
</tr>
<tr>
<td></td>
<td>$k$</td>
<td>0.26 (0.01)</td>
<td>0.22 (0.01)</td>
<td>0.10 (0.01)</td>
<td>0.11 (0.01)</td>
</tr>
<tr>
<td>3</td>
<td>$L_\infty$</td>
<td>849.3 (9.2)</td>
<td>891.3 (11.8)</td>
<td>938.9 (15.0)</td>
<td>978.3 (16.6)</td>
</tr>
<tr>
<td></td>
<td>$k$</td>
<td>0.34 (0.02)</td>
<td>0.30 (0.02)</td>
<td>0.14 (0.01)</td>
<td>0.15 (0.01)</td>
</tr>
<tr>
<td>4</td>
<td>$L_\infty$</td>
<td>903.3 (13.4)</td>
<td>1087.5 (115.8)</td>
<td>1252 (92.1)</td>
<td>1117 (55.8)</td>
</tr>
<tr>
<td></td>
<td>$k_1$</td>
<td>0.23 (0.03)</td>
<td>0.11 (0.02)</td>
<td>0.08 (0.01)</td>
<td>0.10 (0.01)</td>
</tr>
<tr>
<td></td>
<td>$k_2$</td>
<td>0.13 (0.01)</td>
<td>0.04 (0.02)</td>
<td>0.03 (0.01)</td>
<td>0.05 (0.01)</td>
</tr>
<tr>
<td></td>
<td>$t_p$</td>
<td>2.58</td>
<td>7.73</td>
<td>3.35</td>
<td>1.18</td>
</tr>
<tr>
<td>5</td>
<td>$L_\infty$</td>
<td>877.9 (10.5)</td>
<td>928.2 (14.0)</td>
<td>1040 (31.4)</td>
<td>1054 (28.0)</td>
</tr>
<tr>
<td></td>
<td>$k$</td>
<td>0.18 (0.01)</td>
<td>0.15 (0.01)</td>
<td>0.06 (0.01)</td>
<td>0.07 (0.01)</td>
</tr>
</tbody>
</table>

3.3.2 Red Drum

3.3.2.1 Louisiana Data

Growth of Louisiana red drum was sexually dimorphic (Figure 3.3). AIC indicated a better fit to sex-specific models than the pooled sex data (Table 3.4) The best-fit model for both sexes was the double VBGM. For females, parameter estimates (SE) were, $L_\infty$ (mm) = 1059 (12.58), $k_1 =$
0.26 (0.008), \( k_2 = 0.179 \) (0.018), \( t_1 = -0.55 \) (0.059), \( t_2 = -1.98 \) (0.51). For males, parameter estimates (SE) were, \( L_\infty \) (mm) = 1018.9 (17.41), \( k_1 = 0.27 \) (0.01), \( k_2 = 0.15 \) (0.02), \( t_1 = -0.51 \) (0.05), \( t_2 = -3.36 \) (0.87). Observed length-at-age and fitted growth curves are shown in Figure 3.4. Females attained a larger asymptotic size and grew at a slower rate than males. Females reached 65% of \( L_\infty \) at age-4 and 88% of \( L_\infty \) at age-10. Males reached 67% of \( L_\infty \) by age-4 and 86% of \( L_\infty \) by age-10. Parameter estimates for all candidate models are given in Table 3.5. The two best-fit models had 100% support by Akaike weight. The seasonal VBGM was ranked second among candidate models and the VBGM outperformed the Gompertz and logistic models for both females and males.
Table 3.4. AIC and Akaike weight for models fit to red drum length-at-age data. Best-fit model is in bold.

<table>
<thead>
<tr>
<th>State</th>
<th>Sex</th>
<th>Model name</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>LA</td>
<td>Combined</td>
<td>VBGM</td>
<td>27767.11</td>
<td>132.97</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>27905.84</td>
<td>271.70</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>28050.45</td>
<td>416.31</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>27695.80</td>
<td>61.66</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td><strong>Double VBGM</strong></td>
<td><strong>27634.14</strong></td>
<td><strong>0.00</strong></td>
<td><strong>1.00</strong></td>
</tr>
<tr>
<td>LA</td>
<td>Female</td>
<td>VBGM</td>
<td>12160.98</td>
<td>49.65</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>12202.56</td>
<td>91.23</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>12249.07</td>
<td>137.75</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>12133.90</td>
<td>22.57</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td><strong>Double VBGM</strong></td>
<td><strong>12111.33</strong></td>
<td><strong>0.00</strong></td>
<td><strong>1.00</strong></td>
</tr>
<tr>
<td>LA</td>
<td>Male</td>
<td>VBGM</td>
<td>13682.48</td>
<td>51.98</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>13732.08</td>
<td>101.58</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>13786.99</td>
<td>156.50</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>13657.32</td>
<td>26.82</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td><strong>Double VBGM</strong></td>
<td><strong>13630.49</strong></td>
<td><strong>0.00</strong></td>
<td><strong>1.00</strong></td>
</tr>
<tr>
<td>TX</td>
<td>Combined</td>
<td>VBGM</td>
<td>16349.50</td>
<td>43.33</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>16364.73</td>
<td>58.57</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>16412.61</td>
<td>106.45</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td></td>
<td></td>
<td><strong>Double VBGM</strong></td>
<td><strong>16306.17</strong></td>
<td><strong>0.00</strong></td>
<td><strong>1.00</strong></td>
</tr>
<tr>
<td>TX</td>
<td>Female</td>
<td>VBGM</td>
<td>9322.39</td>
<td>48.35</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>9330.76</td>
<td>56.72</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>9360.09</td>
<td>86.05</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td></td>
<td></td>
<td><strong>Double VBGM</strong></td>
<td><strong>9274.04</strong></td>
<td><strong>0.00</strong></td>
<td><strong>1.00</strong></td>
</tr>
<tr>
<td>TX</td>
<td>Male</td>
<td>VBGM</td>
<td>7025.89</td>
<td>10.87</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>7032.56</td>
<td>17.54</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>7051.42</td>
<td>36.40</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td></td>
<td></td>
<td><strong>Double VBGM</strong></td>
<td><strong>7015.02</strong></td>
<td><strong>0.00</strong></td>
<td><strong>1.00</strong></td>
</tr>
</tbody>
</table>
Figure 3.4. Observed red drum length-at-age and best-fit growth curves for Louisiana (top panel) and Texas (bottom panel). Female = red circle points and solid line, Male = blue triangle points and dotted line. All fitted growth curves are the double VBGM. Texas data borrowed from LA are data points > age-10.

3.3.2.2. Texas Data

The addition of Louisiana red drum female data accounted for 2% of the total data used to estimate growth of Texas red drum females and the addition of Louisiana red drum male data also accounted for 2% of the total data used to estimate growth of Texas red drum males.

Growth of Texas red drum was also sexually-dimorphic (Figure 3.3). AIC also indicated a better fit to sex-specific models than the pooled sex data (Table 3.4). The best-fitting model for both sexes was also the double VBGM and parameter estimates (SE) were \( L_\infty (\text{mm}) = 1111.4 \) (29.20), \( k_1 = 0.184 \) (0.01), \( k_2 = 0.096 \) (0.017), \( t_1 = -1.95 \) (0.09), \( t_2 = -6.29 \) (1.25) for females, and \( L_\infty (\text{mm}) = 1035.6 \) (25.90), \( k_1 = 0.224 \) (0.011), \( k_2 = 0.125 \) (0.032), \( t_1 = -1.75 \) (0.07), \( t_2 = -
4.80 (1.73) for males. Observed length-at-age and fitted growth curves are shown in Figure 3.4. Females reached 63% of $L_\infty$ at age-4 and 79% of $L_\infty$ at age-10. Males reached 67% of $L_\infty$ at age-4 and 84% of $L_\infty$ at age-10. For both sexes, the double VBGM also had 100% support by Akaike weight. The traditional VBGM was ranked second among the candidate growth models and the logistic model was ranked last. The seasonal VBGM did not reach convergence for females or males.

Table 3.5. Red drum growth model parameter estimates (and SE) for all candidate models from Louisiana and Texas. Bold text indicates what model was found to be best-fit as determined by AIC. Non-convergence = NC. Model 1= VBGM, 2= Gompertz, 3= Logistic, 4= Double VBGM, and 5= Seasonal VBGM.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>LA female</th>
<th>LA male</th>
<th>TX female</th>
<th>TX male</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$L_\infty$</td>
<td>1034 (10.7)</td>
<td>974.9 (13.1)</td>
<td>1052 (11.9)</td>
<td>1003 (14.3)</td>
</tr>
<tr>
<td></td>
<td>$k$</td>
<td>0.24 (0.01)</td>
<td>0.27 (0.01)</td>
<td>0.21 (0.01)</td>
<td>0.23 (0.01)</td>
</tr>
<tr>
<td>2</td>
<td>$L_\infty$</td>
<td>1020 (10.4)</td>
<td>951.5 (12.7)</td>
<td>1039 (11.4)</td>
<td>991.0 (13.8)</td>
</tr>
<tr>
<td></td>
<td>$k$</td>
<td>0.34 (0.01)</td>
<td>0.39 (0.01)</td>
<td>0.33 (0.01)</td>
<td>0.34 (0.01)</td>
</tr>
<tr>
<td>3</td>
<td>$L_\infty$</td>
<td>1010 (10.3)</td>
<td>930.7 (12.5)</td>
<td>1030 (11.4)</td>
<td>982.7 (13.9)</td>
</tr>
<tr>
<td></td>
<td>$k$</td>
<td>0.45 (0.01)</td>
<td>0.52 (0.02)</td>
<td>0.46 (0.01)</td>
<td>0.47 (0.01)</td>
</tr>
<tr>
<td>4</td>
<td>$L_\infty$</td>
<td>1059 (12.6)</td>
<td>1018.9 (17.4)</td>
<td>1111.4 (29.3)</td>
<td>1035.6 (25.9)</td>
</tr>
<tr>
<td></td>
<td>$k_1$</td>
<td>0.26 (0.01)</td>
<td>0.27 (0.01)</td>
<td>0.18 (0.01)</td>
<td>0.22 (0.01)</td>
</tr>
<tr>
<td></td>
<td>$k_2$</td>
<td>0.18 (0.02)</td>
<td>0.15 (0.02)</td>
<td>0.10 (0.02)</td>
<td>0.13 (0.03)</td>
</tr>
<tr>
<td></td>
<td>$t_p$</td>
<td>2.59</td>
<td>2.99</td>
<td>2.72</td>
<td>2.14</td>
</tr>
<tr>
<td>5</td>
<td>$L_\infty$</td>
<td>1034 (10.5)</td>
<td>974.1 (13.0)</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td></td>
<td>$k$</td>
<td>0.24 (0.01)</td>
<td>0.28 (0.01)</td>
<td>NC</td>
<td>NC</td>
</tr>
</tbody>
</table>

3.3.3 Spotted Seatrout

3.3.3.1. Louisiana Data

Growth of Louisiana spotted seatrout was sexually-dimorphic (Figure 3.5). AIC indicated a better fit to sex-specific models than the pooled sex data (Table 3.6). The best-fitting model for both sexes was the seasonal VBGM. For females, parameter estimates (SE) were, $L_\infty$ (mm) = 789.7 (21.90), $k = 0.218$ (0.013), $t_0 = −1.16$ (0.06), $C = −0.01$ (0.002), $s = 1.72$ (0.02). For males,
Figure 3.5. Observed spotted seatrout length-at-age and best-fit growth curves for Louisiana (top panel) and Texas (bottom panel). Female = red circle points and solid line, Male = blue triangle points and dotted line. Louisiana female and male growth curves are the seasonal VBGM. Texas female growth curve is the logistic model and Texas male growth curve is the power model.

