

9-1-2010

Growth of Atlantic Salmon (*Salmo salar*) in Freshwater

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GROWTH OF ATLANTIC SALMON (*Salmo salar*) IN FRESHWATER

A Dissertation Presented

by

DOUGLAS BRADLEE SIGOURNEY

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

September 2010

Wildlife and Fisheries Conservation

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ACKNOWLEDGEMENTS

I am indebted to many people for their support, advice and encouragement in completing this dissertation. I first would like to thank my advisor Dr. Benjamin Letcher and my unofficial co-advisor Dr. Richard A. Cunjak for offering me this extraordinary opportunity to work on salmon in the Miramachi River system. Both Ben and Rick have an ability to instill a sense of excitement and curiosity in their students. I am deeply grateful for their support and mentorship. I would also like to thank my many committee members. Dr. Paul Barten and my unofficial committee Dr. Martha Mather member were always willing to meet with me and offer advice not only on aspects of my dissertation but also on pursuing a career in the natural resources field. I would also like to thank Dr. Andrew Whiteley for be willing to fill in as a committee member at the last minute. Finally, I would like to thank Dr. Steve Munch for working patiently with me on my third chapter of my dissertation. I have learned a lot from working with Steve and for that I am most grateful.

In addition to my committee, I would like to thank the Natural Resources and Conservation department and in particular our department head Dr. Paul Fissette and our graduate program director Dr. Kevin McGarigal. Both Paul and Kevin were greatly supportive and helpful as I transitioned back to full time status after spending some time away from the university.

The long road to completing this dissertation was faced with many obstacles and difficult times. I was fortunate to have the support of many great friends I met along the way. I would like to thank the many great people I worked with at Catamaran Brook including Tim Upham, Yannick DeSilva, Andre Drapeau, James Connop, Wes and

Tommy Le Bouthillier, Rachel Keeler, Ida Bacon, and Stephan LeBlanc. Peter Hardie deserves particular thanks for his support and encouragement. Finally, I am most grateful to the hard work, patience and excellent attitude of Aaron Fraser. Aaron was in many ways my right hand man during my field work and I am thankful for the many hard hours he put in to helping me with my field work. I consider Aaron a great friend.

In addition to Catamaran, I have met many great people while being a student at the Conte Lab. Gregg Horton was particularly helpful in preparing me for field work. I enjoyed many great conversations with Gregg as we navigated our way through graduate school. I have also have enjoyed many discussions with Jason Coombs, Jamie Pearlstein and other members of the Letcher lab. In addition to Ben's students, I will always have fond memories of working with Todd Dubreuil, Matt O'Donnell and Tyler Evans. We enjoyed many a great time in the field. I would also like to thank the many graduate students I have met during my tenure at UMass. I had the good fortune to meet many wonderful people and I am grateful to for their support during my most trying times. In particular, I would like to thank Kirk Olson who is a great friend.

Finally, I would like to thank my family for their support, faith and patience while I worked diligently on my dissertation.

ABSTRACT

GROWTH OF ATLANTIC SALMON (*Salmo salar*) IN FRESHWATER

SEPTEMBER 2010

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Growth plays a key role in regulating ecological and population dynamics. Life history characteristics such as age at maturity, fecundity and age and size at migration are tightly linked to growth rate. In addition, size can often determine survival and individual breeding success. To fully understand the process of growth it is important to understand the mechanisms that drive growth rates. In Atlantic salmon, growth is critical in determining life history pathways. Models to estimate growth could be useful in the broader context of predicting population dynamics. In this dissertation I investigate the growth process in juvenile Atlantic salmon (*Salmo salar*). I first used basic modeling approaches and data on individually tagged salmon to investigate the assumptions of different growth metrics. I demonstrate the size-dependency in certain growth metrics when assumptions are violated. Next, I assessed the efficacy of linear mixed effects models in modeling length-weight relationships from longitudinal data. I show that combining a random effects approach with third order polynomials can be an effective way to model length-weight relationships with mark-recapture data. I extend this

hierarchical modeling approach to develop a Bayesian growth model. With limited assumptions, I derive a relatively simple discrete time model from von Bertalanffy growth that includes a nonparametric seasonal growth function. The linear dynamics of this model allow for efficient estimation of parameters in a Bayesian framework. Finally, I investigated the role of life history in driving compensatory growth patterns in immature Atlantic salmon. This analysis demonstrates the importance of considering life history as a mechanism in compensatory growth. Information provided in this dissertation will help provide ecologists with statistical tools to estimate growth rates, estimate length-weight relationships, and forecast growth from mark-recapture data. In addition, comparisons of seasonal growth within and among life history groups and within and among tributaries should make a valuable contribution to the important literature on growth in Atlantic salmon.

PREFACE

Understanding how individuals within and among populations perform under different environmental regimes is an important goal of ecologists. One way to assess performance is to focus on biological growth over time. Because of the interaction with environmental conditions, influences on life history, links to survival, and ultimate consequences on population dynamics, growth (somatic and gonadal) has been the subject of many ecological studies (Gaston and Lawton 1988, Werner 1988, Brown 1995, Arendt 1997). For example, growth can influence life history by determining size and age at maturity as well as fecundity (Roff 1992). This influence in turn can strongly impact the population dynamics of a species living in a particular environment. Changes in the mean growth rates of individuals within a population can also have significant impacts on the flow of energy through an ecosystem (Lawton 1971, Odom 1971). Identifying the mechanisms controlling growth in a particular species or population is critical to understanding the dynamics of that population and how it interacts with its community.

The study of salmonids in small stream environments offers an enhanced opportunity to study growth because their environment is relatively accessible and often many individuals can be tagged and recaptured and growth trajectories can be analyzed for individuals (Juanes et al. 2000). Studies on stream salmonids have demonstrated the link between growth and competition (Jenkins et al. 1999), growth and life history pathways (Heggenes and Metcalfe 1991, Berglund 1992, Berglund 1995), and growth and movement (Hughes 1998). The ability to recapture many individuals over time allows the opportunity to use detailed survival models (Lebreton et al. 1992) in

combination with information on growth trajectories to enhance the understanding of how growth and size at particular times of the year influence survival. Combined with new technology to mark and recapture animals such as passive integrated transponder (PIT) tags (Prentice et al. 1990) and portable antennas (Roussel et al. 2001, O'Donnell et al. 2010) a wealth of information can now be accessed with important ecological implications. Untangling the link between growth, survival and life history is not only critical to gaining a complete understanding of a particular species, but may also help illuminate general ecological processes and allow for the testing of ecological theory.

In Atlantic salmon, the need to understand the process of growth is made particularly urgent by the unprecedented decline in abundance throughout its range (Parrish et al. 1998). A crucial goal in freshwater is to understand the causes of variability in smolt production within and among river systems (Power and Power 1994, Whalen et al., 2000). The smolt stage in the life history of Atlantic salmon is a period during the freshwater phase that juveniles begin to undergo a metamorphosis both physiologically and morphologically in order to prepare for life at sea (Hoar 1976, Thorpe 1982, Langdon and Thorpe 1985). Effective management of anadromous salmon populations hinges on the ability to accurately predict the number of smolts a spawning stock can produce (Kennedy and Crozier 1993, Power and Power 1994, Chaput et al. 1998). Many attempts have been made at modeling smolt production (Bagliniere et al. 1993, Chaput et al. 1998). However, these studies generally are descriptive, and thus, are unable to define the mechanisms responsible for variations in the number and size of smolts in a particular year class. Because growth is linked to the timing of smolting and survival to the smolt stage could be size dependent (Quinn and Peterson 1996) a better

understanding of the mechanisms controlling growth may help illuminate population level responses resulting in smolt production.

A number of ecological studies have focused on growth modeling to answer a diversity of questions. In fisheries management, generalized growth models are used to assess the mean growth rate of individuals in a population to assess harvest regulations. Models such as the von Bertalanffy model are based on simple physiological principles and are used to model asymptotic growth from age zero through adulthood. Recent advancements of this basic modeling framework include estimating parameters from mark-recapture data (Wang et al. 1995, Laslett et al. 2002) and accounting for temporal variability (Jones et al. 2002, Szalai et al. 2003). In Atlantic salmon, models based on the basic von Bertalanffy framework have been used to understand variation in growth trajectories and size structure (Jones et al. 2002, Gurney et al. 2007). Continued development of these models holds promise for being able to predict growth and understand the consequences of growth on population dynamics (Gurney et al. 2008).

Objectives

In this dissertation I used data and on individually tagged salmon to investigate the growth process in Atlantic salmon. In order to explore the best ways to model growth and to better understand the growth process in Atlantic salmon I developed the following objectives:

- 1) Evaluate commonly used growth metrics and assess their dependence on size.** I use both models and growth data of individually tagged fish from the field and laboratory to assess the size dependency of different growth metrics
- 2) Develop methods to estimate length-weight relationships from individually tagged fish.** For this objective I take advantage of linear mixed effects models to estimate

length-weight relationships when there are multiple observations for individuals.

3) Develop a seasonal growth model based on first principles and apply Bayesian techniques to estimate parameters and parameter uncertainty. To accomplish this objective I focus on simple von Bertalanffy dynamics but include a seasonal growth function to allow growth to vary over time. The Bayesian framework allows me to take advantage of prior information to estimate parameter values

4) Analyze the interaction between size-dependent growth and life history. I use data from both the field and laboratory to look at the effect of life history on size-dependent growth in juvenile salmon.

Summary and Conclusions

A major goal of ecology is to understand the distribution and performance of individuals in a population over time. Doing so will require the use of appropriate techniques that can deal with complexity in data and make as few assumptions as possible. In chapter 1 I found that the choice of growth metrics carries underlying assumptions about the growth process. The instantaneous growth rate equation tends to scale negatively with size as a consequence of the relationship between size and metabolism. An alternative is the standardized mass-specific growth rate equation which can adjust for the effect of metabolism on growth when the metabolic scaling constant is known. However, both estimates of growth in weight and growth in length may be necessary to understand the growth process depending on the question being asked.

The study of length-weight relationships has long been a cornerstone of fishery science. Length-weight relationships (LWRs) are often estimated from a particular location at a particular time using cross-sectional data. With the advent of technology that allows the efficient mark and recapture of animals, biologists often have multiple measurements of length and weight at the individual level. In chapter 2 I looked at the use of linear mixed effects models to take advantage of repeated measures (i.e.

longitudinal) data when estimating LWRs. I found they can be successfully combined with polynomials to estimate LWRs when longitudinal data are available and the relationship between the log of length and the log of weight is not necessarily linear. Such hierarchical models can be particularly useful because they allow other levels such as location or time to be included in the hierarchy.

In chapter 3 I focused on the development of a growth model with the goal of including a temporal function that would allow inference as to the seasonal variation in growth. I found that a relatively simple discrete time model can be derived from the von Bertalanffy function. The advantage of this model is the dynamics are linear which simplifies estimation of parameters. I adopted a Bayesian framework to estimate parameter values and estimates of uncertainty. I found this model performed well when applied to field data and was able to predict seasonal dynamics and differences between two different life history groups of salmon, early smolts, which do not mature in freshwater, and mature parr, which do mature in freshwater.

The effects of size and growth have long interested ecologists as the nature of this relationship can have important implications for population dynamics. In chapter 4 I focused on the interaction between size and life history on growth rates of immature Atlantic salmon. The results suggest that fish on a smolt life history pathway may undergo a compensatory growth response as early as the fall before migration whereas fish that delay migration a year do not display compensatory growth. The results from this analysis have implications for understanding the dynamics of smolt production and the age and size structure of migrating smolts.

In summary, this dissertation provides some useful tools that can be used by ecologists that study a variety of taxa. In addition, it was my goal to investigate the growth process in Atlantic salmon with the aim of gaining a better understanding of the dynamics of life history on growth. Atlantic salmon have provided a model organism to study in this regard. The ideas and tools provided in this dissertation should be of use to both applied and basic ecologists alike in future studies of growth.