Parameter estimates (SE) were, $L_\infty$ (mm) = 4808 (7102), $k = 0.014$ (0.017), $t_0 = -4.46$ (0.43), $C = 0.002$ (0.003), $s = 3.32$ (2.30). According to model estimates, females attained a smaller asymptotic size and grew at a faster rate than males. Females reached 49% of $L_\infty$ at age-2 and 78% of $L_\infty$ at age-6. Males reached 6% of $L_\infty$ by age-2 and 10% of $L_\infty$ by age-6. Parameter estimates for all candidate models are given in Table 3.7. The two best-fit models had 100% support by Akaike weight. The Gompertz model was ranked second among candidate models for both sexes, while the power model was ranked last.
Table 3.6. AIC and Akaike weight for models fit to spotted seatrout length-at-age data. Best-fit model is in bold.

<table>
<thead>
<tr>
<th>State</th>
<th>Sex</th>
<th>Model name</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>LA</td>
<td>Combined</td>
<td>VBGM</td>
<td>103781.10</td>
<td>84.60</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>103771.90</td>
<td>75.44</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>103775.90</td>
<td>79.40</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>103696.50</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Power</td>
<td>103859.50</td>
<td>162.99</td>
<td>0.00</td>
</tr>
<tr>
<td>LA</td>
<td>Female</td>
<td>VBGM</td>
<td>68758.88</td>
<td>51.11</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>68751.41</td>
<td>43.64</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>68760.47</td>
<td>52.70</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>68707.77</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Power</td>
<td>68802.96</td>
<td>95.19</td>
<td>0.00</td>
</tr>
<tr>
<td>LA</td>
<td>Male</td>
<td>VBGM</td>
<td>29463.33</td>
<td>53.98</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>29462.91</td>
<td>53.57</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>29463.41</td>
<td>54.07</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>29409.34</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Power</td>
<td>29463.90</td>
<td>54.55</td>
<td>0.00</td>
</tr>
<tr>
<td>TX</td>
<td>Combined</td>
<td>VBGM</td>
<td>57422.82</td>
<td>11.54</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>57415.58</td>
<td>4.31</td>
<td>0.10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>57411.27</td>
<td>0.00</td>
<td>0.89</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Power</td>
<td>57443.42</td>
<td>32.15</td>
<td>0.00</td>
</tr>
<tr>
<td>TX</td>
<td>Female</td>
<td>VBGM</td>
<td>35833.81</td>
<td>47.71</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>35806.85</td>
<td>20.75</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>35786.10</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Power</td>
<td>35856.19</td>
<td>70.09</td>
<td>0.00</td>
</tr>
<tr>
<td>TX</td>
<td>Male</td>
<td>VBGM</td>
<td>18738.97</td>
<td>12.41</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gompertz</td>
<td>18744.25</td>
<td>17.69</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Logistic</td>
<td>18749.26</td>
<td>22.70</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Seasonal VBGM</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Power</td>
<td>18726.56</td>
<td>0.00</td>
<td>1.00</td>
</tr>
</tbody>
</table>
Table 3.7. Spotted seatrout growth model parameter estimates (and SE) for all candidate models from Louisiana and Texas. Bold text indicates what model was found to be best-fit as determined by AIC. Non-convergence = NC. Model 1= VBGM, 2= Gompertz, 3= logistic, 4= power model, and 5= seasonal VBGM.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>LA female</th>
<th>LA male</th>
<th>TX female</th>
<th>TX male</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$L_\infty$</td>
<td>781.3 (21.3)</td>
<td>2075.6 (1093.1)</td>
<td>1495.9 (184.5)</td>
<td>730.4 (69.8)</td>
</tr>
<tr>
<td></td>
<td>$k$</td>
<td>0.23 (0.01)</td>
<td>0.03 (0.02)</td>
<td>0.07 (0.01)</td>
<td>0.11 (0.02)</td>
</tr>
<tr>
<td>2</td>
<td>$L_\infty$</td>
<td>682.4 (11.0)</td>
<td>846.4 (81.1)</td>
<td>971.3 (40.3)</td>
<td>654.6 (39.4)</td>
</tr>
<tr>
<td></td>
<td>$k$</td>
<td>0.41 (0.01)</td>
<td>0.16 (0.02)</td>
<td>0.21 (0.01)</td>
<td>0.18 (0.02)</td>
</tr>
<tr>
<td>3</td>
<td>$L_\infty$</td>
<td>639.0 (7.7)</td>
<td>688.67 (37.92)</td>
<td><strong>845.7 (22.1)</strong></td>
<td>618.1 (28.3)</td>
</tr>
<tr>
<td></td>
<td>$k$</td>
<td>0.60 (0.02)</td>
<td>0.28 (0.02)</td>
<td><strong>0.36 (0.01)</strong></td>
<td>0.25 (0.02)</td>
</tr>
<tr>
<td>4</td>
<td>$a^0$</td>
<td>65.6 (17.8)</td>
<td>209.6 (6.2)</td>
<td>244.1 (7.7)</td>
<td><strong>217.0 (17.3)</strong></td>
</tr>
<tr>
<td></td>
<td>$a^1$</td>
<td>38190 (27130)</td>
<td>71.6 (22.8)</td>
<td>161.8 (42.0)</td>
<td><strong>2086 (2277)</strong></td>
</tr>
<tr>
<td></td>
<td>$b$</td>
<td>0.52 (0.03)</td>
<td>0.93 (0.05)</td>
<td>0.88 (0.03)</td>
<td><strong>0.59 (0.06)</strong></td>
</tr>
<tr>
<td>5</td>
<td>$L_\infty$</td>
<td><strong>789.7 (21.9)</strong></td>
<td><strong>4808 (7102)</strong></td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td></td>
<td>$k$</td>
<td><strong>0.22 (0.01)</strong></td>
<td><strong>0.014 (0.02)</strong></td>
<td>NC</td>
<td>NC</td>
</tr>
</tbody>
</table>

3.3.3.2. Texas Data

Growth of Texas spotted seatrout was also best described by sex-specific models (Figure 3.5).

For females, the best-fitting model was the logistic model and parameter estimates (SE) were, $L_\infty$ (mm) = 845.7 (22.10), $k = 0.355$ (0.014), and $t_3 = 2.25$ (0.15). For males, the best-fitting model was the power model and parameter estimates (SE) were, $a^0 = 217$ (17.30), $a^1 = 2086$ (2277), $b = 0.591$ (0.062). Females attained a larger asymptotic size and also grew at a faster rate than males.

Females reached 47% of $L_\infty$ at age-2 and 79% of $L_\infty$ at age-6. Males were modeled best by the power model, which does not estimate an asymptotic length parameter. The logistic model for females had 100% support by Akaike weight, while the power model had 100% support for males. The power model was ranked last for females but was found to be best-fit for males. The seasonal VBGM did not reach convergence for the female or male data.
3.3.4. Model selection

The best-fit models for each species and state combination had 100% Akaike weight. The traditional VBGM and Gompertz model were never selected as best-fit for any species, or for a sex of a species; all other candidate models were chosen at least once as the best-fitting model. From the four state-sex combinations for which growth models were fit for black drum, the double VBGM was always selected as the best-fit. Similarly, for red drum the double VBGM was always selected as the best-fit. For spotted seatrout, the seasonal VBGM was selected the most \((n=2)\), followed by the logistic model \((n=1)\), and the power model \((n=1)\). The VBGM always estimated an asymptotic size larger than the Gompertz model, and the Gompertz always estimated a larger asymptotic length than the logistic model.

3.4. Discussion

In short, the results of my growth analysis determined that more than one growth model may be best-fit when fitted to sciaenid length-at-age data throughout the western GoM and the traditional VBGM may not be the best-fit. I also found that for all three species, growth was sexually dimorphic and generally females were larger at-age than males. Texas fish were estimated to be larger than Louisiana fish, while Louisiana fish grew at a faster rate.

3.4.1. Black Drum

AIC indicated that sex-specific growth models were better fitting than the pooled growth models for black drum in Louisiana and Texas. I found that Louisiana black drum males were estimated to grow to a larger asymptotic size than females, but Texas females were estimated to be larger than Texas males. Sex-specific growth estimates have not previously been reported for black
drum; however, my results suggest growth modeling of combined sexes may not be appropriate for future black drum age and growth studies.

The double VBGM performed best for Texas and Louisiana black drum males and females. The traditional VBGM outperformed the seasonal VBGM except for Louisiana females. The worst-fit model for all state-sex combinations of black drum was the logistic model, which likely could be dropped from further black drum growth analysis. Estimated pivotal age of black drum ranged from 1.18–7.73 which coincides with the age range (2–6) of sexually maturity (Murphy and Taylor 1989; Beckman et al. 1990; Jones and Wells 1998).

My parameter estimates are reasonable compared to other growth studies of black drum. In the past, lower $L_\infty$ estimates from the GoM were found in TX (Doerzbacher et al. 1988) and higher $L_\infty$ estimates have been reported in LA (Beckman et al. 1990). The double VBGM estimated the highest $L_\infty$ in Texas and the lowest in Louisiana. Reported growth for black drum ranged between 798–1173 mm, while my estimates ranged between 903–1252 mm.

3.4.2. Red Drum

AIC indicated that sex-specific growth models were better fitting than the pooled growth models for red drum in Louisiana and Texas. I found that Louisiana and Texas red drum females were estimated to grow to a larger asymptotic size than males. The larger asymptotic length estimates for red drum females I found are supported by previous studies (Beckman et al. 1989; Powers et al. 2012). However, the majority of studies of red drum length-at-age reported parameter estimates for combined sexes and I found that sex-specific models were better fitting. Thus, sex-specific growth modeling for red drum may be appropriate for future analyses. Sex-specific estimates of growth have been reported for red drum (Beckman et al. 1989; Powers et al. 2012);
however, these studies estimated the growth of the offshore adult red drum population, while this study modeled the growth of fish caught from inshore and near coast environments. Murphy and Taylor (1990) found no difference in growth of age 1–3 female and male red drum in coastal Florida. My data included adult red drum that are part of the offshore population but were caught nearshore; therefore, the adult fish in the data could be driving a similar pattern as was observed by Powers et al. (2012).

For red drum, the double VBGM performed best for all state-sex combinations and the seasonal VBGM outperformed the traditional VBGM in Louisiana. I found the seasonal VBGM would not converge for the Texas data, and this is likely because it consisted of whole age data. This is a major downfall of the seasonal VBGM and highlights a strength of the double VBGM as it seems robust to a variety of age data. The double VBGM was a significantly better fit for red drum than the traditional VBGM based on AIC. This supports the idea that growth abruptly changes at some pivotal age, likely due to maturation or environmental changes. Estimated pivotal age ranged from 2.14–2.99, which coincides with estimated age range (1–6) of sexually maturity (Murphy and Taylor 1990; Wilson and Nieland 1994).

My parameter estimates are similar to what has been reported previously. Reported $L_\infty$ estimates for red drum ranged between 717–1163 mm and my estimates ranged from 1018–1111 mm. Porch et al. (2002) fit growth models to fish collected offshore from the adult population and reported the largest $L_\infty$ estimates from Louisiana, while Wakefield and Colura (1983) estimated growth from fish collected from the juvenile population and reported the lowest $L_\infty$ from Texas. My data were collected in estuaries and nearshore environments, but also included adult red drum. Because of this, my estimates are larger than those previously reported from Texas and closer to those reported by Porch et al. (2002).
3.4.3. **Spotted Seatrout**

Sex-specific estimates of growth have been reported for spotted seatrout (Nieland et al. 2002; Dippold et al. 2016). I found that spotted seatrout exhibited sexually dimorphic growth in Louisiana and Texas. Sex-specific growth of Texas spotted seatrout was supported by the selection of two different growth models as best-fit, and AIC supported sex-specific models in Louisiana. However, the Louisiana male spotted seatrout $L_\infty$ estimate had very wide confidence intervals and thus, may be a poor estimate. A visual inspection of the fitted sex-specific growth curves for Louisiana spotted seatrout suggests that growth is sex-specific, with males being smaller at-age, and exhibiting a linear growth trajectory. Spotted seatrout females in Texas were estimated to obtain a larger asymptotic length, while in Louisiana they were estimated to obtain a smaller asymptotic length than males. Once again, the poor estimate for Louisiana male spotted seatrout is the driving factor.