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CHAPTER 1

SIZE-INDEPENDENT GROWTH IN FISH: PATTERNS, MODELS AND METRICS

1.1. Abstract

A combination of a dynamic energy budget (DEB) model, field data on Atlantic salmon *Salmo salar* L. and brown trout *S. trutta* L. and laboratory data on Atlantic salmon was used to assess the underlying assumptions of three different metrics of growth including specific growth rate (G), standardized mass-specific growth rate (G_S) and absolute growth rate in length (G_L) in salmonids. Close agreement was found between predictions of the DEB model and the assumptions of linear growth in length and parabolic growth in weight. Field data comparing spring growth rates of age 1+ year and age 2+ year Atlantic salmon demonstrated that in all years the larger age 2+ year fish exhibited a significantly lower G , but differences in growth in terms of G_S and G_L depended on the year examined. For brown trout, larger age 2+ year fish also consistently exhibited slower growth rates in terms of G but grew at similar rates as age 1+ year fish in terms of G_S and G_L . Laboratory results revealed that during the fall of the age 0+ year the divergence in growth between future smolts and non-smolts was similar in terms of all three metrics with smolts displaying higher growth than non-smolts, however, both G_S and G_L indicated that smolts maintain relatively fast growth into the late fall where G suggested that both smolts and non-smolts exhibit a sharp decrease in growth from October to November. During the spring, patterns of growth in length were

significantly decoupled from patterns of growth in weight. Smolts maintained relatively fast growth through April in length but not in weight. These results suggest G_S can be a useful alternative to G as a size-independent measure of growth rate in immature salmonids. In addition, during certain growth stanzas, G_S may be highly correlated with G_L . The decoupling of growth in weight from growth in length over ontogeny, however, may necessitate a combination of metrics to adequately describe variation in growth depending on ontogenetic stage particularly if life histories differ.

1.2. Introduction

Quantifying individual growth rates in a population is often an important component of ecological studies. Variation in growth can represent differences in competitive ability (Nordwall *et al.*, 2001; Harwood *et al.*, 2002; Byström & Andersson, 2005), life history differences (Rowe & Thorpe, 1990; Letcher & Gries, 2003), or variation in environmental quality (Coghlan & Ringler, 2005). In studies of fish populations, a number of methods can be used to characterize growth rates (Wootton, 1990). Researchers generally focus on changes in weight and/or length over a finite interval. When initial sizes and ages are the same among individuals, comparisons of growth rates are relatively straightforward. However, many studies are interested in interactions among individuals of different sizes and/or ages (Nordwall *et al.*, 2001; Byström & Andersson, 2005). When size differs among individuals, choice of a growth metric is susceptible to underlying assumptions about the physiological relationship between size and growth.

A frequently used metric of growth rate in fish populations is the instantaneous or specific growth rate (G) equation (Ricker, 1979). This growth rate metric somewhat

misleadingly appears to adjust for size differences because it divides instantaneous absolute growth rate by initial size ($\frac{dw}{wdt}$) (Wootton, 1990). For two individuals to express the same G , they must grow at an equal proportion of their instantaneous size. This metric assumes exponential growth (Ricker, 1979), but does not adjust for the scaling of metabolism with size. The allometric relationship between size and metabolism in animals is well established (Peters, 1983; Schmidt-Nielsen, 1984). Studies on fish growth have demonstrated an inverse relationship between size and G which is attributed to the scaling of metabolism with size (Brett, 1974; Elliott, 1975; Buckel *et al.*, 1995). Thus, larger individuals are physiologically constrained to grow at a decreasing proportion of their body size (Winberg, 1975).

Poikilotherms, like fish, often exhibit parabolic growth during the immature phase of their life history, which has been attributed to the relationship between size and metabolism (Winberg, 1971; Ostrovsky, 1995). Under the assumption of parabolic growth, an equation for standardized mass-specific growth rate (G_S), which incorporates growth rate allometry and standardizes growth across size ranges, can be derived (Iwama & Tautz, 1981; Ostrovsky, 1995). Calculating G_S requires knowledge of the allometric growth rate exponent describing the scaling of G with size. The exponent can be derived from the negative relationship between size and G . A number of studies on salmonid growth have estimated a value of approximately 0.31 for salmonids (Elliott, 1975; Elliott & Hurley, 1997). By adopting this value of the exponent, recent studies quantifying growth rates in salmonids have opted to use G_S to calculate individual growth rates in lieu of G (Vollestad *et al.*, 2002; Quinn *et al.*, 2004; Grader & Letcher, 2006).

Although G_S may offer a useful alternative to G to calculate growth rates in terms of weight, growth rates in fishes are often reported in terms of increases in length instead of weight. Information on length may be more complete or reliable and researchers may choose to report information on just one aspect of growth. Weight can often be difficult to measure accurately under field conditions and length measurements may be less prone to measurement error. Although the relationship between size and growth rate in weight in fish has been well documented, the relationship between size and growth in length is less clear and usually dependent upon an assumed relationship between length and weight. Under the assumption that weight is proportional to the cube of length, von Bertalanffy growth predicts a decrease in absolute growth rate in length (G_L) with an increase in length (Ricker, 1979). Ostrovsky (1995) mathematically demonstrated that under specific assumptions of a constant length-weight relationship, growth in length is linear. Ostrovsky (1995) also noted, however, that in some chironomid species growth in length is parabolic. Studies that report growth in length, however, often use the relative growth rate equation, which assumes exponential growth in length, to quantify growth in length (Wootton, 1990). Thus, it is not always clear what growth metric to use when there is size variation in length nor is it clear whether or not growth in length can be used as a surrogate for growth in weight.

Theoretical models of fish bioenergetics offer ways to assess scaling of growth rates both in terms of length and weight with size because they include mechanistic rules for the scaling of physiological processes with size. One method of modelling growth that includes flexibility in energy allocation pathways and has been successfully applied to describe growth in salmonids is based upon the theory of dynamic energy budgets

(Koojiman, 2000; Jones *et al.*, 2002). Broeckhusien *et al.* (1994) initially used this dynamic energy budget (DEB) approach to simulate compensatory growth dynamics of salmonids. Their DEB model divides the weight of an organism into different components, which include an immobilizable, structural component, which cannot be used to meet maintenance requirements and a mobilizable, reserve component, which can be used to meet maintenance requirements. Growth in length is directly related to growth in structural carbon and growth in weight is related to the combined growth of both structure and reserve carbon. Jones *et al.* (2002) applied a variant of this model to field data of individually tagged juvenile Atlantic salmon *Salmo salar* L. Their DEB model decouples growth in weight from growth in length, and thus, a constant length-weight relationship need not be assumed. This DEB model was capable of capturing the seasonal growth dynamics of juvenile Atlantic salmon in both length and weight.

In this paper, the equations of Ostrovsky (1995) are briefly reviewed to demonstrate the relationship between size, G and G_S and the assumptions necessary for linear growth in length. The process-based DEB model of Jones *et al.* (2002) is then used to predict growth trajectories of individuals under constant conditions and compare the use of different growth metrics to quantify growth rates when there is significant size variation. To empirically assess the relationship between size and different metrics of growth rate, an extensive set of field data on spring growth rates of individually tagged age 1+ year and age 2+ year Atlantic salmon and brown trout *Salmo trutta* L. was used. Another topic of interest is how flexible energy allocation strategies may act to decouple growth in length from growth in weight such that growth in one dimension may not be representative of growth in another dimension. Atlantic salmon offer a model species to

explore such questions because individuals of the same age can take on different life history strategies that are highlighted by flexible growth dynamics. To ascertain the influence of flexible energy allocation on the interpretation of different growth metrics, data from a laboratory study of Atlantic salmon expressing two different life histories were used.

The purpose of this study was to compare extent to which different growth metrics exhibit size-dependence when the underlying growth process is not necessarily exponential or parabolic and the relationship between weight and length is not necessarily constant. A second objective was to demonstrate how the decoupling of growth in weight from growth in length may necessitate a combination of metrics to adequately describe variation in growth trajectories.

1.3. Materials and Methods

The equation for G divides instantaneous absolute growth rate in weight ($\frac{dW}{dt}$) by current weight (W). The general equation for G can be written as

$$G_w = \frac{1}{W} \frac{dW}{dt} \quad (1)$$

Under the assumption of parabolic growth, absolute growth rate scales as a function of weight (W) according to the equation

$$\frac{dW}{dt} = \Omega W^{1-b} \quad (2)$$

where Ω is a constant related to the growth of an individual of unit size and b is an allometric scaling constant such that $0 < b < 1$ (Gamito, 1998). Substituting equation 2 into equation 1 (i.e. dividing equation 2 by W), demonstrates that G also scales with size

$$G = \Omega W^{-b} \quad (3)$$

which results in a negative linear relationship on a double logarithmic scale ($\log G$ vs $\log W$) where $\log(\Omega)$ is the intercept and $-b$ is the slope. Studies that aim to quantify growth in the absence of size-dependence are generally interested in calculating Ω . Ostrovsky (1995) showed that under the assumption of allometric growth, an equation for standardized mass-specific growth rate (G_S) can be derived as follows:

$$\Omega = \frac{W_t^b - W_0^b}{b \cdot t} \quad (4)$$

where Ω represent G_S , W_0 represents weight at the start of the growth interval and W_t represents weight at the end of the growth interval. This equation requires that the allometric growth rate exponent b is known. The exponent can be estimated empirically by performing a linear regression $\log(G)$ vs $\log(W)$ over a range of sizes and estimating the slope coefficient.

Ostrovsky (1995) also demonstrated mathematically that if the relationship between length and weight is assumed to be

$$W=aL^{\beta} \quad (5)$$

where a and β are constants, then an equation for growth in length can be derived as

$$\frac{dL}{dt} = (\Omega a^{-b} \beta^{-1}) L^{1-b\beta} = KL^{1-c} \quad (6)$$

where $K=\Omega a^{-b} \beta^{-1}$ and $c=b\beta$ are constants. If $c=1$ (i.e. $\beta = \frac{1}{b}$) then equation 6 is

transformed into a straight line function such that

$$\frac{dL}{dt} = K \quad (7)$$

Thus, absolute growth in length (G_L) is often calculated as the difference in length between two time periods such that

$$G_L = \frac{L_t - L_0}{t} \quad (8)$$

where L_t and L_0 represent final and initial lengths, respectively, and t represents that time interval between measurements.

1.3.1. DEB simulations

Using the DEB growth model of Jones et al. (2002), growth of 30 individuals of different sizes was simulated for a 30 day period. Starting length was selected from a normal distribution with a mean of 10 cm and a standard deviation of two cm to provide a reasonably wide range of initial sizes. Model equations and parameter values are provided in Table 1.1. For all parameters, the same values reported in Jones et al. (2002) for the baseline (population level) model were used. Weight was calculated by assuming each individual started at the same nutritional state (ρ), which was above the "defended" level (ρ_0) or the level below which allocation to reserves increases ($\rho > \rho_0 + \rho_w$, see Table I for definitions). In the version of Jones et al. (2002), the seasonal food function is described by four parameters which estimate the rise and fall and magnitude of food over the course of a year. For the purposes of our simulation, the food environment was fixed to be maximum ($F=1$) and temperature was set constant at 15 °C. Using the predicted initial and final weights, G , G_S and G_L were calculated for each individual. From these simulated results, the allometric growth rate exponent (b) was determined by calculating the slope of the relationship between log weight (W) and log G . Several choices of W can be used when performing the regression including initial mass (W_0) and mean mass (\bar{W}) over the growth period (Elliot & Hurley, 1995). Because the choice of W can lead to spurious estimates of b , the iterative approach suggested by Elliot & Hurley (1995) was used to calculate b . After the value of b was determined, G_S was calculated for each individual and the relationship between log W_0 and log G_S assessed. In addition, the relationship between initial length and G_L was also assessed.

1.3.2. Field Data

Field data on spring growth rates of juvenile Atlantic salmon and brown trout from an ongoing study of individually tagged salmonids were used to empirically examine the relationship between size and different growth metrics. Data were collected from the West Brook River, a tributary to the Connecticut River. Since 1997, a number of samplings were conducted each year to address seasonal variation in growth and survival. All fish were captured by electrofishing. All fish larger than 60 mm fork length and greater than two grams in weight were anesthetized and tagged with a PIT (passive integrated transponder) tag. Further details on the study site and data collection are given elsewhere (Letcher *et al.*, 2002; Letcher & Gries, 2003; Carlson & Letcher, 2003). Spring growth was the focus of the analysis because growth rates are highest during this interval.

To test for a relationship between size and growth rate, one cannot simply run a regression of initial size vs growth rate because measurement error can result in a spurious negative correlation (Lytle, 2001). To circumvent this problem, Lytle (2001) suggests the use of reduced major axis (RMA) regression of initial vs final size. This approach reduces the bias due to sampling error by taking into account error in the x variable as well as the y variable. If all individuals are growing exponentially in weight and linearly in length then a slope of one from the regression of initial vs final natural log (\log_e) weight and from the regression of initial vs final length would reflect a null hypothesis of no size dependence in growth. A slope less than one indicates that smaller individuals are growing relatively faster than larger individuals and vice versa if the slope

is greater than one (Carlson *et al.*, 2004). However, it is unclear what the slope should be if there is measurement error and individuals are displaying parabolic growth. To understand how the slope of initial vs final \log_e weight is affected by both measurement error and parabolic growth, data were simulated over a range of sizes comparable to the range of sizes observed in the field data. An estimate of measurement error was used that is in the range of error expected from our data (Letcher *et al.*, 2003). To simulate parabolic growth the following equation was used

$$W_t = [\Omega bt + W_0^b]^{\frac{1}{b}} \quad (9)$$

where W_0 and W_t are initial and final weight, respectively, Ω is the underlying growth rate and b is the allometric exponent set to a value of 0.31. Growth was simulated to mimic the magnitude of growth observed during the spring growing season. The slopes of initial vs final \log_e weight were calculated using RMA regression on the simulated data. A total of 5000 simulations were performed and the mean slope was calculated as a null expectation of what the slope should be under parabolic growth and a level of measurement error comparable to that observed in the field data. Next, RMA regressions were performed on initial vs final \log_e weight and initial vs final length for spring intervals using individually tagged juvenile Atlantic salmon and brown trout. Individuals in both the age 1+ year and age 2+ year age classes were combined in the analysis to include a range of sizes for both species. The slopes of initial vs final \log_e weight were compared to the *a priori* expectation based on statistical simulations.

To compare growth metrics in distinguishing between differences in growth among groups that differ in initial size G , G_S and G_L were calculated for both age 1+ year and age 2+ year Atlantic salmon and brown trout captured over the spring interval for a number of different years. To calculate G_S an estimate of b reported in the literature for juvenile Atlantic salmon ($b=0.31$, Elliot & Hurley, 1997) and brown trout ($b=0.308$, Elliot, 1975) were used. It is possible that estimates of the allometric exponent may vary among populations, however, Iwama & Tautz (1981) report that inaccuracy in the estimate of b should have little effect on the estimate of growth rate. The interest was in comparing these metrics when there are differences in the size of the two groups being compared. For each growth metric, a two-way ANOVA was performed with growth rate as the response variable and year and age as categorical predictor variables. An honest significance difference (HSD) *post-hoc* test was used to test for differences among age groups within each year.

Another method that can be employed to compare specific growth rates among groups when there is a range of sizes is to use initial size as a covariate to control for the effect of size on growth rate (Bacon *et al.*, 2005). To assess the utility of this method and to adjust for differences in the length of the growth interval, general linear models (GLM) were constructed using $\log_e G$ as the response variable, year and age as categorical predictor variables and \log_e initial weight and length of the growth interval as covariates.

1.3.3. Laboratory Data

The analysis used to compare growth metrics in the field data was repeated on a set of laboratory data on growth of juvenile Atlantic salmon. The data were collected in

an experiment investigating differences in growth rates between smolts and non-smolts raised in a laboratory environment (see Obedzinski & Letcher, 2004 for details).

Differences in growth, shape and body condition among smolts and non-smolts has previously been well described (Thorpe, 1977; Rowe & Thorpe, 1990; Huntingford *et al.*, 1992; Letcher, 2003). The intention of this analysis is to bring attention to the possible decoupling of growth in length from growth in weight over ontogeny and provide another example of comparing growth metrics when sizes differ among groups of the same age.

All fish used in this analysis were from the same stock and the same cohort. Fish were initially tagged in the fall of their age 0+ year at a size greater than 6 cm and a weight greater than 2 grams. Length and weight were recorded for each fish at approximately one month intervals from October to June resulting in a total of eight growth intervals.

By the late spring sample fish were easily assigned a life history status based on a combination of size and morphological characteristics (Thorpe, 1977; Nicieza, 1995).

For each growth interval, G , G_S and G_L were calculated and compared as metrics for quantifying differences in growth among the two life history groups. To calculate G_S , a value of b for Atlantic salmon reported in the literature was used (Elliot & Hurley, 1997).

As with analysis of field data, we performed a two-way ANOVA on each growth metric with growth rate as the response variable and sampling interval and life history group as categorical predictor variables. An HSD *post-hoc* test was used to test for differences among life history groups within each growth interval.

1.4. Results

1.4.1. DEB Simulations

A tight negative relationship between initial weight and G was predicted by the DEB growth model of Jones et al. (2002) ($\log_e G = -2.54 - 0.23 \log_e W_0$, $r^2 = 0.99$). Using the iterative approach of Elliot & Hurley (1995), a value of 0.2828 was estimated for the allometric growth rate exponent b . With this value of b , the G_S equation appropriately adjusted estimates of growth rate in weight such that there was no relationship between size and growth rate ($\log_e G_S = -2.19 + 1.64 \times 10^{-5} \log_e W_0$, $r^2 = 0.005$). A slight negative relationship between initial length and G_L was predicted by the model; however, the slope was close to zero such that differences in G_L between the largest individual and smallest individual were negligible ($G_L = 0.92 - 0.0005 L_0$, $r^2 = 0.99$).

1.4.2. Field Data

Statistical simulations indicated that under parabolic growth with an allometric exponent of 0.31, the slope of initial vs final \log_e weight is approximately 0.84 with estimates ranging from 0.81 to 0.87 when there is measurement error in both initial and final weight. For juvenile Atlantic salmon slopes from the RMA regression of initial vs final \log_e weight were below this value suggesting that larger fish were growing slower than smaller fish even after adjusting for the effects of parabolic growth (Table 1.2). RMA regressions of initial vs final length produced slopes that were generally less than one also suggesting slower growth by larger fish in terms of length (Table 1.2). For the brown trout data, the slopes of the RMA regressions of initial vs final \log_e weight were generally within the range of our null expectation for size-independent parabolic growth, suggesting that large and small fish were growing at the same mass specific rate (Table

1.3). These results were in agreement with results from the analysis of initial vs final length, where slopes were consistently around one indicating no size dependence in growth in length (Table 1.3).

Differences in growth rates among age classes depended on the growth metric analyzed as well as on the year and species. For Atlantic salmon there was a significant effect of age and year on G (Table 1.4). Age 1+ year fish consistently had a higher G than age 2+ year fish for all years (Figure 1.1a). For G_S , a significant age and year effect as well as an interaction between age and year was also detected (Table 1.4). However, in contrast to G , in some years there were no differences in growth among age classes and in other years age 1+ year fish grew faster than age 2+ year fish (Figure 1.1b). There was also a significant effect of age and year on G_L (Table 1.4). For most years, the results for growth in length mirrored the results from the analysis of G_S . In years when age 1+ year fish grew faster than age 2+ year fish in G_S they also grew faster in G_L , with the exception of 1999 where there was no significant difference in G_L but there was a significant difference in G_S (Figure 1.1c).

For the brown trout, analysis there was a significant effect of age on G (Table 1.5). As with juvenile Atlantic salmon, the larger age 2+ year class had significantly lower G than the smaller age 1+ year class in all years examined (Figure 1.2a). For G_S , there was no significant age effect (Table 1.5). Although growth rates varied among years, there were no significant differences among age classes within years (Figure 1.2b). The results for G_L were similar to G_S except a significant age x year interaction was present (Table 1.5). In years of slow growth, age 2+ year fish seemed to have lower growth rates than age 1+ year fish and in years with fast growth, age 2+ year fish seemed

to exhibit faster growth than smaller age 1+ year fish (Figure 1.2c). However, similar to the results from G_S , there was no significant difference in growth among age classes within years.

The GLM model indicated a significant age and size effect on G (Table 1.6). The interaction term was also significant suggesting that the relationship between size and G differs among age classes. For Atlantic salmon, there was a significant negative correlation between length of the growth interval and G . The effect of growth interval was only marginally significant for brown trout.

1.4.3. Laboratory Data

For all growth metrics examined, there was a significant effect of life history status and sample date as well as a significant interaction between the two predictor variables (Table 1.7). Over the first growth interval (October), future smolts displayed faster growth rates than future non-smolts in terms of all three metrics (Figure 1.3). During the proceeding interval (November), both smolts and non-smolts undergo a substantial decrease in G (Figure 1.3a); however, G_S suggested that smolts only exhibited a minor decrease in growth (Figure 1.3b). This pattern is similar in terms of G_L , with smolts displaying only a minor decrease in growth from October to November (Figure 1.3c). Thus, the pattern in growth during the first two intervals are similar for both G_S and G_L with smolts exhibiting faster overall growth than non-smolts and maintaining relatively fast growth during the late fall interval. The pattern of growth over the winter intervals is similar in terms of all three metrics, with both life history groups displaying lower growth rates overall and smolts maintaining higher growth than non-smolts. By

February differences in growth in weight were similar in terms of both G_S and G with no significant difference among life history groups, although during the March intervals, G suggests that non-smolts had surpassed smolts in terms of growth rate whereas G_S suggests that smolts still maintained a higher growth rate than non-smolts. Growth in length; however, suggest that smolts maintained significantly faster growth rates than non-smolts until the April interval. By May non-smolts grew faster than smolts in terms of all three metrics.

1.5. Discussion

One goal of this paper was to compare different growth metrics when neither exponential growth nor parabolic growth is explicitly assumed in the growth process and the relationship between length and weight is not necessarily constant. To simulate growth in length and weight in a manner that does not rely on these assumptions, a mechanistic process-based model, which includes a simple rule for energy allocation, was used. This model was chosen because it decouples growth in weight from growth in length, is based on dynamic energetic budget theory of growth, and was found to accurately predict growth trajectories in both length and weight of juvenile Atlantic salmon. There was strong agreement between model predictions and the assumption of parabolic growth under constant conditions. The model also predicted a linear growth trajectory in length. Application of the G_S equation to the simulated growth trajectories appeared to successfully standardize growth rates across size ranges such that growth rate in weight was not size dependent. This result lends credence to the use of the G_S equation as a size-independent measure of growth rate in salmonids and suggests that an

assumption of linear growth in length may be valid for salmonids during the immature phase of growth.

Testing for size dependence in growth rates in the wild can be difficult because error in measured variables can result in a negative bias (Lytle 2001). One way to address this problem is to use RMA regression on initial vs final size. The RMA regressions on field data generally suggested that during most spring intervals, growth in juvenile Atlantic salmon was size dependent with larger individuals growing at a slower rate than smaller individuals both in terms of weight and length, but that growth in brown trout was generally not size dependent. For Atlantic salmon, slopes of initial vs final length were less than one in all but one year and slopes of initial vs final \log_e weight were less than 0.84. This result suggests that there is size dependence in growth over these intervals. A possible explanation for this size/age dependence is discussed in the following paragraph. For brown trout, the slopes of initial vs final length were generally around one and the slope of initial vs final \log_e weight were generally around 0.84. Although this does not definitively prove that brown trout are growing linearly in length and parabolically in weight (with an allometric exponent of 0.31), it is consistent with our null expectation. In a study on growth rates in brown trout, Elliot (1975) found a strong support for parabolic growth in weight over a range of sizes. This relationship has been established in other salmonids (Brett, 1974) including Atlantic salmon (Elliot & Hurley, 1997). There is a paucity of information, however, investigating the relationship between size and growth in length in fishes. When quantifying growth in length some studies report relative growth in length (Rowe & Thorpe, 1990; Metcalfe *et al.*, 2002), which assumes exponential growth whereas other studies report absolute growth in length

(Whalen & Parrish, 1999; Steingrímsson & Grant, 2003), which assumes linear growth. The present investigation of this relationship is more consistent with an assumption of linear growth in length.