The linear trajectory of growth for males may make estimating an asymptotic length challenging. This linear growth trajectory of males has been observed here and elsewhere (Murphy and Taylor 1994; Nieland et al. 2002), and suggests that the concept of asymptotic growth may not apply to spotted seatrout males. Furthermore, the next best-fit model was the Gompertz model and it too had wide confidence intervals and showed no difference between sexes. Because my data included fish up to age-10 and the maximum age of spotted seatrout has been estimated at 18 years (Froese et al. 2017) it is possible that I did not observe enough old fish to capture the asymptote of the models. Nonetheless, spotted seatrout are heavily targeted and harvested in the recreational fishery and so it may be unlikely to observe a fish approaching maximum age or size. Therefore, it may be more important to best estimate the growth of
younger fish and worry less about the estimation of a maximum size because these fish are unlikely to reach this length.

The spotted seatrout growth analysis revealed that the seasonal VBGM was best-fit for Louisiana male and females and the logistic and power models were best-fit for Texas females and males, respectively. Interestingly, the power model was ranked last for all spotted seatrout state-sex combinations, except for Texas male spotted seatrout where it was found to be best-fit. My results are similar to previous studies that have found linear models (Nieland et al. 2002), and sigmoidal models (logistic and Gompertz) described the growth of spotted seatrout best (Murphy and Taylor 1994; Dippold et al. 2016). The variety of models found to describe spotted seatrout growth best, underscores the importance of evaluating multiple models for length-at-age analyses.

My parameter estimates for spotted seatrout are similar to what has been reported in the literature. Reported $L_\infty$ ranged between 574–839 mm, while my estimates ranged between 789–845 mm (excluding Louisiana males). My Louisiana male estimate of 4808 mm is biologically unreasonable and likely inaccurate. The Gompertz model was ranked second among candidate models for Louisiana males and estimated an $L_\infty$ of 846 mm, which is more biologically reasonable. Maceina et al. (1987) reported the largest $L_\infty$ for spotted seatrout in Texas, and Dippold et al. (2016) reported the lowest $L_\infty$ in Mississippi. To the best of my knowledge, this is the first study that has evaluated the seasonal VBGM and power model for fit with spotted seatrout length-at-age data, and their utility in describing growth of spotted seatrout appears promising for future studies.

I did not find any difference between states in regard to the $L_\infty$ estimate for spotted seatrout. Although not statistically different, Texas females were estimated to be larger than
Louisiana females. Also, three different models were chosen as best-fit out of the four possible state-sex combinations. This suggests that while fish grow to approximately the same length, they have very different paths to get there. Some fish are described best by sigmoidal models (e.g., logistic model) suggesting rapid growth at younger ages, others by linear models suggesting continuous growth throughout life, and others by sinusoidal, asymptotic models which suggests a seasonal component to growth. Louisiana spotted seatrout were best-fit by a seasonal model but Texas spotted seatrout were not. Because I used whole age data for Texas spotted seatrout, the seasonal model did not converge and thus, I cannot speculate whether or not their growth exhibits a seasonal component. However, spotted seatrout growth has been found to be positively correlated with estuarine salinity (Bortone 2003), and thus in Louisiana where freshwater input has a seasonal component growth may also show seasonal variation. Louisiana estuaries have more freshwater input than Texas estuaries and this positive correlation of spotted seatrout growth with salinity may explain my larger estimated $L_\infty$ in Texas. I believe future studies should further evaluate linear, seasonal, and sigmoidal growth models for fit with spotted seatrout length-at-age data.

3.4.4. Biphasic growth

The concept of a change in an individual’s growth rate is rooted in biological and life history theory, whereby at some stage or age fish reduce the amount of somatic growth to increase their reproductive growth. This phenomenon is accompanied by a change in habitat for black and red drum, which mature and leave estuarine habitats between ages 2–6 (Beckman et al. 1990; Powers et al. 2012). Given this life history, the double VBGM, which allows growth to change at a given age, seems like a biologically reasonable growth model. The double VBGM
has been shown to be a good fit for many species including striped trumpeter *Latris lineata* (Tracey and Lyle 2005), spiny dogfish *Squalus acanthias* (Tribuzio et al. 2010), and Atlantic sturgeon *Acipenser oxyrinchus* (Balazik et al. 2012) as well as red drum (Ross et al. 1995; Porch et al. 2002). Porch et al. (2002) developed a seasonal growth model which outperformed the double VBGM, although my parameterization of seasonal VBGM (Haddon 2001) did not. However, one major downfall of the seasonal VBGM, is the failure to converge when whole age data are used (as opposed to biological age), and thus, the seasonal VBGM did not converge for the Texas red drum analysis.

In most cases, for black and red drum the traditional VBGM was a better fit than the Gompertz and logistic models, which were always ranked as the last two models based on AIC. Porch et al. (2002) found similar results regarding the poor fit of the Gompertz and logistic models with red drum. However, early life growth of black and red drum may be described well by the Gompertz or logistic models, and this has been documented as being a good fit for younger, faster growing fishes (Gamito 1998). Furthermore, Beckman et al. (1990) found that juvenile black drum data were best-fit by a power model. While I found the double VBGM to be a better fit to length-at-age data of black and red drum, future studies should consider biphasic models with a power or logistic function to model the growth of juvenile fish.

At least 25 biphasic growth models have been proposed for use in fisheries age and growth studies (Wilson et al. 2018). These models can have a discontinuous (or discrete) change in growth with age, where the growth rate changes at some pivotal age, or continuous change in growth which allows a fish to smoothly change between growth phases throughout their life (Minte-Vera et al. 2016). Biphasic models have been used to describe the change in growth rate as a function of maturity, habitat shift, and diet shift (Wilson et al. 2018). Because my estimated
pivotal age of black and red drum coincided with the estimated age-at-maturity, I believe it may be investment in reproductive output that is the driving force for this change in growth rate among black and red drum, and not the habitat shift from estuaries to offshore (although they may be confounded). Additionally, ontogenetic shifts to adult prey items in black and red drum occur very early in their life history (Peters and McMichael Jr. 1987) and thus, shifts in diet are unlikely to be a driving force for a change in growth at the pivotal ages I estimated.

The form of double VBGM selected allowed only a single discontinuous change in growth at a pivotal age. Continuous double VBGM and discontinuous (or discrete) double VBGM have nearly equal usage in the literature (Wilson et al. 2018); however, more recently continuous biphasic models have gained more attention (Ohnishi et al. 2012; Minte-Vera et al. 2016). Porch et al. (2002) developed a growth model for red drum in which the change in growth rate with age was continuous, and this model fitted the data better than the double VBGM; thus, evaluation of multiple biphasic growth models should be a focus of future research.

Additionally, biphasic growth models can accommodate multiple models for the first and second growth phases. Lester et al. (2004) used a linear model for juvenile growth and a VBGM curve for adult growth; Day and Taylor (1997) fit a power model for juvenile growth and a VBGM for adult growth; and Scott and Heikkonen (2012) fit separate linear models for juvenile and adult growth. Biphasic growth models have been used to describe the growth of many species in both freshwater and marine environments. Their flexibility and ability to accommodate a change in growth rate due to environmental or biological factors typically improve the fit to the data. These models have gained popularity in recent years and may represent a significant improvement from the traditional uniphasic growth models (e.g. VBGM).
3.4.5. Borrowed data

I used old, large fish from my Louisiana data to help anchor my \( L_\infty \) parameter for black and red drum, and as such comparisons between the two states are confounded. I found that between sexes, Texas black and red drum grew to larger size than Louisiana drums. However, in preliminary analyses when the old, large Louisiana data were excluded from the analysis, Texas drums were estimated to be significantly smaller than Louisiana drums. Although this is not an ideal scenario, I feel that by anchoring the \( L_\infty \) parameter I obtained more accurate estimates of growth for Texas fish. While growth may vary between states and even among estuaries in early-life (Scharf 2000), for long-lived species such as black and red drum, this growth variation is likely to be dampened later in life, especially because these fish leave estuaries and enter the GoM. Thus, at older ages I believe that growth between the two states is similar, and that some fish caught in Louisiana at older ages could very well have been spawned within Texas estuaries. This is supported by tagging studies that show large neighborhood areas of 700–900 km (Gold and Turner 2002). However, complete sampling of the life history in Texas drums would increase the ability for researchers to evaluate and compare growth between Louisiana and Texas.

3.4.6. Model selection

I found that all of the best-fit models gained 100% Akaike weight, and thus model-averaging was not possible for any species-sex set of candidate models. For this reason, and that model-averaging can only average the \( L_\infty \) parameter (because the \( k \) parameter is not directly comparable between growth models) I feel it may be of little utility. For example, in the case of my spotted seatrout analysis, the power model cannot be model averaged and thus, if it was given any
Akaike weight, it would be ignored and could not be model averaged. While MMI and model-averaging has shown to be a useful tool in making robust parameter estimates and reducing uncertainty (Katsanevakis 2006; Katsanevikis and Maravelias 2008), I found it to provide no additional insight. Model-averaging may be more useful when working with small data sets, or when growth is highly variable between individuals of a population. Despite my disappointment with model-averaging, I found the use of Akaike weights to be an easily interpretable measure of uncertainty regarding model selection. The variation among model selection techniques and appropriate usage of each, is an interesting topic that is substantially debated in ecology (Brewer et al. 2016; Galipaud et al. 2017). However, currently for age and growth analyses in fisheries, AIC is the dominant method of model selection.

3.4.7. Conclusion

The use of the traditional VBGM may result in poor estimates of sciaenid growth in the GoM. Future studies should consider a framework similar to this when performing length-at-age analyses. I found the use of multiple models to be much more informative than if I had chosen a single growth model. Furthermore, I believe that evaluating multiple growth models can aid fisheries managers by reducing uncertainty and allowing them to estimate growth more confidently. Future studies should consider spatial and sex-specific variation and compare the VBGM to alternative growth models when estimating fish growth. By evaluating multiple growth models and considering the spatial and sex-specific variation of growth among populations, fisheries managers will perform robust analyses and thereby reduce uncertainty when setting fisheries regulations, resulting in better management of fish populations.
3.5. References


Matich, P., and coauthors. 2017. Factors shaping the co-occurrence of two juvenile shark species along the Texas Gulf Coast. Marine Biology 164(6).


CHAPTER 4. SPATIAL VARIATION AND DRIVERS OF SCIAENID GROWTH IN THE GULF OF MEXICO

4.1. Introduction

Growth is a basic life history trait and the product of many physiological, biological, and environmental processes. Fish growth rates (e.g., the increase in length with age) are used in the management of fisheries populations (Ricker 1975; Methot and Wetzel 2013) because individual growth is a major source of gains to biomass of populations, and growth is related to other life history variables such as survival and reproduction (Beverton and Holt 1957; Beverton 1992). However, fish growth rates vary between species and within species. Spatial variation of growth among fish populations has been a focus of fisheries research for some time (DeVries and Grimes 1997; Wagner et al. 2007; Midway et al. 2015). This is because the growth of fish may vary even between nearby waterbodies and be regulated under the same management regime, which could lead to poor management of fisheries stocks. Additionally, understanding the spatial variation of fish populations can inform managers how populations will react to different management actions, or during shifting environmental conditions (Rypel 2012; Massie et al. 2018). Therefore, understanding the spatial variability in fish populations dynamics is an important component of fisheries ecology, conservation, and management, especially for species that are heavily harvested, both recreationally and commercially.

Spatial variation of fish growth may arise due to a wide range of factors. Previous research into drivers of spatial variation of fish growth has focused on genetics (Chandrapavan et al. 2010; Lorenzen 2016), habitat (Baltz et al. 1998; Stunz et al. 2002a), and environmental factors (Wagner et al. 2007; Forrester 2003; Morriengiello 2014). More recently, attention has been given to cross-scale interactions (Soranno et al. 2014) and macrosystems ecology (Heffernan et al. 2014) to evaluate drivers of ecological processes on different spatial scales that
interact and influence local response variables. New methodologies (e.g., Bayesian estimation) made possible by an increase in computational power have emerged as a way to examine macrosystems and cross-scale interactions (Levy et al. 2014). This is an emerging field in fisheries that has shown promise identifying broad-scale drivers of ecological processes such as local and regional land-use driving lake phosphorus (Soranno et al. 2014).