In a comparison of growth metrics, differences in growth rate depended on the growth metric used for both Atlantic salmon and brown trout. For both species, the larger age 2+ year classes always exhibited slower growth in weight when growth rate was quantified using G . The observed slower growth of the larger age class is consistent with previous studies that report an inverse relationship between size and G (Elliot, 1975; Jobling, 1983; Elliot & Hurley, 1997). Using just this metric of growth, it would be unclear if differences among age classes are the result of ecological factors (e.g. limited food availability for larger fish) or solely due to the effect of size on G . When growth in weight was quantified using G_S , there was no effect of age on growth for brown trout whereas differences in growth rates among age classes of Atlantic salmon depended on the year examined. Also, the pattern in growth in length in terms of G_L was consistent with the pattern in growth in G_S . For brown trout, there was no age effect and for Atlantic salmon in years when age 2+ year fish grew slower in G_S they also exhibited slower growth in G_L . These results are qualitatively similar to the RMA regressions in suggesting an age effect in growth for salmon but not for brown trout. In a study on growth rate of brown trout in Norwegian streams, Vollestad *et al.* (2002) found that G_S tended to decrease with age, however, their study covered a wider range of age classes throughout the summer and fall, when maturity may have influenced differences in growth rates among age classes. The apparent slower growth of age 2+ year salmon is not surprising given the complex life histories of salmon in the Westbrook. Most of the

fast growing salmon emigrate as age 2+ year smolts in the spring (Letcher *et al.*, 2002; Letcher & Gries, 2003). Thus, slower growing individuals are left during the spring interval. This pattern of smolting and emigration may explain why age 1+ year fish exhibit faster spring growth than age 2+ year fish.

Although RMA regressions generally agreed with analyses of growth metrics, some discussion of the inconsistencies is warranted. Under our null expectation, if there is no size-dependence in G_L or G_S , then the slope of initial vs final length should be one and the slope of initial vs final loge weight regressions should be approximately 0.84. This expectation was generally met for brown trout, but for Atlantic salmon slopes from RMA regressions indicated slower growth of larger fish in most years in both length and weight, but analysis in terms of G_L and G_S indicated in some years there was no difference among age classes. This discrepancy may partly be an artifact caused by variation in the growth rate interval. Growth over the spring likely varies as environmental conditions such as flow, water temperature and food availability change. If the growth interval varies, it may appear that individuals with a shorter growth interval are growing at a faster rate. Results from the GLM indicated that length of the growth interval was a significant predictor of growth in Atlantic salmon data, but only marginally significant in brown trout. A cursory examination of growth intervals revealed that age 2+ year Atlantic salmon were often captured over shorter time intervals than age 1+ year Atlantic salmon, which may have biased their growth rates upward. This effect of differences in the growth rate interval may partly explain the discrepancy between the RMA regressions and the analysis of the growth rate metrics

Results from the GLM were difficult to interpret because of a significant interaction between age and initial weight for both Atlantic salmon and brown trout. Using initial size as a covariate offers an advantageous alternative to adjust for the effect of size on G because an estimate of b is not needed. This approach has been used in other studies as a way to adjust for differences in initial size when G is the response variable (Bacon *et al.*, 2005; Jonsson & Jonsson, 2007). However, if the relationship between size and G is non-linear due to ecological constraints for example, then the rate of decrease in growth in one group may be different from the rate of decrease in growth in another group leading to non-parallel slopes and complicating interpretation of growth rate differences.

Differences in growth between smolts and non-smolts depended not only on the time of year and the ontogenetic stage, but also on the growth metric used to quantify growth rate. During the age 0+ fall, future smolts exhibited faster growth than non-smolts regardless of the metric used. However, from the October to November both G_S and G_L suggested that future smolts only exhibit a minor decrease in growth where as G suggested a substantial decrease in growth for both groups. Similar to the field data, characterization of the magnitude and timing of divergence in growth rate using G_L closely matched those using G_S , and hence, use of either growth metric would result in the same conclusion about timing and magnitude of divergence in growth among these groups. Furthermore, the close relationship between G_S and G_L indicates that rapid growth in length accompanies rapid growth in weight over this growth period. In the spring the choice of a growth metric was found to influence conclusions about differences in growth among life history groups. Both G and G_S indicated no significant

difference in growth rates among life history groups, although G suggests that non-smolts surpass smolts in March in growth where as G_S suggest that smolts are still growing faster. Faster growth in length, however, is maintained by smolts late into the spring and it is not until the last interval that non-smolts surpass smolts in growth rate in terms of length. Overall, these results suggest that during the spring, growth in length is significantly decoupled from growth in weight among these life history groups. A number of studies have suggested that during certain life stages or seasons growth in length is decoupled from growth in weight (Edmundson & Mazumder, 2001; Bacon *et al.*, 2005). Using only one measure of growth may obscure interpretation of growth rate differences, and thus, a combination of both metrics may be necessary to more completely describe variation in the growth trajectory.

The dynamic growth trajectories of Atlantic salmon through ontogeny offer one example of how variable energy allocation strategies can separately influence growth in length and growth in weight. A growing body of literature is beginning to unravel the complex relationship between growth rates in fish and plasticity in energy allocation decisions (Post & Parkinson, 2001; Hurst & Conover, 2003; Garvey *et al.*, 2004). For example, research on compensatory growth shows that fish recovering from starvation may prioritize energy allocation to replenishing lipid reserves over growth in structural tissue (Nicieza & Metcalfe, 1997; Metcalfe *et al.*, 2002). In temperate fishes, body size and season can interact with selection pressures in determining energy allocation strategies. For example, Garvey *et al.* (2004) found that growth in length during winter might be selectively advantageous for smaller members of a cohort when predation is high. Similarly, Post & Parkinson (2001) found that for rainbow trout *Oncorhynchus*

mykiss (Walbaum) entering the winter season, selection favors energy allocated to somatic growth for small fish, but for large fish an energy storage strategy is more profitable. Thus, selective pressure to grow in length or weight may differ among individuals of different sizes independent of metabolic constraints. For Atlantic salmon, life history plays a significant role as fish that are preparing to enter the marine environment undergo a series of physiological and morphological changes to prepare for life at sea (McCormick & Saunders, 1987). In this study, a prioritization towards growth in length was observed in fish that were transitioning to the smolt stage. The plasticity in growth demonstrated by studies of growth in fishes highlight the importance of considering energy allocation strategies when comparing growth rates among individuals from different size classes and environments. Future studies that aim to relate environmental conditions to growth rate should be careful to consider the influence of energy allocation patterns when quantifying growth rate and correlating variation in growth to environmental variables.

Growth is a metabolic process and therefore subject to metabolic constraints (Brett, 1979; Winberg, 1971). A number of studies have demonstrated a clear inverse relationship between G and body size in fish (Brett, 1974; Elliot, 1975), which has been attributed to the scaling of metabolism with size (Peters, 1983). It is important, however, to note that in ecological settings, other constraints on growth might dominate the size-growth rate relationship. For example, ontogenetic niche shifts in diet may lead to an increase in growth with size as fish transition to piscivory (Olson, 1996; Post, 2003). In such cases morphological constraints dictate the size-growth rate relationship. Nonetheless, size represents an important influence on growth rates. Many important

studies aim to quantify difference in growth performance among groups of different sizes including studies on interspecific competition (Harwood *et al.*, 2001), intercohort competition (Byström & Andersson, 2005) and compensatory growth (Ali *et al.*, 2003). It is fundamental to studies of this nature that the effect of size on growth rate is taken into account when interpreting differences in growth performance. There are a number of methods and approaches to quantifying growth in fishes, but each is dependent upon underlying assumptions of the growth process (Ricker, 1979; Ostrovsky, 1995). The results of the present study generally supported an assumption of parabolic growth in weight and linear growth in length during juvenile development in salmonids. In addition, growth in length appears to be tightly coupled with growth in weight early in ontogeny, and therefore, substituting one measure of growth for another may not compromise interpretation of growth rate differences among individuals or groups even when there is size variation. Differences in life history strategies and the effects of maturity may, however, result in changing energy allocation strategies over ontogeny (Vollestad *et al.*, 2002). During later life history stages, flexible energy allocation strategies may decouple growth in length from growth in weight. To fully describe growth, simultaneous analysis of both growth in length and weight may be necessary to provide a more complete description of variation in growth trajectories.

Table 1.1. Equations and parameter values from the dynamic energy (DEB) model.

<i>state variables</i>	<i>Definition</i>	
S	Structural Mass	
R	Reserve Mass	
L	Length (cm)	
W	Weight (g)	
<i>global parameters</i>	<i>Definition</i>	<i>Value</i>
W_0	Weight scale	0.01394
β	Weight-length power	0.684
γ	Weight-carbon power	0.72
A_0	Assimilation scale	0.095
M_0	Basal metabolic rate scale	0.014
P	Basal metabolic rate power	0.75
T_m	Basal metabolic rate temperature	6.0
T_a	Assimilation temperature	12.0
α	Length-structure power	0.248
L_0	Length-scale power	2.35
ρ_0	Defended reserve ratio	2.44
ρ_w	Allocation switch width	0.362
k_0	Max. proportion of assimilate allocated to S	0.232
F	Food	1
Equation	Definition	Equation No.
	Net carbon assimilation rate	
$A=A_0FS^p\exp[\frac{T}{T_a}]$		(10)
	Maintenance cost	
$M=M_0(R+S)^p\exp[\frac{T}{T_m}]$		(11)
$\rho=\frac{R}{S}$	Reserve to structure ratio	(12)
$\frac{dS}{dt}=kA$	Rate of change of structural carbon	(13)
$\frac{dR}{dt}=A-M-\frac{dS}{dt}$	Rate of change of reserve carbon	(14)
$L=L_0S^\alpha$	Relationship between structural carbon (S) and length	(15)
$W=W_0L^\beta(R+S)^\gamma$	Relationship of wet mass (W) to length (L) and total carbon mass (R+S)	(16)
$k=\begin{cases} k_0 & \rho > \rho_0 + \rho_w \\ k_0(\rho - \rho_0)^+ / \rho_w & otherwise \end{cases}$	k-rule determining the amount of assimilate allocated to structure as a function of the R to S ratio	(17)

Table 1.2. Results from reduced major axis (RMA) regressions of (a) initial length (L_0) vs final length (L_t) and (b) natural log of initial weight ($\text{Log}_e W_0$) vs natural log of final weight ($\text{Log}_e W_t$) for individually tagged juveniles Atlantic salmon captured over eight different spring sampling intervals. Age 1+ year and age 2+ year fish were combined in all analyses.

Regression	Sample (year)	n	Slope Coefficient (SD)	r
(a) L_0 vs L_t	9 (1998)	218	0.90 (0.01)	0.98
	18 (1999)	342	0.85 (0.01)	0.97
	25 (2000)	327	1.02 (0.02)	0.96
	32 (2001)	207	0.88 (0.01)	0.98
	38 (2002)	266	0.94 (0.02)	0.96
	43 (2003)	286	0.83 (0.02)	0.94
	48 (2004)	390	0.83 (0.02)	0.94
	52 (2005)	325	0.90 (0.02)	0.89
(b) $\text{Log}_e(W_0)$ vs $\text{Log}_e(W_t)$	9 (1998)	218	0.68 (0.01)	0.97
	18 (1999)	341	0.64 (0.01)	0.94
	25 (2000)	327	0.73 (0.01)	0.94
	32 (2001)	207	0.69 (0.01)	0.96
	38 (2002)	266	0.76 (0.02)	0.93
	43 (2003)	286	0.62 (0.01)	0.93
	48 (2004)	390	0.65 (0.01)	0.93
	52 (2005)	324	0.74 (0.02)	0.84

Table 1.3. Results from reduced major axis (RMA) regressions of (a) initial length (L_0) vs final length (L_t) and (b) natural log of initial weight ($\text{Log}_e W_0$) vs natural log of final weight ($\text{Log}_e W_t$) for individually tagged brown trout captured over six different spring sampling intervals. Age 1+ year and age 2+ year fish were combined in all analyses.

Regression	Sample		Slope Coefficient	
	(year)	n	(S.D.)	r
(a) L_0 vs L_t	25 (2000)	40	1.06 (0.03)	0.98
	32 (2001)	80	0.96 (0.02)	0.98
	38 (2002)	99	1.02 (0.02)	0.98
	43 (2003)	34	1.03 (0.03)	0.98
	48 (2004)	42	0.97 (0.03)	0.98
	52 (2005)	137	1.01 (0.02)	0.97
(b) $\text{Log}_e(W_0)$ vs $\text{Log}_e(W_t)$	25 (2000)	41	0.81 (0.07)	0.82
	32 (2001)	81	0.84 (0.08)	0.61
	38 (2002)	100	0.86 (0.05)	0.83
	43 (2003)	35	0.75 (0.07)	0.85
	48 (2004)	43	0.77 (0.10)	0.64
	52 (2005)	137	0.78 (0.05)	0.71

Table 1.4. Results from a two-way ANOVA on spring growth rates of juvenile Atlantic salmon where age (1+ year or 2+ year) and year are included as independent variables and the dependent variable is either a) G , b) G_S or c) G_L .