Because so many confounding abiotic and biotic factors exist that could potentially affect fish growth, relating spatial variation of growth to environmental characteristics requires that individuals have been separated from one another in areas that differ in some way environmentally. For this reason, lakes (closed, inland systems that function as ecological islands) offer a nice framework for evaluating spatial differences between populations and the majority of previous research has focused on relating landscape and environmental characteristics to life history traits such as growth and reproductive success in freshwater lake environments (Wagner et al. 2007; Hansen et al. 2018). Although not completely separate from one another, estuaries offer a similar framework of fish subpopulations. Midway et al. (2015) found spatial variation of flounder growth and concluded that environmental conditions within estuaries was likely driving the observed variation of growth rates. Estuaries are unique and dynamic environments (Orlando et al. 1993; Engle et al. 2007; Minello et al. 2017) and their importance as nursery habitat and to fisheries production is well-documented, yet they are among the most modified and threatened aquatic environments (Blaber et al. 2000; Able 2005; Amara et al. 2009). The physical, chemical, anthropogenic, and hydrologic characteristics of estuaries influence habitat conditions and even forage, which may result in indirect effects on the growth rates of fish inhabiting these estuaries.
Black drum (*Pogonias cromis*), red drum (*Sciaenops ocellatus*), and spotted seatrout (*Cynoscion nebulosus*) are economically and recreationally important estuarine-dependent species that are found throughout the Gulf of Mexico (GoM). Black drum and red drum inhabit estuaries as juveniles and leave upon maturation, usually between age 3–6 to join the adult offshore population (Richards 1973; Beckman et al. 1990; Murphy and Taylor 1990; Powers et al. 2012). These fish return to estuaries in the spring (black drum) and fall (red drum) to spawn. Tagging studies have shown that black drum exhibit little inter-bay movement (Osburn and Matlock 1984) and spotted seatrout will typically live within a single estuary and adjacent coast lines for their entire lives (Iversen and Tabb 1962; Walters et al. 2009). Because these species inhabit estuaries for all or part of their lives, their growth rate may be related to environmental characteristics within those estuaries.

Because many environmental conditions within estuaries (e.g., salinity, temperature, dissolved oxygen) vary temporally, I was interested in variables that I hypothesized to remain static within the relevant timescale (e.g., estuary drainage area, latitude, etc.). Henceforth, I will refer to these types of factors (temporally invariant abiotic variables) as static spatial drivers. My objectives are (1) to evaluate the variation of sciaenid growth rate among GoM estuaries, and (2) to identify static spatial drivers of estuaries that have an effect on the growth rate of sciaenids by directly incorporating hypothesized drivers into growth models. I considered static spatial drivers for inclusion into my model based on the hypothesized relationships (and previous evidence of effect) of those drivers on fish growth rate.
4.1.1. Hypotheses

I hypothesized that the growth rate of fishes would vary among estuaries based on the static spatial drivers of estuary drainage area, distance of marsh edge habitat, area of freshwater habitat, and relative depth. Further justification for each variable is given below.

H1: Estuary drainage area. — The drainage area of a watershed is a major factor in estuarine productivity (Mallin et al. 1993) and links between terrestrial inputs and aquatic food webs are well-documented (Pace et al. 2004; Abrantes and Sheaves, 2008). Factors within a watershed such as rainfall and river discharge will affect the rate of freshwater, detritus, and nutrient input into an estuary, estuarine circulation and coastal-ocean exchanges, and regulate primary productivity and production at higher trophic levels (Mallin et al. 1993). For humid areas such as this study region, I hypothesized that the growth rate for all three species would be positively related to total estuary drainage area due to higher primary productivity rates resulting from increased detritus and nutrient inputs.

H2: Relative freshwater habitat. — A preference for freshwater habitats has been observed for juvenile black drum, red drum, and spotted seatrout (Whaley et al. 2016; Thomas and Smith 1973). Freshwater habitats also offer refuge for juveniles from large marine predators (Stewart and Scharf 2008), thereby increasing feeding opportunities. Lab and aquaculture experiments have shown that several fishes exhibit optimum growth at certain salinities (Boeuf and Payan 2001). Fishes that spend time in salinities that are outside their optimum salinity range may have increased metabolic costs that will decrease growth rate. I hypothesized that the amount of freshwater area within an estuary would increase the growth rate of all three species. Although
there is a temporal component to this variable on a finer-scale (e.g., estuary salinity), I am considering it from a broad scale using long-term averaged data. Furthermore, the estimated freshwater area among individual estuaries did not vary widely from year to year in these data.

H3: Marsh edge habitat. — The marsh edge ecotone is an important nursery habitat for many larval and juvenile estuarine fishes (Baltz et al. 1993; Stunz et al. 2002b). Larval and juvenile fishes use the marsh edge habitat as shelter from predators and because it is a food-rich environment (Baltz et al. 1998). I hypothesized that the total distance of marsh edge within an estuary would be positively related to growth rate, such that more marsh edge habitat would result in higher growth rates in all three species.

H4: Relative depth. — Many estuarine fish species seek shallow water habitat as juveniles (Weinstein 1979; Stunz et al. 2002a). The physical characteristics of an estuary such as depth and volume may also affect the growth of fish due to increased predators with increasing depth and volume, and increased prey diversity and habitat-availability (e.g., shelter from predators) in shallower habitats. Furthermore, shallower estuaries may be warmer, resulting in higher rates of primary productivity than in deeper estuaries. I hypothesize that the relative depth (an area-adjusted depth variable) of an estuary would affect the growth rate of fishes, such that estuaries with higher relative depth (shallower estuaries) will have increased growth rate for all three species.
4.2. Methods

4.2.1. Length-at-age data

To evaluate the spatial variation of fish growth among estuaries of the GoM, I used data collected from fisheries-independent sampling programs, including Florida Fish and Wildlife Conservation Commission (FWC), Louisiana Department of Wildlife and Fisheries (LDWF), and Texas Parks and Wildlife Department (TPWD). Data were available from a variety of gears (e.g., both fisheries-dependent and -independent sampling); however, to reduce the effect of gear selectivity (Taylor et al. 2005) I used only fish collected from fishery-independent gill net, seine, trammel net, and trawl surveys (see Appendix C). Red drum and spotted seatrout length-at-age data were available for 18 estuaries in Texas, Louisiana, and Florida (Figure 4.1). Black drum length-at-age data were available for 12 of those 18 estuaries and each state was represented.

Figure 4.1. Map of the US Gulf of Mexico region and the 18 estuaries (yellow dots) represented in the Chapter 4 analysis.
In Florida, the FWC conducts monthly stratified-random sampling (Fisheries-Independent Monitoring (FIM) program) and uses a 21.3-m seine in water depths of 1.8 m or less, while the trawl typically samples water depths of 1.8 m or greater. Larger sub-adult and adult fishes are collected using 183-m haul seines in water depth of 3.0 m or less\(^1\).

In Louisiana, fish were collected using gill nets, trawls, seines, and trammel nets. The LDWF uses a 228.6-m long experimental monofilament gill net to sample finfish. The net is 2.4 m in depth and composed of five 45.7 m long panels of 51, 64, 76, 89, and 102 mm stretch mesh (LDWF 2002). A 15.2-m long bag seine of 6.3 mm bar mesh is used to sample juvenile finfish. The seine is 1.8-m in depth and has a 1.8-m by 1.8-m bag in the middle of the net. The trammel nets are 228.6-m in length and 1.8-m in depth, consists of 3 walls, and are constructed of treated nylon. The inner wall has 41.2 mm bar mesh, a #6 twine meshes deep. The two outer walls have 15.2 cm bar black net dip size and is 35 mesh, #9 twine size, and measures 7 meshes deep. The 4.8-m flat otter trawl is attached to a 6.3 mm diameter nylon rope or stainless-steel tow line and bridle. The length of the bridle is 2–3 times the trawl width. Tow line length is normally at least 4–5 times the maximum depth of water. The trawl is towed for ten minutes (measured from the time when the trawl first begins to move forward to the time when it stops forward movement) at a constant speed and in a weaving or circular track to allow the prop wash to pass on either side of the trawl.

In Texas, a 183-m long experimental monofilament gill net is used to sample finfish. The net is 1.2 m in depth and composed of four 45.7 m panels of 76, 102, 127, and 152 mm stretch mesh (Matich et al. 2017). Sample sizes of fish varied by species, estuary, and years collected (see Appendix B). See section 3.2.1 for details on otolith aging, fork length to total length

\(^1\) http://myfwc.com/research/saltwater/fish/research/fim-stratified-random-sampling/
conversions, and outlier removal. Because biological ages were not available for all datasets, the models used whole ages for all datasets, for consistency.

Black drum and red drum remain in natal estuaries as juveniles for around 3–6 years before maturing and moving offshore to join the adult population (Richards 1973; Beckman et al. 1990; Murphy and Taylor 1990; Powers et al. 2012). Because I wanted the growth rate of the fish to reflect the environment in which it was assumed to be, I truncated the length-at-age data to include only up to age-3 for all species. Once fish leave estuaries and join the adult population offshore, the effect of estuary-specific static spatial drivers is likely to be dampened and thus, adult data (age > 3) were excluded. Although spotted seatrout typically do not move between estuaries and the effect of estuary-specific static spatial drivers on growth may be present and detectable for all ages, I hypothesized that the greatest effect of static spatial drivers would occur at younger ages.

4.2.2. Static spatial driver data

I used environmental variables that I considered to be temporally invariant. Because I was not evaluating temporal trends in the data, it was not necessary to have environmental data for the exact years of fish sampling. The estuary drainage area, estuary surface area, and depth are all characteristics that I considered to be constant throughout time. I recognize that freshwater habitat varies temporally; however, this temporal variability was beyond the scope of my study as I sought to quantify any overall trends and average gradients among GoM estuaries. I assumed the environmental gradients that I observed in my environmental data would be present from year to year.
I compiled data from the USEPA Environmental Monitoring and Assessment Program (EMAP), NOAA’s Coastal Assessment and Database Synthesis system (CA&DS), and NOAA’s Coastal Change Analysis Program (C-CAP) for the 18 estuaries in which I had fish length-at-age data. I used average depth (m) obtained from USEPA EMAP (averaged over time and space) and estuary area (km²; represents the area of open water in a watershed; from NOAA CA&DS). For more information regarding the collection of these data see Engle et al. (2007). I divided estuary area by average depth to create a relative depth variable. Lower index values indicate area-adjusted deeper estuaries and higher index values indicated area-adjusted shallower estuaries.

Additionally, I used data from NOAA C-CAP for area of freshwater (ha), total estuary drainage area (ha), and distance of marsh edge (km). Data were available for four years (1996, 2001, 2006, and 2010) and I averaged the data over the four years of sampling. For more details on this approach, see Minello et al. (2017). All covariates (x; Table 4.1) were log-transformed, mean-centered, and scaled by (\([\log(x)] – \text{mean}[\log(x)] / \text{sd}[\log(x)]\)). The transformation resulted in centered covariate variables (z).