	Effect	d.f.	MSE	F	P
(a)	Intercept	1	0.292	42058.73	<0.0001
	Year	7	0.002	243.76	<0.0001
	Age	1	0.014	2085.16	<0.0001
	Year x Age	7	0.0001	16.64	<0.0001
	Error	2344	0.00001		
(b)	Intercept	1	1.470	43863.00	<0.0001
	Year	7	0.008	250.38	<0.0001
	Age	1	0.004	121.91	<0.0001
	Year x Age	7	0.001	23.31	<0.0001
	Error	2344	0.00003		
(c)	Intercept	1	291.37	43619.94	<0.0001
	Year	7	1.06	157.90	<0.0001
	Age	1	0.99	148.30	<0.0001
	Year x Age	7	0.14	21.36	<0.0001
	Error	2346	0.01		

Table 1.5. Results from a two-way ANOVA on spring growth rates of brown trout where age (1+ year or 2+ year) and year are included as independent variables and the dependent variable is either a) G , b) G_S or c) G_L .

	Effect	d.f.	MSE	F	P
(a)	Intercept	1	0.044	6820.54	<0.0001
	Year	5	0.0002	33.35	<0.0001
	Age	1	0.002	325.24	<0.0001
	Year x Age	5	0.00001	1.35	0.24
	Error	423	0.00001		
(b)	Intercept	1	0.245	7385.47	<0.0001
	Year	5	0.001	33.19	<0.0001
	Age	1	0.00002	0.53	0.47
	Year x Age	5	0.00005	1.48	0.20
	Error	423	0.00003		
(c)	Intercept	1	49.454	8092.80	<0.0001
	Year	5	0.171	27.91	<0.0001
	Age	1	0.0002	0.04	0.85
	Year x Age	5	0.018	2.93	<0.05
	Error	423	0.006		

Table 1.6. Results from a general linear model (GLM) using \log_e specific growth rate (G) as the response variable, age and year of sampling as fixed effects and \log_e initial weight and length of the growth interval as covariates for both a) juvenile Atlantic salmon and b) brown trout captured during multiple spring seasons. Only age 1+ year and age 2+ year fish were used in the analysis for both species.

	Effect	d.f.	MSE	F	P
(a)	Intercept	1	46.13	723.73	<0.0001
	Year	7	7.11	111.58	<0.0001
	Age	1	3.62	56.82	<0.0001
	$\log_e(W_0)$	1	26.69	418.67	<0.0001
	Interval	1	0.58	9.03	0.003
	Year x Age	7	1.34	21.00	<0.0001
	Age x $\log_e(W_0)$	1	3.53	55.31	<0.0001
	Error	2338	0.06		
(b)	Intercept	1	16.13	481.55	<0.0001
	Year	5	0.68	20.24	<0.0001
	Age	1	1.05	31.44	<0.0001
	$\log_e(W_0)$	1	6.84	204.10	0.07
	Interval	1	0.11	3.26	<0.0001
	Year x Age	5	0.02	0.46	0.80
	Age x $\log_e(W_0)$	1	0.98	29.24	<0.0001
	Error	420	0.03		

Table 1.7. Results from a two-way ANOVA on growth rates of Atlantic salmon grown under laboratory conditions over several growth intervals from age 0+ fall to age 1+ spring. Independent variables are sample and smolt group (smolt or non-smolt) and the dependent variable is either a) G b) G_S or c) G_L .

	Effect	d.f.	MSE	F	P
(a)	Intercept	1	0.016	9904.08	<0.0001
	Smolt Group	1	0.00002	11.39	<0.001
	Sample	7	0.0008	535.98	<0.0001
	Smolt Mode x Sample	7	0.0002	127.23	<0.0001
	Error	923	0.000002		
(b)	Intercept	1	0.329	9046.80	<0.0001
	Smolt Mode	1	0.001	33.76	<0.0001
	Sample	7	0.012	315.91	<0.0001
	Smolt Mode x Sample	7	0.005	130.10	<0.0001
	Error	923	0.00004		
(c)	Intercept	1	89.942	12943.69	<0.0001
	Smolt Mode	1	1.783	333.51	<0.0001
	Sample	7	2.318	256.63	<0.0001
	Smolt Mode x Sample	7	0.431	62.03	<0.0001
	Error	888	0.007		

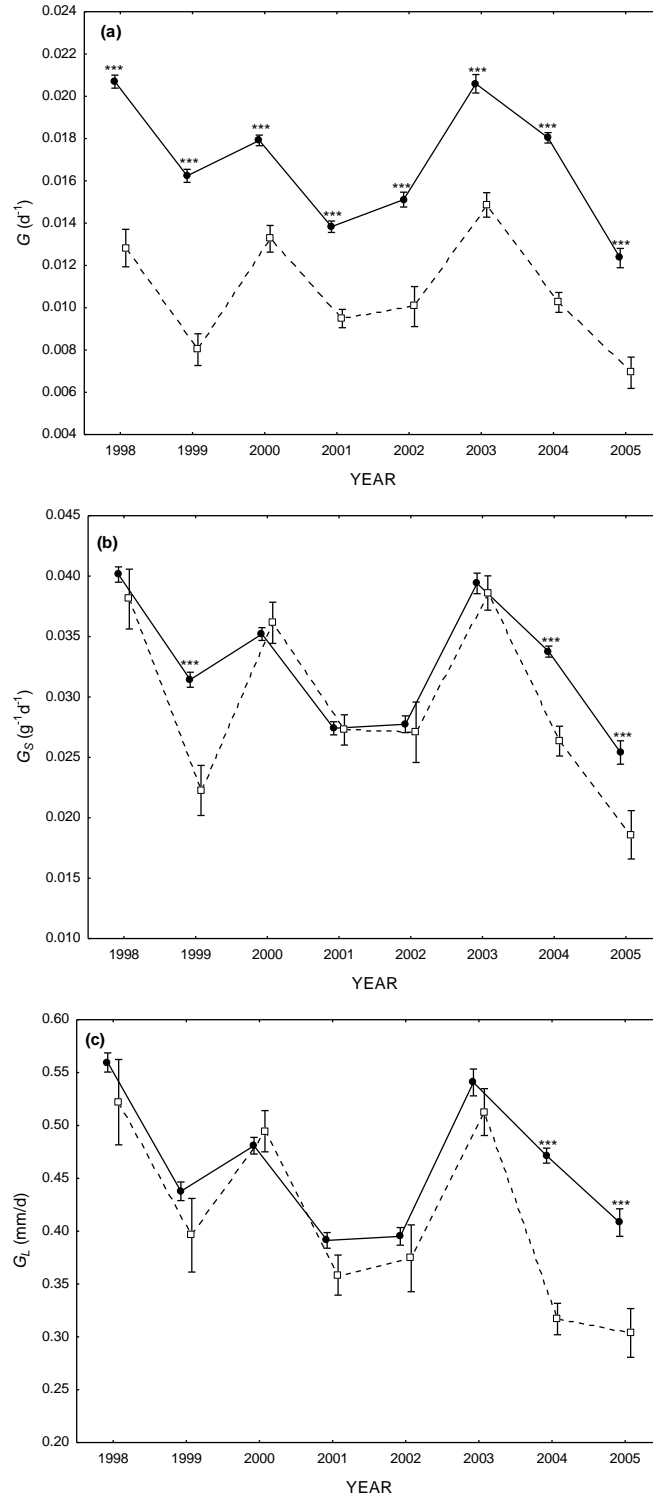


Figure 1.1: Mean \pm 95% CI growth rates in terms of (a) specific growth rate (G) (b) standardized mass-specific growth rate (G_S) and (c) growth rate in length (G_L) for age 1 (\bullet) and age 2 (\square) Atlantic salmon captured over spring intervals for eight consecutive years (***) indicates a significant difference ($P < 0.0001$) determined from a HSD *post-hoc* test).

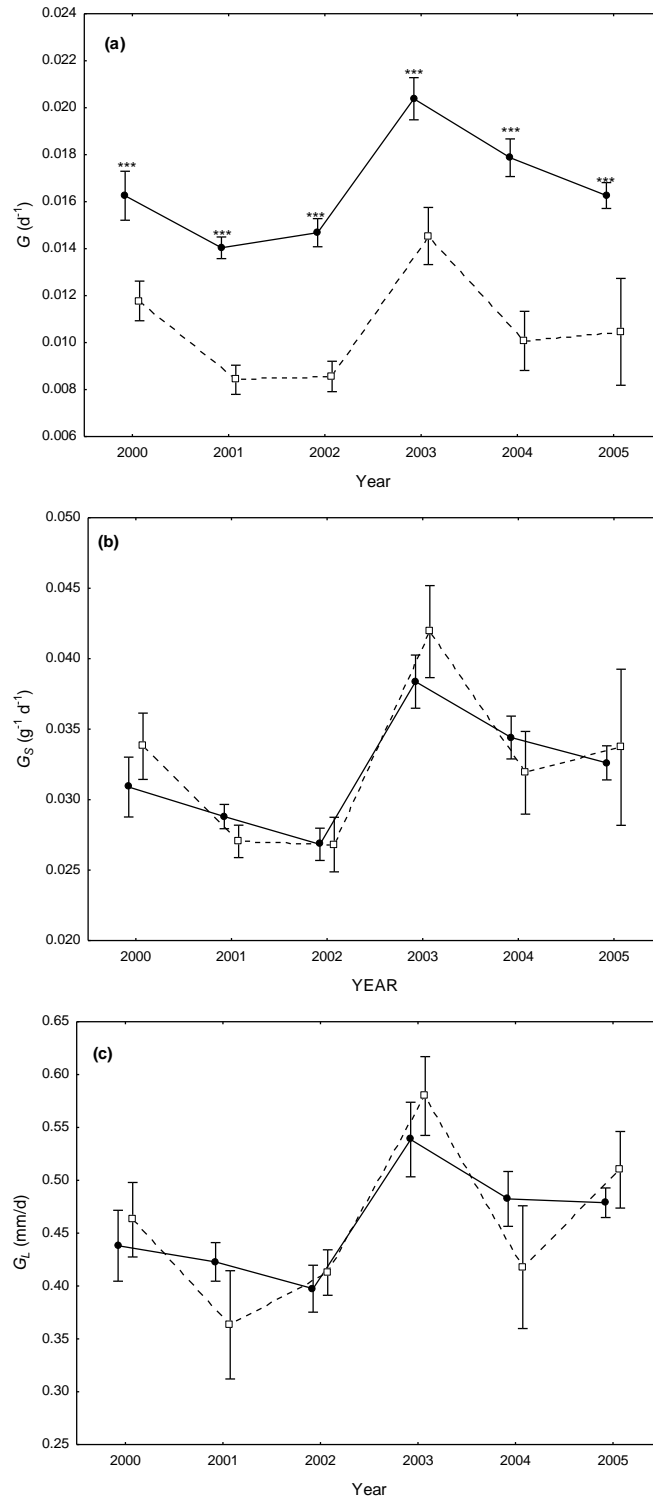


Figure 1.2: Mean $\pm 95\%$ CI growth rates in terms of (a) specific growth rate (G) (b) standardized mass-specific growth rate (G_S) and (c) growth rate in length (G_L) for age 1 (\bullet) and age 2 (\square) brown trout captured over spring intervals for six consecutive years (***) indicates a significant difference ($P < 0.0001$) determined from a HSD *post-hoc* test).