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Mean</th>
<th>Range</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>x1 drainage area (ha)</td>
<td>941,208</td>
<td>183,839–2,024,217</td>
<td>NOAA C-CAP¹</td>
</tr>
<tr>
<td>x2 marsh edge (km)</td>
<td>2,567</td>
<td>76–10,951</td>
<td>NOAA C-CAP¹</td>
</tr>
<tr>
<td>x3 relative depth (unitless)</td>
<td>420</td>
<td>103–1,061</td>
<td>Average depth (m); USEPA EMAP² Estuary Area (km²); NOAA CA&amp;DS²</td>
</tr>
<tr>
<td>x4 freshwater area (ha)</td>
<td>10,354</td>
<td>269–46,942</td>
<td>NOAA C-CAP¹</td>
</tr>
</tbody>
</table>

4.2.3 Models and model justification

I sought a model for each species that best captured the shape of growth over the ages in which the estuary environment is hypothesized to play a role. I fit hierarchical linear models to
observed length-at-age data. A linear model was used for three reasons; (1) the visual fit of linear models to the data, (2) the parsimony of comparison and interpretability of the linear model parameters, and (3) the known extremely rapid and linear growth of black drum, red drum, and spotted seatrout at young ages (Murphy and Taylor 1989; Nieland et al. 2002; Porch et al. 2002). Spotted seatrout growth was fitted with sex-specific models because they are known to mature quickly and exhibit sexually dimorphic growth (Nieland et al. 2002; Dippold et al. 2016; Chapter 3). Furthermore, Callihan et al. (2013) found that females have higher rates of fidelity to estuarine environments which makes them more vulnerable to estuarine-specific drivers. Model equations are given below.

Linear model

Level 1: $y_i \sim N(\alpha_j + \beta_j x_i, \sigma_j^2)$, for $i = 1, \ldots, n$

Level 2: $\begin{pmatrix} \alpha_j \\ \beta_j \end{pmatrix} \sim \text{MVN} \left( \begin{pmatrix} \gamma_0^\alpha \\ \gamma_0^\beta \end{pmatrix} + \gamma_{1-4}^\theta \times z_{1-4} \right), \begin{pmatrix} \sigma_\alpha^2 & \rho \sigma_\alpha \sigma_\beta \\ \rho \sigma_\alpha \sigma_\beta & \sigma_\beta^2 \end{pmatrix}$ for $j = 1, \ldots, J$

Where $\alpha_j$ is the intercept for estuary $j$, $\beta_j$ is the slope for estuary $j$, $\sigma_j^2$ is the variance, and error is normally distributed. The $\alpha_j$ and $\beta_j$ parameters are assumed to come from a multivariate normal distribution (MVN). The parameters $\gamma_0^\alpha$ and $\gamma_0^\beta$ are the population level mean $\alpha$ and $\beta$ parameter estimates, respectively, and the $\gamma_{1-4}^\theta$ parameters describe the effects of estuary-specific covariates ($z$) on $\beta_j$ for $z=1-4$; (1) estuary drainage area (km$^2$), (2) distance of marsh edge (km), (3) relative depth (unitless), and (4) area of freshwater habitat (km$^2$). Parameters $\sigma_\alpha^2$ and $\sigma_\beta^2$ are the conditional variances for $\alpha_j$ and $\beta_j$ respectively, and $\rho \sigma_\alpha \sigma_\beta$ is the covariance between $\alpha_j$ and $\beta_j$, and $\rho$ describes the correlation of $\alpha_j$ and $\beta_j$. 
I used diffuse normal prior distributions for $\gamma_0^b$, $\gamma_0^g$, and $\gamma_1^b$, uniform priors for $\sigma$, and the scaled inverse-Wishart distribution for the variance-covariance matrix. I ran 3 Markov chains with different starting values, each with 10,000 iterations. Of those iterations, the first 7,000 were discarded as burn-in, and then were thinned so that every third value was retained for a final total of 1,000 values for analysis. Convergence of posterior distributions were assessed with the Gelman–Rubin statistic ($\hat{R}$), such that values > 1.1 indicated non-convergence (1.0 at convergence). The JAGS analysis was performed within R (R Core Team 2016) using the rjags package (Plummer 2016). I examined 95% and 90% credible intervals (CI) and determined significance by examining whether or not the 95% and 90% CI for the estuary-specific estimates ($\beta_j$) overlapped each other and whether or not the ($\gamma_1^b$) estimates overlapped zero. I considered differences at the 95% level to indicate strong evidence and at the 90% level to indicate moderate evidence of an effect or significant difference. Additionally, I calculated the Pearson correlation coefficient ($r$) between the estuary-specific growth rates ($\beta_j$) of the three species to evaluate the inter-species variation in growth rate among estuaries.

4.3. Results

The data included 1,958 black drum, 14,218 red drum, 12,120 spotted seatrout females, and 5,465 spotted seatrout males from 18 estuaries within Florida, Louisiana, and Texas that were sampled between 1989–2015. Black drum and spotted seatrout had the largest sample sizes from Louisiana and the largest red drum sample size was from Texas. For all three species the lowest sample size was from Florida, and the most sampled estuary was the Terrebonne estuary in Louisiana. Age ranged from 0–3 years for all three species (black drum mean = 2.0 years, red drum = 1.6, and spotted seatrout female and male = 1.7 and 1.6, respectively). Length of black
drum ranged from 117–879 mm (mean = 417 mm), length of red drum ranged from 80–1013 mm (mean = 503 mm), and length of spotted seatrout females and males ranged from 94–671 mm (mean= 396 mm), and 67–618 (mean= 324 mm), respectively.

4.3.1. Black Drum

The estimated estuary-specific linear growth fits show variability among GoM estuaries (Figure 4.2). Estuary-specific growth rate varied from 32–103 mm/yr. (Table 4.2). Vermilion-Teche had the lowest estimated growth rate and was significantly different from the population level mean (Figure 4.3). The highest estimate was in Cedar Key, but it was not significantly different from

Figure 4.2. Observed length (mm) at age (yr.) and fitted estuary-specific (gray) and population mean (red) linear growth models for black drum (A), red drum (B), and spotted seatrout females (C) and males (D). Data are jittered along the x-axis to show contrast between individual points.
the population level mean slope. Barataria was the only estuary to have an estimate higher than and significantly different from the population level mean. The growth rates of many individual estuaries differed significantly from each other.

At the 95% credible interval level, I did not find any significant effects of the static spatial driver covariates on black drum growth (Figure 4.4). However, at the 90% CI level relative depth had a significant negative effect (e.g., slower growth in shallower estuaries). Relative depth and freshwater area were negatively related to growth, with relative depth having

Figure 4.3. Estimated estuary-specific slope ($\beta_j$ [mm/yr.]; black dot), 95% CI (thin vertical line), 90% CI (thick vertical line) and population mean 95% CI (dark gray area) and 90% CI (light gray area) for black drum. Points are arranged by geographic location such that the left x-axis is south Texas and the right x-axis is south Florida.
the larger negative effect (Table 4.3). Estuary drainage area and distance of marsh edge were both positively related to growth, and distance of marsh edge was predicted to have the larger positive effect. The largest overall effect was found for relative depth (higher relative depths indicate shallower estuaries). Interestingly, the estuary with the largest estimated slope (Cedar Key) has relatively small estuary drainage area and distance of marsh edge and the lowest relative depth and freshwater habitat. Additionally, the estuary with the smallest estimated slope (Vermilion-Teche) has relatively large estuary drainage area and distance of marsh edge and the highest relative depth and freshwater habitat.

Figure 4.4. Black drum relationship between estuary-specific slope (growth rate) and estuary drainage area, marsh edge, relative depth, and freshwater area. Points are estimated posterior means and vertical bars are 95% CIs. Solid blue line is the hierarchical regression line for the effect of the covariate on slope and light blue area is the 95% credible region.
Table 4.2. Estuary-specific intercept ($\alpha_j$) and slope ($\beta_j$) estimates for black drum, red drum, and spotted seatrout.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estuary</th>
<th>Black drum</th>
<th>Red drum</th>
<th>Seatrout Female</th>
<th>Seatrout Male</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\alpha_j$</td>
<td>Apalachicola, FL</td>
<td>222.34</td>
<td>305.8</td>
<td>257.15</td>
<td>233.18</td>
</tr>
<tr>
<td></td>
<td>Aransas Bay, TX</td>
<td>NA</td>
<td>289.61</td>
<td>214.88</td>
<td>213.2</td>
</tr>
<tr>
<td></td>
<td>Barataria, LA</td>
<td>236.89</td>
<td>236.37</td>
<td>271.7</td>
<td>248.63</td>
</tr>
<tr>
<td></td>
<td>Calcasieu, LA</td>
<td>201.21</td>
<td>339.63</td>
<td>288.15</td>
<td>271.4</td>
</tr>
<tr>
<td></td>
<td>Cedar Key, FL</td>
<td>226.83</td>
<td>302.52</td>
<td>264.14</td>
<td>253.5</td>
</tr>
<tr>
<td></td>
<td>Charlotte Harbor, FL</td>
<td>305.83</td>
<td>354.12</td>
<td>258.48</td>
<td>271.76</td>
</tr>
<tr>
<td></td>
<td>Corpus Christi, TX</td>
<td>NA</td>
<td>303.89</td>
<td>276.01</td>
<td>274.14</td>
</tr>
<tr>
<td></td>
<td>E. Matagorda, TX</td>
<td>254.88</td>
<td>338.96</td>
<td>301.26</td>
<td>330.69</td>
</tr>
<tr>
<td></td>
<td>Galveston, TX</td>
<td>NA</td>
<td>356.38</td>
<td>273.84</td>
<td>277.01</td>
</tr>
<tr>
<td></td>
<td>Lower Laguna Madre, TX</td>
<td>NA</td>
<td>316.76</td>
<td>275.47</td>
<td>279.6</td>
</tr>
<tr>
<td></td>
<td>Matagorda, TX</td>
<td>243.65</td>
<td>314.2</td>
<td>252.67</td>
<td>253.53</td>
</tr>
<tr>
<td></td>
<td>Pontchartrain, LA</td>
<td>372.32</td>
<td>308.24</td>
<td>264.12</td>
<td>247.5</td>
</tr>
<tr>
<td></td>
<td>Sabine, LA/TX</td>
<td>NA</td>
<td>337.03</td>
<td>265.02</td>
<td>263.63</td>
</tr>
<tr>
<td></td>
<td>San Antonio, TX</td>
<td>NA</td>
<td>299.06</td>
<td>240.15</td>
<td>250.22</td>
</tr>
<tr>
<td></td>
<td>Tampa Bay, FL</td>
<td>282.48</td>
<td>270.04</td>
<td>268.93</td>
<td>271.43</td>
</tr>
<tr>
<td></td>
<td>Terrebonne, LA</td>
<td>330.06</td>
<td>325.42</td>
<td>272.24</td>
<td>246.21</td>
</tr>
<tr>
<td></td>
<td>Upper Laguna Madre, TX</td>
<td>214.53</td>
<td>310.25</td>
<td>260.95</td>
<td>296.47</td>
</tr>
<tr>
<td></td>
<td>Vermilion-Teche, LA</td>
<td>394.62</td>
<td>361.02</td>
<td>308.71</td>
<td>276.05</td>
</tr>
<tr>
<td>$\beta_j$</td>
<td>Apalachicola, FL</td>
<td>71.01</td>
<td>103.7</td>
<td>75.49</td>
<td>37.64</td>
</tr>
<tr>
<td></td>
<td>Aransas Bay, TX</td>
<td>NA</td>
<td>109.43</td>
<td>82.12</td>
<td>59.95</td>
</tr>
<tr>
<td></td>
<td>Barataria, LA</td>
<td>92.64</td>
<td>134.38</td>
<td>68.2</td>
<td>34.72</td>
</tr>
<tr>
<td></td>
<td>Calcasieu, LA</td>
<td>87.53</td>
<td>119.16</td>
<td>92.4</td>
<td>59.33</td>
</tr>
<tr>
<td></td>
<td>Cedar Key, FL</td>
<td>103.2</td>
<td>121.52</td>
<td>65.46</td>
<td>41.93</td>
</tr>
<tr>
<td></td>
<td>Charlotte Harbor, FL</td>
<td>65.44</td>
<td>105.9</td>
<td>58.28</td>
<td>30.94</td>
</tr>
<tr>
<td></td>
<td>Corpus Christi, TX</td>
<td>NA</td>
<td>105.67</td>
<td>62.85</td>
<td>44.51</td>
</tr>
<tr>
<td></td>
<td>E. Matagorda, TX</td>
<td>50.41</td>
<td>103.91</td>
<td>68.96</td>
<td>33.03</td>
</tr>
<tr>
<td></td>
<td>Galveston, TX</td>
<td>NA</td>
<td>119.2</td>
<td>74.97</td>
<td>46.08</td>
</tr>
<tr>
<td></td>
<td>Lower Laguna Madre, TX</td>
<td>NA</td>
<td>119.9</td>
<td>66.04</td>
<td>38.05</td>
</tr>
<tr>
<td></td>
<td>Matagorda, TX</td>
<td>43.26</td>
<td>104</td>
<td>75.44</td>
<td>43.39</td>
</tr>
<tr>
<td></td>
<td>Pontchartrain, LA</td>
<td>66.55</td>
<td>123.53</td>
<td>73.44</td>
<td>35.35</td>
</tr>
<tr>
<td></td>
<td>Sabine, LA/TX</td>
<td>NA</td>
<td>118.71</td>
<td>67.81</td>
<td>39.78</td>
</tr>
<tr>
<td></td>
<td>San Antonio, TX</td>
<td>NA</td>
<td>112.65</td>
<td>81.36</td>
<td>44.87</td>
</tr>
<tr>
<td></td>
<td>Tampa Bay, FL</td>
<td>73.74</td>
<td>138.81</td>
<td>69.22</td>
<td>36.55</td>
</tr>
<tr>
<td></td>
<td>Terrebonne, LA</td>
<td>58.94</td>
<td>108.94</td>
<td>71.11</td>
<td>36.55</td>
</tr>
</tbody>
</table>

(table cont’d.)
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estuary</th>
<th>Black drum</th>
<th>Red drum</th>
<th>Seatrout Female</th>
<th>Seatrout Male</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\beta_j$</td>
<td>Upper Laguna Madre, TX</td>
<td>70.78</td>
<td>116.5</td>
<td>58.9</td>
<td>35.14</td>
</tr>
<tr>
<td></td>
<td>Vermilion-Teche, LA</td>
<td>32.05</td>
<td>101.34</td>
<td>74.17</td>
<td>52.42</td>
</tr>
</tbody>
</table>

### 4.3.2. Red Drum

The estuary-specific linear fits of growth show the variability in red drum grow rate among GoM estuaries (see again Figure 4.2). Estimated estuary-specific growth rate ranged from about 101–138 mm/yr. (see again Table 4.2). Vermilion-Teche again had the smallest estimated slope and was significantly different from the population level mean along with Matagorda Bay and East Matagorda Bay (Figure 4.5). The largest slope was estimated for Tampa Bay but it was not

![Figure 4.5](image-url)

Figure 4.5. Estimated estuary-specific slope ($\beta_j$ [mm/yr.]; black dot), 95% CI (thin vertical line), 90% CI (thick vertical line) and population mean 95% CI (dark gray area) and 90% CI (light gray area) for red drum. Points are arranged geographically such that the left x-axis is southern Texas and the right x-axis is southern Florida.
significantly different from the population level mean estimate. Barataria was the only estuary to have an estimated growth rate significantly larger than the population level mean growth rate. The slopes of many individual estuaries differed significantly from each other.

All static spatial driver covariates were found to not have a significant effect in predicting the variation in growth rate among estuaries (Figure 4.6). Estuary drainage area and distance of marsh edge each were predicted to have positive effects on growth, and distance of marsh edge had the largest positive effect (see again Table 4.3). Relative depth and freshwater area were predicted to have negative effects on growth, and relative depth had the largest negative effect. The overall largest effect was found in distance of marsh edge.

Figure 4.6. Red drum relationship between estuary-specific slope (growth rate) and estuary drainage area, marsh edge, relative depth, and freshwater area. Points are estimated posterior means and vertical bars are 95% CIs. Solid blue line is the hierarchical regression line for the effect of the covariate on slope and light blue area is the 95% credible region.
4.3.3. Spotted Seatrout

The estuary-specific linear growth fits show variability of growth rate for spotted seatrout females among GoM estuaries (see again Figure 4.2). Estimated growth rates ranged from about 58–92 mm/yr. (see again Table 4.2). The smallest slope for female spotted seatrout was estimated for Charlotte Harbor, and the greatest was estimated for Calcasieu. Calcasieu was the only estuary to have an estimated growth rate that was significantly different from the population mean growth rate and was also significantly different from most other estuaries (Figure 4.7). The 95% credible intervals for the estuary-specific growth rate estimates shows significant variation in spotted seatrout female growth rate among GoM estuaries.

Table 4.3. Posterior mean estimates and 95% credible intervals for population level intercept ($\gamma_0^g$), population level slope ($\gamma_0^\beta$), effect of drainage area ($\gamma_1^\beta$), effect of marsh edge ($\gamma_2^\beta$), effect of relative depth ($\gamma_3^\beta$), and effect of freshwater area ($\gamma_4^\beta$).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Black drum</th>
<th>Red drum</th>
<th>Seatrout female</th>
<th>Seatrout male</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\gamma_0^g$</td>
<td>261.38</td>
<td>313.11</td>
<td>266.27</td>
<td>262.79</td>
</tr>
<tr>
<td></td>
<td>(213.84–303.21)</td>
<td>(295.94–330.24)</td>
<td>(250.78–279.85)</td>
<td>(246.43–278.80)</td>
</tr>
<tr>
<td>$\gamma_0^\beta$</td>
<td>68.87</td>
<td>115.20</td>
<td>71.65</td>
<td>41.84</td>
</tr>
<tr>
<td></td>
<td>(52.53–84.35)</td>
<td>(108.93–122.26)</td>
<td>(66.03–77.25)</td>
<td>(35.75–47.90)</td>
</tr>
<tr>
<td>$\gamma_1^\beta$</td>
<td>3.82</td>
<td>2.24</td>
<td>-0.46</td>
<td>2.33</td>
</tr>
<tr>
<td></td>
<td>(-20.12–26.61)</td>
<td>(-5.99–10.76)</td>
<td>(-8.11–6.96)</td>
<td>(-5.87–10.70)</td>
</tr>
<tr>
<td>$\gamma_2^\beta$</td>
<td>8.99</td>
<td>2.71</td>
<td>4.78</td>
<td>2.23</td>
</tr>
<tr>
<td>$\gamma_3^\beta$</td>
<td>-15.06</td>
<td>-2.42</td>
<td>4.10</td>
<td>1.08</td>
</tr>
<tr>
<td></td>
<td>(-31.67–0.67)</td>
<td>(-8.76–3.74)</td>
<td>(-2.39–10.65)</td>
<td>(-6.46–8.80)</td>
</tr>
<tr>
<td>$\gamma_4^\beta$</td>
<td>-6.17</td>
<td>-0.44</td>
<td>-5.31</td>
<td>-5.40</td>
</tr>
</tbody>
</table>

All static spatial driver covariates were found to be insignificant at the 95% credible interval level for female spotted seatrout (Figure 4.8). Relative depth and distance of marsh edge was positively related to growth, and marsh edge had the largest positive effect (see again Table 4.3). Distance of marsh edge was not significant at the 95% credible interval level, but was
significant at the 90% level. Estuary drainage area and freshwater area were negatively related to depth and freshwater area had the largest negative effect. Freshwater area had the largest overall effect.

The estuary-specific linear growth fits show variability of growth rate for spotted seatrout males among GoM estuaries (see again Figure 4.2). Estimated estuary-specific growth rate

![Graph](image)

Figure 4.7. Estimated estuary-specific slope ($\beta_j$ [mm/yr.]; black dot), 95% CI (thin vertical line), 90% CI (thick vertical line) and population mean 95% CI (dark gray area) and 90% CI (light gray area) for female (A) and male (B) spotted seatrout. Points are arranged by geographic location such that the left x-axis is south Texas and the right x-axis is south Florida.

ranged between about 30–59 mm/yr. The lowest estimated growth rate was found for Charlotte Harbor, but it differed insignificantly from the population level mean. The highest growth rate was estimated in Aransas Bay. Aransas, Calcasieu, and Vermilion-Tecche each had estimated
growth rates that differed significantly from the population level mean. The 95% credible intervals for the estuary-specific growth rate estimates show significant variation in spotted seatrout male growth rate among GoM estuaries (see again Figure 4.7).

I found that the effects of the static spatial driver covariates were insignificant for male spotted seatrout growth (Figure 4.9). Drainage area, marsh edge, and relative depth each had a positive effect on growth and freshwater area had a negative effect (see again Table 4.3). Estuary drainage area had the largest positive effect and freshwater area had the largest overall effect.

Figure 4.8. Female spotted seatrout relationship between estuary-specific slope (growth rate) and estuary drainage area, marsh edge, relative depth, and freshwater area. Points are estimated posterior means and vertical bars are 95% CIs. Solid blue line is the hierarchical regression line for the effect of the covariate on slope and light blue area is the 95% credible region.
4.3.4. Correlation of growth rates

I calculated the Pearson correlation coefficient ($r$) of growth rates of the three species between estuaries to evaluate whether growth varies among species within given estuaries. Spotted seatrout female and male estuary-specific growth rates were highly correlated ($r = 0.79$) and black and red drum estuary-specific growth rates were also highly correlated ($r = 0.68$). The growth rates of black drum and red drum were not correlated with spotted seatrout growth rates (Table 4.4).

---

Figure 4.9. Male spotted seatrout relationship between estuary-specific slope (growth rate) and estuary drainage area, marsh edge, relative depth, and freshwater area. Points are estimated posterior means and vertical bars are 95% CIs. Solid blue line is the hierarchical regression line for the effect of the covariate on slope and light blue area is the 95% credible region.
Table 4.4. Pearson correlation coefficient ($r$) of growth rates between black drum, red drum, and spotted seatrout females and males.

<table>
<thead>
<tr>
<th></th>
<th>Black Drum</th>
<th>Red Drum</th>
<th>Seatrout Female</th>
<th>Seatrout Male</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black Drum</td>
<td>1</td>
<td>0.68</td>
<td>−0.02</td>
<td>−0.04</td>
</tr>
<tr>
<td>Red Drum</td>
<td>0.68</td>
<td>1</td>
<td>−0.04</td>
<td>−0.12</td>
</tr>
<tr>
<td>Seatrout Female</td>
<td>−0.02</td>
<td>−0.04</td>
<td>1</td>
<td>0.79</td>
</tr>
<tr>
<td>Seatrout Male</td>
<td>−0.04</td>
<td>−0.12</td>
<td>0.79</td>
<td>1</td>
</tr>
</tbody>
</table>

4.4. Discussion

4.4.1. Spatial variability in growth rate

Understanding the spatial variation and drivers of fish growth is important to fisheries conservation and management. In recent years, the role of environmental and other factors unrelated to fishery exploitation, such as climate change (Rypel 2012; Hansen et al. 2018), landscape variables (Wagner et al. 2007), and pollution (Amara et al. 2009) have been of increasing concern for fisheries managers. Additionally, focus has been given to macrosystems ecology (Heffernan et al. 2014; Levy et al. 2014) and cross-scale interactions (Soranno et al. 2014) to examine how ecological processes that operate on continental scales influence local ecological processes. These types of studies represent a shift toward a desire to manage populations in ecologically relevant units and align policy with spatial patterns of population dynamics, rather than pooling a collection of substocks based on political boundaries.

Additionally, by considering macrosystems ecology and cross-scale interactions managers may gain an understanding of broad-scale ecological processes that effect fish populations and assess the impact of various management regimes (Soranno et al. 2014; Heffernan et al. 2014).