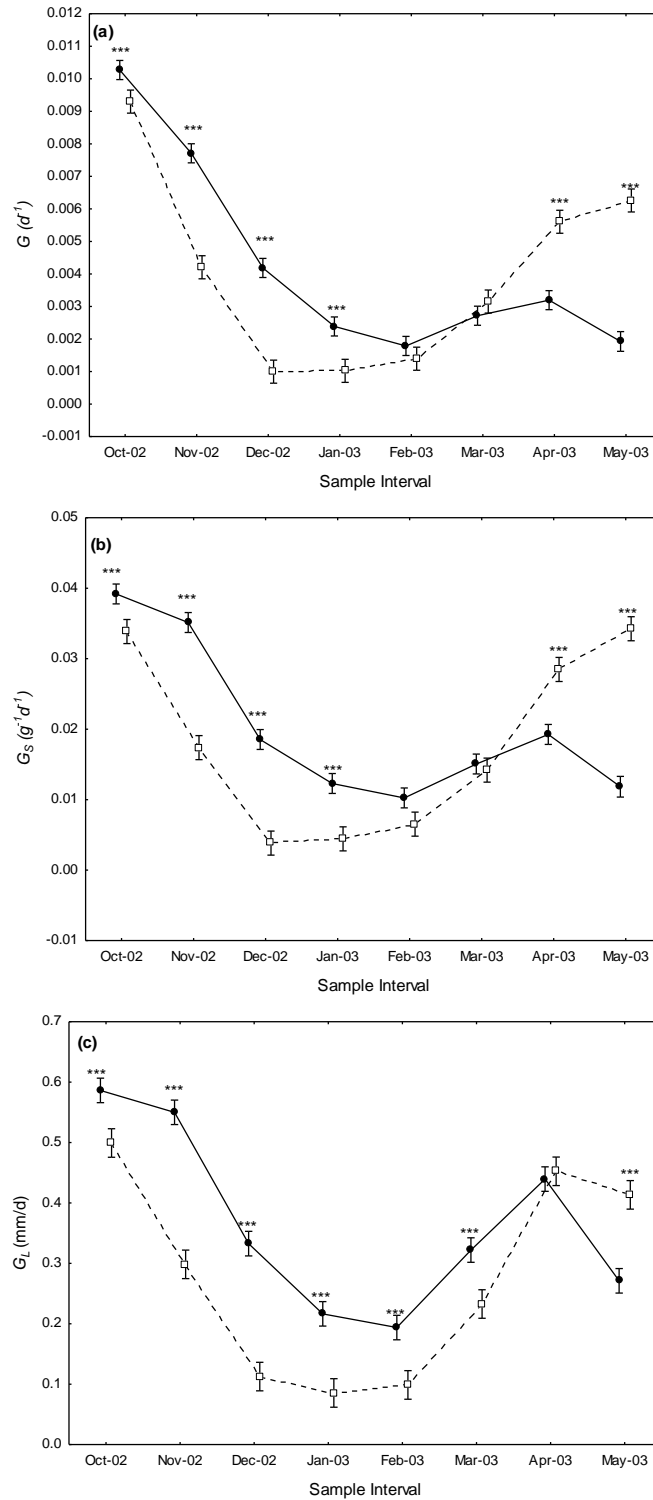


Figure 1.3: Mean $\pm 95\%$ CI growth rates in terms of (a) specific growth rate (G) (b) standardized mass-specific growth rate (G_s) and (c) growth rate in length (G_L) for smolts (\bullet) and non-molts (\square) grown under laboratory conditions from age 0 fall to age 1 spring (***) indicates a significant difference ($P < 0.0001$) determined from a HSD *post-hoc* test).

CHAPTER 2

INDIVIDUAL VARIATION IN LENGTH-WEIGHT RELATIONSHIPS: APPLICATION OF A HIERARCHICAL APPROACH TO THE STUDY OF LENGTH-WEIGHT RELATIONSHIPS

2.1. Abstract

The study of length-weight relationships has long been a cornerstone in fisheries science. Information can be used in production models and in quantifying body condition and hence overall health of a population. Recently, standard approaches to estimating length-weight and condition in fishes have received more scrutiny and hierarchical approaches have been proposed. However, few studies have addressed the mechanisms that cause variation in length-weight relationships at different levels. In this paper, we review causes of individual variation in length-weight relationships through a set of simulations. We found that a dynamic allometry not only gives rise to a nonlinear relationship between log length and log weight but also can result in individual variation when individuals are growing at different rates. We suggest that a random effects approach using polynomials can capture both the individual level variation and changes in morphology that may occur over ontogeny. We applied this approach to laboratory data on growth of individually marked juvenile Atlantic salmon and found that an LME model with a 3rd order polynomial provided the best fit to the data. Finally, we use this hierarchical approach to study the dynamics of length-weight relationships among three separate populations of Atlantic salmon that vary along a latitudinal gradient. We discuss advantage and disadvantages to this approach in contrast to other existing methods.

2.2. Introduction

The estimation of length-weight relationships (LWRs) has long been an important component of fishery science (Ricker 1975, Quinn and Derisio 1999). Information from LWRs can serve two main purposes 1) to provide estimates of biomass from length data and 2) to provide estimates of condition and hence the overall health of a group or population (Winters and Wheeler 1994, Marshall et al. 2004, Kimmerer et al. 2005). The study of length-weight relationships has a long history in the fisheries literature as accurate estimation of LWRs is often vital to proper management of fisheries (Lai and Hesler 2004, Froese 2006, He et al. 2008). The importance of LWRs to both basic and applied fisheries science warrants a clear understanding of the dynamics of LWRs and careful consideration of methods to accurately estimate them.

Despite its importance, fishery scientists have traditionally paid little attention to estimation of LWRs as they are generally estimated with simple ordinary least squares (OLS) regression techniques on log transformed data (Hillborn and Walters 2001, Robertis and Williams 2008). This method assumes a constant length-weight allometry. Recently, however, criticism of the simplicity of this method has resulted in a renewed interest in developing appropriate modeling techniques (Lai and Hesler 2004, He et al. 2008, Robertis and Williams 2008). For example, Robertis and Williams (2008) demonstrated that the OLS method can produce bias predictions of weight for different length categories which can in turn result in a size-dependent bias in biomass estimates for a given size-class. In addition, many studies have observed that length-weight relationships can vary over spatial and temporal scales (Winters and Wheeler 1994, Brodziak and Mikus 2000, Kimmerer et al. 2005, Gerritsen and McGrath 2007). Some *ad*

hoc methods for estimating length-weight relationships include running separate regressions for categories based on size classes, times and locations over which the data were collected. However, such approaches generally require large amounts of data which are difficult to collect and ignore the hierarchical structure of the data (He et al. 2008).

An alternative way to deal with multiple levels of variation is to apply linear mixed effects (LME) models. LME approaches are becoming increasingly common in the fisheries and ecological literature as they offer a robust statistical approach to deal with complex data sets that can be readily subdivided into multiple hierarchical levels (Clark 2003, Rivot et al. 2004). A number of studies have recently proposed the use of LME models as a way to deal with multiple levels of variation in LWRs and address violations of assumptions that are often ignored in simpler approaches (Lai and Hesler 2004, He et al. 2008).

Although these new approaches have offered sophisticated techniques to deal with multiple levels of variation, few studies have addressed the fundamental biological reasons for variation in LWRs. A more thorough understanding of the growth process that gives rise to observed LWRs could help illuminate the levels at which significant variation may occur. Numerous studies have outlined the connection between size, metabolism and growth in mass; however, studies of LWRs rarely address these concepts explicitly. General scaling laws predict a decline in metabolic demands with an increase in size (Peters 1983, Schmidt-Nielsen 1984). As a result in temperate fishes there tends to be an inverse relationship between size and energy depletion (Shuter and Post 1990, Schultz and Conover 1999). In addition, smaller fish are often more susceptible to predation. A growing body of literature is beginning to reveal how these competing

selective pressures give rise to dynamic energy allocation patterns (Post and Parkinson 2001, Hurst and Conover 2003, Garvey et al. 2004). These studies suggest that size, season and even the presence or absence of predators can often determine if it is more profitable to grow in length vs mass (Hurst and Conover 2003). This dynamic energy allocation can have direct consequences for LWRs, for example, in a study of age 0 rainbow trout rainbow trout (*Onchyrhynchus mykiss*), Post and Parkinson (2001) found that even over a relatively narrow size range there is evidence of a bi-phasic allometry which they attributed to the flexibility of energy allocation as fish grow. Therefore, the scaling relationship between size and metabolism and the role of energy allocation decisions may result in dynamic LWRs even within an individual over time.

Understanding how these processes affect variation can help guide the modeling process.

Because this pattern of energy allocation is size and environment specific it may be reasonable to suspect that within a cohort there may be individual differences in LWRs depending on growth rate and local environment. Traditionally, studies of LWRs only include cross-sectional data where only one data point is recorded for each individual. Developing technology has led to an increasing ability to individually mark animals and gather longitudinal data where multiple records of length and weight information for an individual are recorded (Juanes et al. 2000, Gamble et al. 2008). Consequently, capture mark-recapture (CMR) studies are becoming pervasive in the ecological and fisheries literature. Previous applications of LME methods to estimation of length-weight relationships have looked at different levels of variation among groups in time or space (Lai and Hesler 2004 , He et al. 2008); however, we are not aware of any papers that have estimated LWRs at the level of the individual. The increasing number

of CMR studies with individuals illuminates the need to develop methods that appropriately handle the complexity of longitudinal data.

In this paper we take a mechanistic approach to investigate variation in LWRs. We first use basic simulations to demonstrate how a changing allometry can influence the LWRs both within a single individual and among individuals that are growing at different rates. We then use Atlantic salmon as a model species to investigate complexity in the length-weight relationship. Atlantic salmon are an ideal species in this respect as they exhibit considerable flexibility in their energy allocation throughout ontogeny (Metcalf 1998, Thorpe et al. 1998). For example, prior to entering the marine environment migrating individuals undergo a morphological change becoming longer and thinner (McCormick et al. 1998, Letcher 2003). In addition, in laboratory settings they are known to exhibit seasonal changes in appetite entering a period of anorexia where they lose weight despite being fed (Simpson et al. 1996). All these factors make their LWRs challenging to model. Finally, there are many studies of juvenile Atlantic salmon *in situ* where longitudinal data are available because they are easy to mark and recapture probabilities are often high. Ultimately, this paper has three goals 1) to illuminate mechanisms responsible for variation in LWRs at the individual level and 2) offer a statistical modeling approach to deal with this variation and 3) apply the new modeling approach to investigate variation in LWRs of individually marked juvenile Atlantic salmon sampled across three streams that vary in latitude.

2.3. Materials and Methods

2.3.1. Simulations

To simulate growth under a dynamic allometry we used the allometric scaling of age 0+ rainbow trout estimated in Post and Parkinson 2001 as a baseline model. In their study, they found the length-weight allometry was bi-phasic with a switch to a steeper allometry at ~100 mm fork length. To simulate growth rate we used a baseline value of 0.5 mm/day which approximates the maximum growth rate observed in Atlantic salmon in our field data. We simulated growth for 120 days which is roughly equivalent to the length of the growth season for Atlantic salmon in the streams we sampled. To mimic seasonal growth in length we used a linear model starting at 0.5 mm/d and extending to 0 mm/d as growth towards the end of the growth season approaches 0 in our study systems. We assumed an allometric relationship between length and weight such that

$$W=aL^b \quad (1)$$

Under this relationship growth in weight ($\frac{dW}{dt}$) can be derived from growth in length

($\frac{dL}{dt}$) through an application of the chain rule

$$\frac{dW}{dt} = \frac{dW}{dL} * \frac{dL}{dt} = b * a * L^{b-1} * \frac{dL}{dt} \quad (2)$$

To solve for W_t equation 2 was integrated numerically using Heun's method. We used the following algorithm to simulate a switch in allometry

$$\begin{cases} \frac{dW}{dt} = b_1 * a * L^{b_1-1} * \frac{dL}{dt} & \text{If } L \leq 100\text{mm} \\ \frac{dW}{dt} = b_2 * a * L^{b_2-1} * \frac{dL}{dt} & \text{If } L > 100\text{mm} \end{cases} \quad (3)$$

where $b_1=2.903$ and $b_2=3.278$.

We first examined the results for growth of one individual to compare the degree to which a single individual's LWR deviates from an assumed log linear relationship. Next, to assess the effect of variation in growth in producing variation in LWRs among individuals we simulated growth under increasing levels of growth variation using a sample size of 10 individuals. The degree of growth variation between each simulation was adjusted by increasing the coefficient of variation (CV) of mean growth rate such that the CV was 10%, 20% and 50% of the mean for the three simulations respectively. In each simulation growth rate was autocorrelated such that the slowest growing individual always had the slowest growth rate and the fastest growing individual always had the fastest growth rate. Autocorrelation in growth rate is known to occur in a natural setting therefore we felt justified in including it in our simulations (Pfister and Peacor 2003). We compare estimated LWRs graphically.