Furthermore, identifying ecological processes that are important for the growth of fish will aid managers in the future given uncertain environmental conditions (e.g. sea-level rise, reduced freshwater input; Robins et al. 2006; Rypel 2012).
Macroscale processes and cross-scale interactions are difficult to quantify because they require years of sampling and large amounts of data to detect a significant interaction (Soranno et al. 2014; Heffernan et al. 2014). However, previous research has found that estimated von Bertalanffy growth model parameters of bass populations were related to latitudinal gradients (Helser and Lai 2004), and measures of lake productivity were related to the variation in mean length-at-age of fish in Michigan lakes (Wagner et al. 2007). My results suggest that sciaenid growth varies among GoM estuaries; however, static spatial drivers such as estuary drainage area, distance of marsh edge, relative depth, and relative freshwater area are not strong, significant drivers of that variation. However, I did find evidence of a moderate effect of relative depth on black drum growth and distance of marsh edge for female spotted seatrout growth.

4.4.2. Static Spatial Drivers

The distance of marsh edge within an estuary was found to have a moderately significant effect on female spotted seatrout growth rate. For all three species, distance of marsh edge was predicted to have a positive effect on growth rate. I hypothesized this relationship because marsh edge habitat has been shown to be important for estuarine species (Baltz et al. 1993, 1998). Previous research found that red drum growth rate was highest in salt marsh and seagrass habitats (Stunz et al. 2002a) and my results suggest a positive relationship between sciaenid growth and distance of marsh edge. However, I did not have data for estuarine seagrass bed area, which might have been useful to incorporate into these models. It has also been suggested that the arrangement and complexity of estuarine habitats are more important than one single characteristic (MacRae and Cowan 2010) and perhaps a measure of habitat complexity would be more informative than one single characteristic.
Relative depth was found to have a moderately significant effect on black drum growth rate but not in the direction I expected. I hypothesized that relative depth would be positively related to growth rate, yet for both drum species growth rate was negatively related to relative depth (larger, shallower habitats result in slower growth rates). This may be because drums reach relatively large sizes early in life and do not need to seek refuge from predators, thus allowing them to exploit better feeding opportunities in deeper water. Additionally, shallower estuaries may have higher temperatures that are outside of thermal optima and results in decreased growth and increase metabolic stress. The mechanisms behind the relationship of relative depth and growth rate are not entirely clear, yet it is clear that aspects of bathymetry (e.g. depth and volume) should be investigated further.

I did not detect an effect of estuary drainage area or freshwater area on sciaenid growth for any of the three species. This is surprising because the importance of freshwater habitat to juvenile sciaenids is well documented (Smith et al. 2008; Purtlebaugh and Allen 2010; Flaherty-Walia et al. 2015). It is possible that freshwater habitats are more important in early life but decrease in importance at later ages. Perhaps access to prey-rich marine waters becomes more important than seeking refuge in freshwater habitats with age. The least influential of all the environmental covariates appears to be estuary drainage area. This is surprising because estuaries with larger drainage basins are likely to have increased terrigenous inputs and, therefore, higher primary production (Mallin et al. 1993). Despite known relationships between estuaries and their watersheds, I was unable to relate the estuarine drainage area of estuaries to the observed variation of sciaenid growth to age-3. Perhaps metrics of rainfall within an estuary drainage area would better explain spatial variation than estuary drainage area, but rainfall has a temporal aspect to it, which I avoided in this study.
This study is limited because it does not account for any biological or temporally-variable drivers. Biological drivers such as anthropogenic influence (Forrester et al. 2003), predator-prey dynamics (Scharf 2000), density dependence (Bacheler et al. 2012), and fishing mortality have been previously hypothesized to affect the growth of estuarine fishes. Additionally, temporally-variant and finer-scale environmental factors such as salinity, temperature, dissolved oxygen, sediment structure, and food availability also likely contribute to fish growth (Sogard 1992; Baltz et al. 1998). The effects of environmental factors on growth are well documented in the literature; however, evaluating many of these variables is best done in a controlled laboratory or mesocosm setting (Craig et al. 1995; Fontaine et al. 2007). Nevertheless, future analyses may consider these drivers.

Although I failed to identify a major driver of sciaenid growth, I anticipated the possibility of this outcome because quantifying the relationships between environmental conditions and fish populations is difficult (Rose 2000), because so much noise is present in natural systems detecting a strong signal of an effect can be challenging. Despite a failure to identify strong, significant effects of static spatial drivers on sciaenid growth rate, I did find variation in growth rate among GoM estuaries. Therefore, future studies should continue to further evaluate the spatial variation and drivers of fish growth within estuaries of the GoM. The emergence of macrosystems (Heffernan et al. 2014; Levy et al. 2014) and cross-scale approaches (Soranno et al. 2014) in fisheries will allow researchers to answer ecological questions on regional and local scales and better understand the spatial variation of fish populations. These new macrosystem approaches will foster management of ecologically relevant populations based on population dynamics, and an alignment of policy with spatial patterns of population dynamics.
4.4.3. Conclusion

This study represents an initial step toward understanding the drivers of spatial variation in growth rate of sciaenids in the GoM. I found significant variation in growth rate among GoM estuaries, and that distance of marsh edge and relative depth were best at describing the observed variation in estuary-specific growth rate. Therefore, future studies should further evaluate habitat, bathymetric, and other new variables to determine drivers of sciaenid growth. Because sciaenids are economically and culturally important fish species in the GoM a deep understanding of their growth dynamics is necessary to ensure sustainable management.

4.5. References


Forrester, G. E., and coauthors. 2003. Growth of estuarine fish is associated with the combined concentration of sediment contaminants and shows no adaptation or acclimation to past conditions. Marine Environmental Research 56(3):423–442.


Matich, P., and coauthors. 2017. Factors shaping the co-occurrence of two juvenile shark species along the Texas Gulf Coast. Marine Biology 164(6).


CHAPTER 5. GENERAL CONCLUSIONS

5.1. Thesis Summary

Given the ubiquity and overall importance of growth modeling to fisheries science, knowledge of the methodological trends is useful when evaluating the growth of fishes. Additionally, when assessing populations on a large scale, recognizing the spatial and sex-specific variation of growth can improve growth model fit (DeVries and Grimes 1997; Curtis and Shima 2005; Williams et al. 2012), and investigating macrosystems processes (Heffernan et al. 2014) and cross-scale interactions (Soranno et al. 2014) can offer insight into the ecological drivers of those processes. Studies such as this—which include all of these components—better evaluate the dynamics of growth and obtain a deeper understanding of study species than those that simply estimate and compare von Bertalanffy parameters (Bertalanffy 1938; Beverton and Holt 1957).

This study sought to examine historical trends in growth modeling in fisheries science and evaluate the growth of three, culturally and economically important sciaenid species in the Gulf of Mexico using a suite of growth modeling techniques. In Chapter 2, I examined historical trends in the use of growth models in peer-reviewed fisheries literature and compared those trends to the trends in approach to growth modeling in NOAA stock assessments. I found a recent shift in the peer-reviewed fish growth literature to increased use in multi-model frameworks and an accompanying shift in model selection methods from general goodness-of-fit procedures to Akaike Information Criterion (Akaike 1973) and other information theoretic options. Despite these advances in the peer-reviewed fish growth literature, I did not see a commensurate shift in approaches in NOAA stock assessments. Additionally, when considering species taxa, maximum size, and habitat I did not detect any trends in relation to modeling approaches.
In Chapter 3, I evaluated the fit of multiple growth models on black and red drum, and spotted seatrout. Prior research has indicated that the von Bertalanffy growth model (VBGM) may not fit sciaenid life history dynamics well (Ross et al. 1995; Porch et al. 2002; Dippold et al. 2016). This study confirms that the VBGM is not the best growth model to describe the growth of these species. A biphasic model (double von Bertalanffy) better described the growth of drums in Louisiana and Texas, and linear, sigmoidal, and seasonal growth models better fit spotted seatrout length-at-age data. I also found that Texas fishes were estimated to grow to a larger mean maximum size than Louisiana fishes, and Louisiana fishes grew at a faster rate than Texas fishes. Furthermore, I evaluated sex-specific growth models for all three species and found that they each exhibited sexually dimorphic growth.

In Chapter 4, I evaluated the variation of growth rate for subadult fishes in the estuaries of the Gulf of Mexico. Estuaries are unique environments (Orlando et al. 1993; Engle et al. 2007; Minello et al. 2017) and the conditions within those estuaries have been hypothesized to affect the growth of inhabitant species (Baltz et al. 1998; Scharf 2000; Midway et al. 2015). I found that black drum, red drum, and spotted seatrout growth rate varies significantly among Gulf of Mexico estuaries, but was unable to relate variation in growth rate to static spatial drivers of estuaries. The static spatial drivers of estuary drainage area, distance of marsh edge, relative depth, and area of freshwater habitat did not explain the variation in growth rate. However, relative depth and distance of marsh edge had a moderately significant effect for some species. Thus, habitat and bathymetry characteristics within estuaries may potentially play a role in fish growth and further research should be directed in this area.

Overall, this thesis has identified major trends in the methodology in growth modeling, provided an in-depth analysis of growth models on sciaenid species, and evaluated hypotheses
regarding spatial drivers of sciaenid growth by linking spatial drivers to length-at-age analyses. Because of the recreational, cultural, and economic importance of sciaenids across their range, and the importance of accurately estimating growth of fishes to fisheries management, I believe this research will be of interest to fisheries researchers and managers not only along the Gulf coast but also in other regions where sciaenids are found. Although further studies will be necessary, this thesis serves as an initial step toward understanding the spatial variation of sciaenid growth and the effect of spatial drivers on sciaenid growth in the estuaries of the Gulf of Mexico.

5.2. References


### APPENDIX A. CHAPTER 3 SUPPLEMENTAL MATERIAL

Table A.1. Parameter estimates, growth models used, study location, and sample sizes from age and growth studies of red drum in the literature. \( L_\infty \) estimates are in mm. Superscripts in location are 1= Lower Laguna Madre, 2= Matagorda Bay, 3= Galveston Bay. Model 1= VBGM, 2= double VBGM, and 3= Porch model. Matlock estimates based on data from 1= Pearson (1929), and 2= Theiling and Loyacano Jr. (1976). C= combined sexes.

<table>
<thead>
<tr>
<th>Study</th>
<th>Location</th>
<th>Sex</th>
<th>Model</th>
<th>( L_\infty )</th>
<th>( k )</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Matlock (1984)¹</td>
<td>TX</td>
<td>C</td>
<td>1</td>
<td>1068</td>
<td>0.30</td>
<td></td>
</tr>
<tr>
<td>Matlock (1984)²</td>
<td>SC</td>
<td>C</td>
<td>1</td>
<td>945</td>
<td>0.45</td>
<td>62</td>
</tr>
<tr>
<td>Rohr (1980)</td>
<td>LA</td>
<td>C</td>
<td>1</td>
<td>950</td>
<td>0.37</td>
<td>62</td>
</tr>
<tr>
<td>Wakefield and Colura (1983)</td>
<td>TX¹</td>
<td>C</td>
<td>1</td>
<td>717</td>
<td>0.52</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>TX²</td>
<td>C</td>
<td>1</td>
<td>835</td>
<td>0.35</td>
<td>339</td>
</tr>
<tr>
<td></td>
<td>TX³</td>
<td>C</td>
<td>1</td>
<td>804</td>
<td>0.41</td>
<td>23</td>
</tr>
<tr>
<td>Doerzbacher et al. (1988)</td>
<td>TX</td>
<td>C</td>
<td>1</td>
<td>918</td>
<td>0.42</td>
<td>2010</td>
</tr>
<tr>
<td>Beckman et al. (1989)</td>
<td>GoM</td>
<td>M</td>
<td>1</td>
<td>909</td>
<td>0.14</td>
<td>1544</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>1</td>
<td>1013</td>
<td>0.09</td>
<td></td>
</tr>
<tr>
<td>Murphy and Taylor (1990)</td>
<td>FL</td>
<td>C</td>
<td>1</td>
<td>934</td>
<td>0.45</td>
<td></td>
</tr>
<tr>
<td>Ross et al. (1995)</td>
<td>NC</td>
<td>C</td>
<td>2</td>
<td>1163</td>
<td>0.30 (k₁)</td>
<td>843</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.07 (k₂)</td>
<td></td>
</tr>
<tr>
<td>Porch et al. (2002)</td>
<td>LA</td>
<td>C</td>
<td>1</td>
<td>958</td>
<td>0.32</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>1102</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Powers et al. (2012)</td>
<td>AL</td>
<td>M</td>
<td>1</td>
<td>923</td>
<td>0.11</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>1</td>
<td>965</td>
<td>0.11</td>
<td></td>
</tr>
</tbody>
</table>

717–1102 0.09–0.52

Table A.2. Parameter estimates, growth models used, study location, and sample sizes from age and growth studies of black drum in the literature. \( L_\infty \) estimates are in mm. All estimates are from the VBGM and pooled sexes.

<table>
<thead>
<tr>
<th>Study</th>
<th>Location</th>
<th>( L_\infty )</th>
<th>( k )</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Doerzbacher et al. (1988)</td>
<td>TX</td>
<td>798</td>
<td>0.22</td>
<td>383</td>
</tr>
<tr>
<td>Murphy and Taylor (1989)</td>
<td>FL</td>
<td>1172</td>
<td>0.12</td>
<td>397</td>
</tr>
<tr>
<td>Beckman et al. (1990)</td>
<td>LA</td>
<td>1100</td>
<td>0.04</td>
<td>1072</td>
</tr>
<tr>
<td>Jones and Wells (1998)</td>
<td>Chesapeake Bay</td>
<td>1173</td>
<td>0.11</td>
<td>871</td>
</tr>
</tbody>
</table>

798–1173 0.04–0.22
Table A.3. Parameter estimates, growth models used, study location, and sample sizes from age and growth studies of spotted seatrout in the literature. $L_\infty$ estimates are in mm. Model 1= VBGM; 2= Linear regression; 3= Gompertz; 4= Logistic. Superscripts in location, 1= Charlotte Harbor, 2= Indian River Lagoon, and 3= Apalachicola Bay.

<table>
<thead>
<tr>
<th>Study</th>
<th>Location</th>
<th>Sex</th>
<th>Model</th>
<th>$L_\infty$</th>
<th>$k$</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maceina et al. (1987)</td>
<td>TX</td>
<td>M</td>
<td>1</td>
<td>664</td>
<td>0.18</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>1</td>
<td>687</td>
<td>0.51</td>
<td></td>
</tr>
<tr>
<td>Murphy and Taylor (1994)</td>
<td>FL¹</td>
<td>M</td>
<td>2</td>
<td>TL = 267.3 + 33.96(Age)</td>
<td>657</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>3</td>
<td>698</td>
<td>0.36</td>
<td>1102</td>
</tr>
<tr>
<td></td>
<td>FL²</td>
<td>M</td>
<td>2</td>
<td>TL = 286.5 + 42.52(Age)</td>
<td>631</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>3</td>
<td>839</td>
<td>0.36</td>
<td>1195</td>
</tr>
<tr>
<td></td>
<td>FL³</td>
<td>M</td>
<td>2</td>
<td>TL = 249.8 + 51.26(Age)</td>
<td>476</td>
<td></td>
</tr>
<tr>
<td>Nieland et al. (2002)</td>
<td>LA</td>
<td>M</td>
<td>2</td>
<td>TL = 211.4 + 41.28(Age)</td>
<td>601</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>2</td>
<td>TL = 231.2 + 70.12(Age)</td>
<td>1451</td>
<td></td>
</tr>
<tr>
<td>Dippold et al. (2016)</td>
<td>MS</td>
<td>M</td>
<td>4</td>
<td>575</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>4</td>
<td>605</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

575–839 0.18–0.51
Table A.4. Sample description for black drum, red drum, and spotted seatrout data used in multi-model growth analysis. All sizes are in mm and ages in years. Whole age data are denoted with (*).

<table>
<thead>
<tr>
<th>Black drum</th>
<th>LA female</th>
<th>LA male</th>
<th>LA combined</th>
<th>TX female</th>
<th>TX male</th>
<th>TX combined</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>( n )</td>
<td>452</td>
<td>275</td>
<td>727</td>
<td>277</td>
<td>247</td>
<td>524</td>
<td>1251</td>
</tr>
<tr>
<td>mean size</td>
<td>499</td>
<td>530</td>
<td>511</td>
<td>375</td>
<td>374</td>
<td>375</td>
<td>454</td>
</tr>
<tr>
<td>age range</td>
<td>0.5–41.6</td>
<td>0.5–41</td>
<td>0.5–41.6</td>
<td>0.9–9.1</td>
<td>0.9–9.9</td>
<td>0.9–9.9</td>
<td>0.5–41.6</td>
</tr>
<tr>
<td>mean age</td>
<td>5.5</td>
<td>6.25</td>
<td>5.8</td>
<td>3.4</td>
<td>3.4</td>
<td>3.4</td>
<td>4.8</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Red drum</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>( n )</td>
<td>1131</td>
<td>1271</td>
<td>2402</td>
<td>837</td>
<td>635</td>
<td>1472</td>
<td>3874</td>
</tr>
<tr>
<td>mean size</td>
<td>585</td>
<td>547</td>
<td>565</td>
<td>484</td>
<td>490</td>
<td>487</td>
<td>535</td>
</tr>
<tr>
<td>age range</td>
<td>0.7–30.9</td>
<td>0.9–37.4</td>
<td>0.7–37.4</td>
<td>0–5*</td>
<td>0–4*</td>
<td>0–5*</td>
<td>0–37*</td>
</tr>
<tr>
<td>mean age</td>
<td>3.1</td>
<td>2.7</td>
<td>2.9</td>
<td>1.2*</td>
<td>1.2*</td>
<td>1.2*</td>
<td>1.9*</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Spotted seatrout</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>( n )</td>
<td>6515</td>
<td>2835</td>
<td>9350</td>
<td>3260</td>
<td>1804</td>
<td>5064</td>
<td>14414</td>
</tr>
<tr>
<td>mean size</td>
<td>398</td>
<td>325</td>
<td>376</td>
<td>457</td>
<td>386</td>
<td>432</td>
<td>395</td>
</tr>
<tr>
<td>age range</td>
<td>0.2–7.7</td>
<td>0.2–8.6</td>
<td>0.2–8.6</td>
<td>0–10*</td>
<td>0–9*</td>
<td>0–10*</td>
<td>0–10*</td>
</tr>
<tr>
<td>mean age</td>
<td>2.1</td>
<td>2.3</td>
<td>2.2</td>
<td>2.7*</td>
<td>2.9*</td>
<td>2.8*</td>
<td>2.1*</td>
</tr>
</tbody>
</table>
APPENDIX B. CHAPTER 4 SUPPLEMENTAL MATERIAL

Table B.1. Estuary-specific sample sizes (n) for black drum, red drum, and spotted seatrout for all sampling years between 1989–2015.

<table>
<thead>
<tr>
<th>Estuary</th>
<th>Black drum</th>
<th>Red drum</th>
<th>Seatrout Female</th>
<th>Seatrout Male</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apalachicola, FL</td>
<td>6</td>
<td>41</td>
<td>11</td>
<td>9</td>
</tr>
<tr>
<td>Aransas Bay, TX</td>
<td>NA</td>
<td>1090</td>
<td>235</td>
<td>99</td>
</tr>
<tr>
<td>Barataria, LA</td>
<td>296</td>
<td>844</td>
<td>1694</td>
<td>929</td>
</tr>
<tr>
<td>Calcasieu, LA</td>
<td>172</td>
<td>553</td>
<td>914</td>
<td>368</td>
</tr>
<tr>
<td>Cedar Key, FL</td>
<td>21</td>
<td>56</td>
<td>23</td>
<td>8</td>
</tr>
<tr>
<td>Charlotte Harbor, FL</td>
<td>22</td>
<td>61</td>
<td>11</td>
<td>9</td>
</tr>
<tr>
<td>Corpus Christi, TX</td>
<td>NA</td>
<td>918</td>
<td>141</td>
<td>105</td>
</tr>
<tr>
<td>E. Matagorda, TX</td>
<td>74</td>
<td>1027</td>
<td>226</td>
<td>70</td>
</tr>
<tr>
<td>Galveston, TX</td>
<td>NA</td>
<td>1161</td>
<td>214</td>
<td>194</td>
</tr>
<tr>
<td>Lower Laguna Madre, TX</td>
<td>NA</td>
<td>1020</td>
<td>372</td>
<td>188</td>
</tr>
<tr>
<td>Matagorda, TX</td>
<td>22</td>
<td>955</td>
<td>706</td>
<td>216</td>
</tr>
<tr>
<td>Pontchartrain, LA</td>
<td>98</td>
<td>1076</td>
<td>2308</td>
<td>869</td>
</tr>
<tr>
<td>Sabine, LA/TX</td>
<td>NA</td>
<td>911</td>
<td>134</td>
<td>118</td>
</tr>
<tr>
<td>San Antonio, TX</td>
<td>NA</td>
<td>1010</td>
<td>205</td>
<td>121</td>
</tr>
<tr>
<td>Tampa Bay, FL</td>
<td>13</td>
<td>20</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>Terrebonne, LA</td>
<td>771</td>
<td>1596</td>
<td>3006</td>
<td>1438</td>
</tr>
<tr>
<td>Upper Laguna Madre, TX</td>
<td>317</td>
<td>951</td>
<td>186</td>
<td>114</td>
</tr>
<tr>
<td>Vermilion-Teche, LA</td>
<td>146</td>
<td>928</td>
<td>1729</td>
<td>603</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>1958</strong></td>
<td><strong>14218</strong></td>
<td><strong>12120</strong></td>
<td><strong>5465</strong></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Year</th>
<th>Black Drum</th>
<th>Red Drum</th>
<th>Spotted Seatrout</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FL</td>
<td>LA</td>
<td>TX</td>
</tr>
<tr>
<td>1989</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1992</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1993</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1994</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1995</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1996</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1997</td>
<td>0</td>
<td>151</td>
<td>0</td>
</tr>
<tr>
<td>1998</td>
<td>0</td>
<td>264</td>
<td>0</td>
</tr>
<tr>
<td>1999</td>
<td>0</td>
<td>348</td>
<td>0</td>
</tr>
<tr>
<td>2000</td>
<td>0</td>
<td>328</td>
<td>0</td>
</tr>
<tr>
<td>2001</td>
<td>0</td>
<td>155</td>
<td>0</td>
</tr>
<tr>
<td>2002</td>
<td>0</td>
<td>225</td>
<td>0</td>
</tr>
<tr>
<td>2003</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2005</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2007</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2008</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2009</td>
<td>0</td>
<td>0</td>
<td>48</td>
</tr>
<tr>
<td>2010</td>
<td>0</td>
<td>0</td>
<td>46</td>
</tr>
<tr>
<td>2011</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2012</td>
<td>8</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>2013</td>
<td>29</td>
<td>4</td>
<td>84</td>
</tr>
<tr>
<td>2014</td>
<td>24</td>
<td>0</td>
<td>80</td>
</tr>
<tr>
<td>2015</td>
<td>0</td>
<td>0</td>
<td>333</td>
</tr>
<tr>
<td>Total</td>
<td>62</td>
<td>1483</td>
<td>413</td>
</tr>
</tbody>
</table>
APPENDIX C. GEAR SELECTIVITY HISTOGRAMS

Figure C.1. Black drum female gear selectivity from Florida, Louisiana, and Texas.
Figure C.2. Black drum male gear selectivity from Florida, Louisiana, and Texas.
Figure C.3. Red drum female gear selectivity from Florida, Louisiana, and Texas.
Figure C.4. Red drum male gear selectivity from Florida, Louisiana, and Texas.
Figure C.5. Spotted seatrout female gear selectivity from Florida, Louisiana, and Texas.
Figure C.6. Spotted seatrout male gear selectivity from Florida, Louisiana, and Texas.
Shane Alexander Flinn was born in Lansing, Michigan in 1988. He earned his Associate of Science in Biology from Lansing Community College in 2013 and a Bachelor of Science in Fisheries and Wildlife from Michigan State University in 2016.