2.3.2. Laboratory Data

We used a set of laboratory data for juvenile Atlantic salmon to explore how LWRs vary among individuals and over size ranges among two distinct life history groups. These data offer several advantage including having several observations for each fish, being able to unambiguously assign each individual to one of two life history groups (smolt or parr) based on its morphology at the end of the experiment, limited measurement error and equally spaced growth intervals. These data were collected in a separate experiment investigating the differences in growth and morphology between two life history groups. Details of the experiment are described elsewhere (Obedzinski and Letcher 2004, Pearlstein et al. 2007, Sigourney et al. 2008). Briefly, all fish were anesthetized in MS-222, measured for length and weight and a PIT tag was inserted in the peritoneal cavity. Fish were randomly placed into one of four circular tanks in a manner that ensured equal biomass among tanks. At the end of the experiment parr could be easily distinguished from smolts as they exhibited a longer thinner shape, and difference in coloration. In addition, most smolts were significantly larger than parr at the start of the experiment.

We fit several different models to the data which included 3rd order polynomials and simpler linear models which excluded higher order polynomials. To compare models we used Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002). For each model, delta AIC values were computed by taking its AIC value subtracting it from the AIC value of the top model (Burnham and Anderson, 2002). All models were fit using restricted error maximum likelihood (REML). Although it is possible to fit models with random coefficients, preliminary analyses showed little variation was explained by

including random coefficients, therefore, we only considered models with random intercepts in the final analysis. For the top model we assessed the importance of the random effects with a likelihood ratio test (LRT). Because LRTs cannot be applied when using REML we used maximum likelihood (ML) to fit the top model with and without random effects and then compared the two models with a LRT (Pinheiro and Bates, 2000).

2.3.3. Field Data

Using a similar LME approach as applied to the laboratory data, we estimated LWRs and seasonal changes in condition among three different streams for which we have mark-recapture data. The streams occur along a latitudinal gradient from Massachusetts to New Brunswick, Canada and include the West Brook (WB) a 3rd order tributary to the Connecticut River located in Whately, Massachusetts USA (42°25'N 72°39'W), Shorey Brook (SB) a 2nd order tributary to the Narraguagus River located in Beddington, Maine USA (44°49'N 68°03'W) and Catamaran Brook (CB) a 3rd order tributary to the Little Southwest Miramichi River located in Renous, New Brunswick Canada (46°52'N 66°06'W). Data from all three streams were collected in a manner consistent with the sampling design outlined by Juanes et al. 2000. Fish were captured using backpack electrofishing. Captured fish greater than 60 mm fork length and 2 g in weight were anesthetized and tagged interperitoneally with a 11.5 mm passive integrated transponder (PIT) tag. Fish were then returned to the same section of stream from which they were captured (see Letcher and Gries 2003 and Horton et al. 2009 for more details

on sample design). In all three streams there were four primary sampling occasions (spring, summer, fall, prewinter) (Table 2.1).

We used data collected from the 2001 sampling season as it provided the most comprehensive dataset of tagged individuals. We compared a number of models which varied in complexity. For example, we included maturity status and season as predictor variables because condition is known to fluctuate as a function of these variables. We also tested for river effects and differences in scaling relationships among rivers as well as seasons. This analysis would allow us to assess changes due to river or season and whether or not changes are consistent among rivers. Finally, we compared 3rd order polynomial models to simpler linear models to test whether a more complicated nonlinear model is necessary to capture the relationship between log transformed length and log transformed weight across the size ranges within the data. As outlined above, we used AIC as a model selection criterion for models with different fixed effects. To address the importance of random effects we used the same procedure as outlined above for the laboratory data.

2.4. Results

2.4.1. Simulations

Our simulations showed that a dynamic allometry not only results in a nonlinear relationship between log length and log weight over ontogeny but also demonstrated how variation in growth rates can act as a mechanism to increase variation in LWRs. Simulation results for one individual illustrates how the LWR deviates from a linear relationship even over a relatively narrow size range (Figure 2.1). Repeating the

simulations with ten individuals suggested that with a small amount of variation in growth ($CV=10\%$) the resulting variation in individual slopes and intercepts was negligible (Figure 2.2a). However, a doubling of the growth rate variation ($CV=20\%$) produced a more noticeable variation in slopes and intercepts (Figure 2.2b). Finally, large variation in growth ($CV=50\%$) translated into large differences in estimated slopes and intercepts (Figure 2.2c).

2.4.2. Laboratory Data

Our exploratory analysis of the laboratory data yielded two prominent growth patterns in terms of the relationship between length and weight. First, we found that there was considerable variation in LWRs among individuals as evidenced by variation in individual intercepts (Figure 2.3a) and slopes (Figure 2.3b). In addition to this individual level variation, the two life history groups (smolts and parr) separated out into separate, distinct groups in terms of the mode and distribution of estimated slopes and intercepts. These empirical histograms appeared to follow a Gaussian distribution suggesting that an LME approach might be appropriate for these data. The second pattern we found is a distinct change in LWRs from pre-winter to post-winter. During the pre-winter phase both parr and smolts follow similar LWRs with overall slopes close to three for both life history groups (Figure 2.4). During the post-winter phase the estimated allometry for smolt LWRs was considerably less than three as individuals following this pathway become longer and thinner whereas the estimated allometry for parr LWRs was greater than three as larger fish become more rotund as they grow.

The full LME model with higher (3rd) order polynomial effects, life history effects and sample effects had the lowest AIC indicating that the most complex model was also the most parsimonious (Table 2.2). Also, a likelihood ratio test indicated that inclusion of random effects provided significant improvement to model fit ($P < 0.0001$). We found close agreement between predicted and observed log weights for a randomly chosen smolt (Figure 2.5a) and a randomly chosen parr (Figure 2.5b).

2.4.3. Field Results

Analysis of field data suggested considerably variation in LWRs among rivers, seasons and life history groups. Although the most complex model had the lowest AIC, parameter estimates and standard errors were nonsensical suggesting a problem with convergence, therefore, we excluded this model from further analysis. After excluding the most complex model we found the top model did not include a higher order polynomial effect (Table 2.3). We found 3rd order polynomial models were among the top models in our candidate set, however, delta AIC values indicated little support for these models. Individual variation appeared to be significant as indicated by a likelihood ratio test ($P < 0.0001$) and a decomposition of variance components. The top model included effects of log length, river, season and maturity as well as interactions among these variables (Table 2.4). Within rivers, there was evidence of seasonal changes in LWRs (Table 2.4). Among rivers LWRs were similar in most seasons except in spring where the allometric slope for CB was less than that for the other rivers and SB appeared to have a significantly lower intercept indicating lower condition (Figure 2.6). Mature and immature parr had similar LWRs in spring and early summer but the onset of

maturation leads to significant increases in condition for weight of mature parr in fall (Table 2.4). Finally, our results also suggest some interesting differences in seasonal changes in condition among rivers for immature parr. In WB, where fish attain the largest sizes, there appeared to be a significant drop in condition from early summer to fall (Figure 2.7a). This pattern of decreasing summer condition was similar in SB (Figure 2.7b). Comparisons of estimated LWRs for CB, however, suggested little change in condition between summer and fall (Figure 2.7c).

2.5. Discussion

One goal of this paper was to demonstrate the effect of a dynamic allometry on LWRs both within and among individuals. Fishery scientists have long recognized that LWRs can differ as fish enter different growth stanzas (Ricker 1975, Froese 2006), but it is rare that the mechanisms behind these changing LWRs are discussed. Population level studies often tend to look at variation in LWRs at large temporal or spatial scales and over large size ranges (Winters and Wheeler 1994, Brodziak and Mikus 2000, Kimmerer et al. 2005, Gerritsen and McGrath 2007). These studies often attribute observed variation to large scale environmental fluctuations (Winters and Wheeler 1994, Brodziak and Mikus 2000, Gerritsen and McGrath 2007). However, on a smaller scale, dynamic allometry can arise from individuals switching their energy allocation tactic as they grow. An increasing body of literature is beginning to support this notion of flexible energy allocation in young fishes (Post and Parkinson 2001, Hurst and Conover 2003, Garvey et al. 2004). For example, the theory of dynamic energy budgets decouples growth in length from growth in weight via an energy allocation rule (Broekhuizen et al. 1994,

Koojiman 2000, Jones et al. 2002). In a physiological context, this rule recognizes that individual organisms may be capable of making decisions about how to allocate energy to growth in structural mass or growth in energy reserves. Depending on the ecological context different allocation strategies may be more optimal than others and result in a dynamic allometry between length and weight. Our simple simulations using bi-phasic allometry demonstrated how variation in growth rates among individuals can result in variation in LWRs over a narrow size range.

Recognition of the complexity of LWRs has led to a recent resurgence of methods to deal with different levels of variation; however, we are not aware of any studies that have explicitly addressed this combined problem of individual variation and dynamic allometry. With the increasing number of CMR studies, the need for appropriate modeling approaches to handle variation among individuals is apparent. Hierarchical or LME approaches are quickly becoming common in the literature as sophisticated methods to deal with multiple levels of variation. Hai and Hesler (2004) showed that they can be readily applied to the study of LWRs when there are different levels of variation among groups. However, the underlying assumption is that within a group the allometry is static (linear). Using higher order polynomials help to relax the assumption of a linear relationship between log length and log weight but are rarely used when modeling the relationship between size and weight (but see Hochachka and Smith 1991 and Weatherhead et al. 1996 for examples). Including higher order polynomials has the advantage of being nonlinear in the mathematical sense but linear in the statistical sense and therefore amenable to a LME modeling framework.

Exploratory analysis of laboratory data on Atlantic salmon growth revealed evidence of both individual variation in LWRs and a life history dependent dynamic allometry. Atlantic salmon represent a challenging species for which to study LWRs because their complex life history includes a morphological change as they prepare to switch environments (McCormick et al. 1998, Letcher 2003). Other aspects of the salmon life history include bimodal variation in growth rates and winter starvation which tends to uncouple the otherwise tight relationship between length and weight even in a laboratory setting. We tested our modeling approach on this laboratory data set and found that the most complex model with a sample (seasonal) effect and a higher order (3rd) polynomial effect was the most parsimonious model. We further found for a given individual of both life history groups, the model was able to capture the overall variation in weight as a function of length. This result lends credence to this modeling approach as a potential method to capture variation in LWRs and speaks to the underlying complexity in LWRs that can arise from dynamic life history tactics.

Another advantage of the LME approach is that it is readily applicable to field situations where there are likely missing observations resulting in unbalanced designs (Gillies et al. 2006). Our analysis of field data on three separate Atlantic salmon populations did not detect a polynomial effect ($\Delta AIC > 10$); however, variation among individuals was significant suggesting that a general LME approach was appropriate. One reason why a higher order polynomial was not needed in the field data is possibly because the size range is too narrow within any given season and river combination. We did find, however, that LWRs are complex with slope coefficients varying among rivers and among seasons within a river. Because our dataset only included three rivers and one

year we did not include temporal or spatial hierarchical effects. However, it is common on surveys to have multiple levels (tributaries) collected over multiple years. This can readily be put into a hierarchical framework where quantifying the random variation may be of interest. Using this approach we were able to use one model with all individuals that accurately reflects the data structure to estimate the best model describing LWRs.

Our comprehensive analysis of this complex dataset allowed us to reveal interesting differences among streams in terms of LWRs and condition within a unified modeling framework. Our results suggest that condition decreases from summer to fall in WB and SB but remains steady and even increased slightly in CB. This result is intriguing as summer temperatures are generally higher in Catamaran routinely exceeding 20° C which is presumably more stressful for Atlantic salmon (Breau et al. 2007). However, when coupled with cross-tributary comparison of summer growth, this result is not surprising as fish in CB maintain positive growth rates over summer where as fish in both WB and SB exhibit negligible and occasionally negative growth in mass over summer (Letcher and Gries 2003, Sigourney et al. 2006, Horton et al. 2009). Therefore, changes in condition may partly reflect differences in summer feeding. In addition, these differences in fall condition may partly reflect changes in energy allocation strategies in response to winter conditions. Because winters are longer in CB energy allocation strategies may differ such that parr put more energy into lipid accumulation in the fall to survive longer winters. There is increasing evidence in the literature that energy allocation strategies may be flexible, and therefore, adaptable among populations (Post and Parkinson 2001, Metcalfe et al. 2002, Hurst and Conover 2003, Garvey et al. 2004).

Therefore, adaptation to longer winters may partly explain why juvenile Atlantic salmon in CB have higher condition in the fall than in the more southern streams.

Sophisticated statistical techniques to deal with data complexity are continuing to evolve in the fisheries and ecological literature. New methods come with advantages and disadvantages. In this study we aimed to resolve the mechanisms of variation in LWRs at the individual level and design an appropriate modeling approach to deal with this variation. Our modeling approach allows us to relax some assumptions about LWRs so that they are not necessarily linear on a log-log scale and they can vary among individuals. This approach should be applicable among a wide variety of species especially because metabolic scaling is a common mechanism dictating scaling relationships in all species (Peters 1983, Schmidt-Nielsen, 1984). Other approaches offer some advantages such as not assuming constant variance over the entire size range (see He et al. 2008). Such complexity could be combined with our modeling strategy in a Bayesian framework; however, the tradeoff might be tractability.

Table 2.1. Median dates for each electrofishing sample conducted in 2001 in which age 1 Atlantic salmon were captured in West Brook (Massachusetts, USA), Shorey Brook (Maine, USA) and Catamaran Brook (New Brunswick, Canada).

River	Season	Median Sample Date
West	spring	3/13/2001
Shorey	spring	4/23/2001
Catamaran	spring	5/19/2001
West	summer	6/9/2001
Shorey	summer	6/6/2001
Catamaran	summer	6/28/2001
West	fall	9/8/2001
Shorey	fall	9/14/2001
Catamaran	fall	9/10/2001
West	prewinter	12/6/2001
Shorey	prewinter	11/24/2001
Catamaran	prewinter	10/26/2001

Table 2.2. Summary of the top LME models fit to laboratory data of repeated measurements of length and weight for individual Atlantic salmon where log length (L), life history (LH) and sample date (SD) were used to predict log weight. L^3 indicates a 3rd order polynomial was used for log length. The percentage of variation between individuals (%B) and within individual (%W) is shown where * indicates that significant ($P < 0.05$) variation was explained by inclusion of a random intercept in the model.

Model	ΔAIC_c	% B	% W
$L^3 * LH * SD$	0	73*	27
$L * LH + SD$	165	71*	29
$L^3 * LH + SD$	300	67*	33
$L^3 + SD$	612	57*	43
$L^3 + LH + SD$	617	56*	44

Table 2.3. Summary of top LME models fit to field data of individually tagged juvenile Atlantic salmon where log length (L), river (R), maturity status (M) and season (S) were used to predict log weight. L^3 indicates a 3rd order polynomial was used for log length. The percentage of variation between individuals (%B) and within individual (%W) is shown where * indicates that significant ($P < 0.05$) variation was explained by inclusion of a random intercept in the model.

Model	ΔAIC	%B	%W
$L^*R^*S+S^*M+R^*M$	0	43*	57
$L^3+S^*M+R^*M$	18	40*	60
$L^3*R+S^*M+R^*S$	23	40*	60
$L^*M+R^*S+S^*M$	26	40*	60
$L^3*M+R^*S^*M$	30	40*	60

Table 2.4. Estimated coefficients and standard errors from top LME model fit to field data of individually marked juvenile Atlantic salmon. The slope and intercept represent the LWR for immature juvenile Atlantic salmon captured in the fall in Catamaran Brook. WB and SB represent the river effect of West Brook and Shorey Brook, respectively. PP represents the effect of mature salmon. The effects of season (spring, summer, prewinter) with respect to the fall season are also included.

Parameter	Estimate	Std.Error	DF	p-value
Intercept	-10.714774	0.239814	1085	<0.0001
Slope	2.827914	0.054816	947	<0.0001
SB	-0.192917	0.530745	1085	0.7163
WB	-0.575452	0.308322	1085	0.0623
summer	-1.099731	0.312392	947	0.0005
spring	2.617004	0.469756	947	<0.0001
prewinter	0.415703	0.315729	947	0.1883
PP	0.078036	0.00794	1085	<0.0001
LogL*SB	0.045468	0.118246	947	0.7007
LogL*WB	0.135787	0.068253	947	0.0469
LogL*summer	0.248766	0.072231	947	0.0006
LogL*spring	-0.635565	0.111723	947	<0.0001
LogL*prewinter	-0.103094	0.072034	947	0.1527
SB*summer	0.418172	0.634719	947	0.5102
WB*summer	1.254467	0.397486	947	0.0016
SB*spring	-3.551435	0.714008	947	<0.0001
WB*spring	-2.179792	0.530881	947	<0.0001
SB*prewinter	-1.39637	0.742214	947	0.0602
WB*prewinter	-1.105183	0.413743	947	0.0077
summer*PP	-0.044764	0.006513	947	<0.0001
spring*PP	-0.05796	0.007932	947	<0.0001
prewinter*PP	0.00611	0.007689	947	0.427
SB*PP	-0.025578	0.014396	1085	0.0759
WB*PP	-0.013501	0.00897	1085	0.1326
LogL*SB*summer	-0.072239	0.142854	947	0.6132
LogL*WB*summer	-0.252025	0.088998	947	0.0047
LogL*SB*spring	0.836381	0.165388	947	<0.0001
LogL*WB*spring	0.54296	0.124293	947	<0.0001
LogL*SB*prewinter	0.308975	0.165248	947	0.0618
LogL*WB*prewinter	0.238051	0.091264	947	0.0092

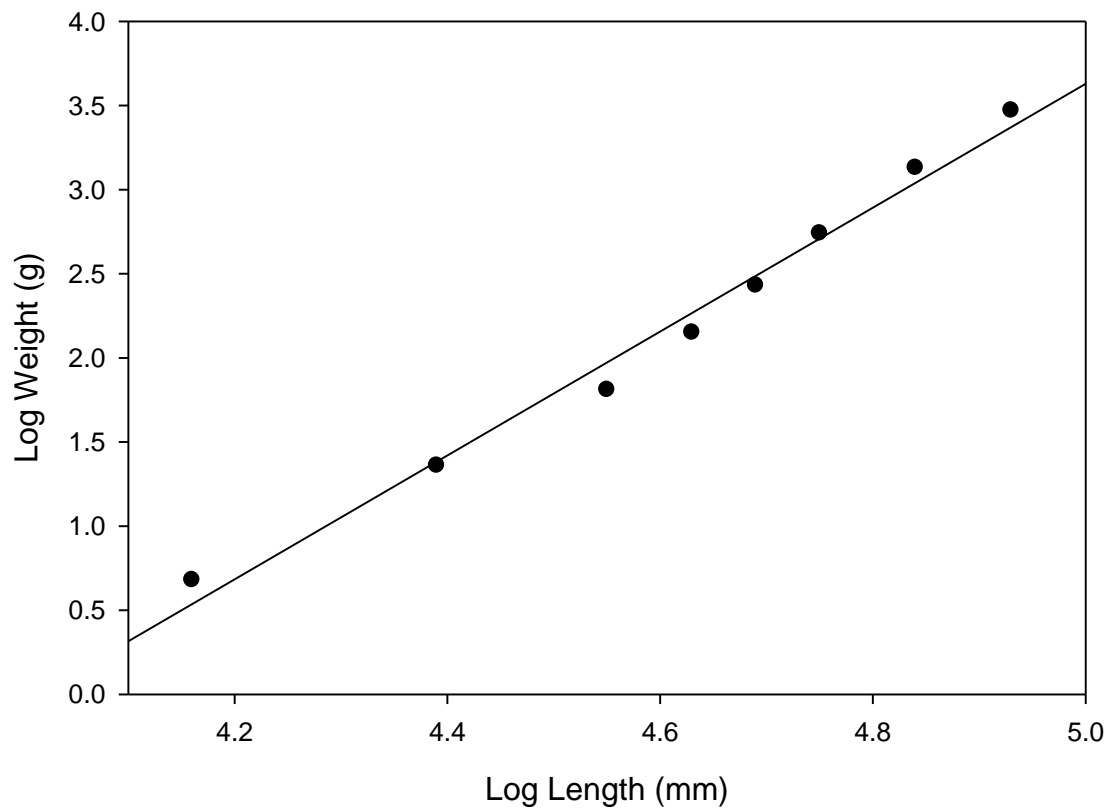


Figure 2.1: Simulated length-weight relationship for one individual with bi-phasic allometry.

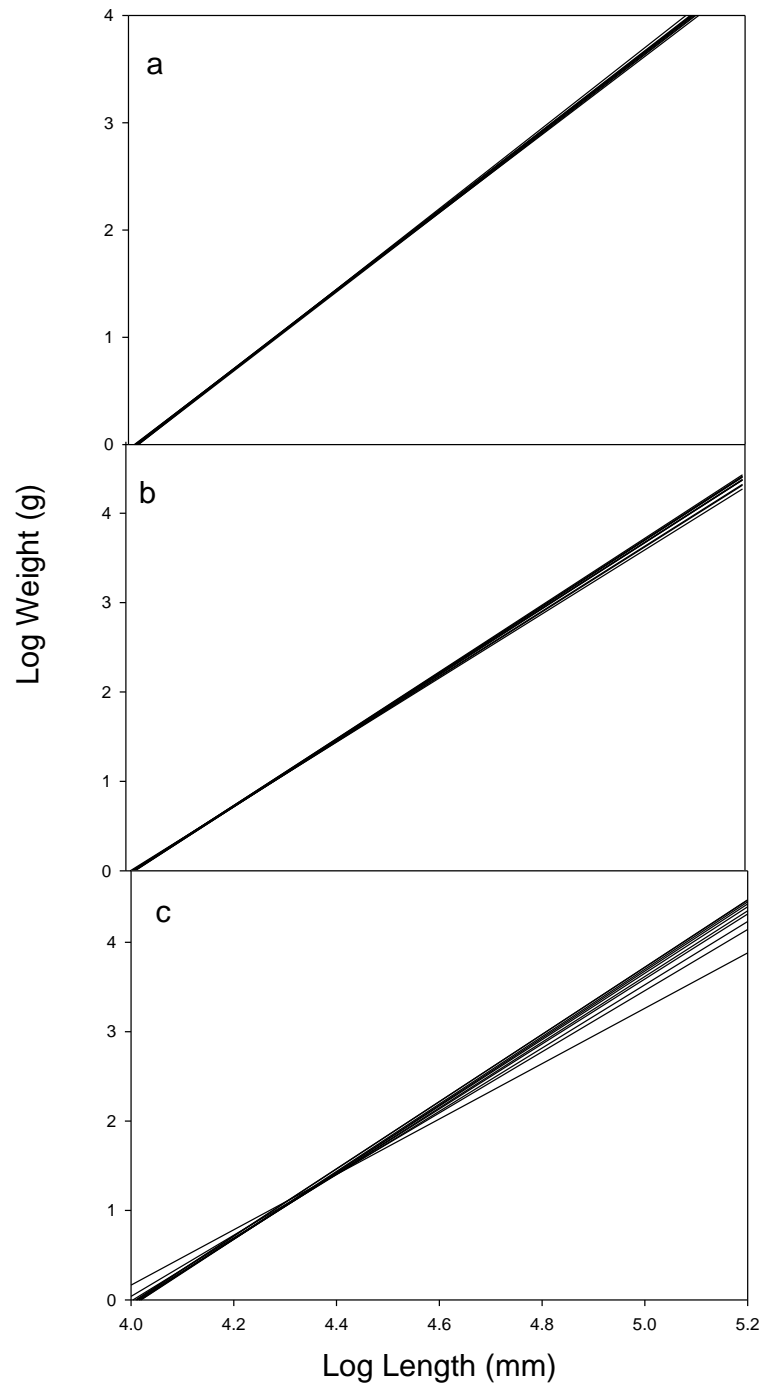


Figure 2.2: Results of estimated length-weight relationships for 10 simulated individuals growing with biphasic allometry where the coefficient of variation in growth rates among individuals is (a) 10%, (b) 20% and (c) 50%.

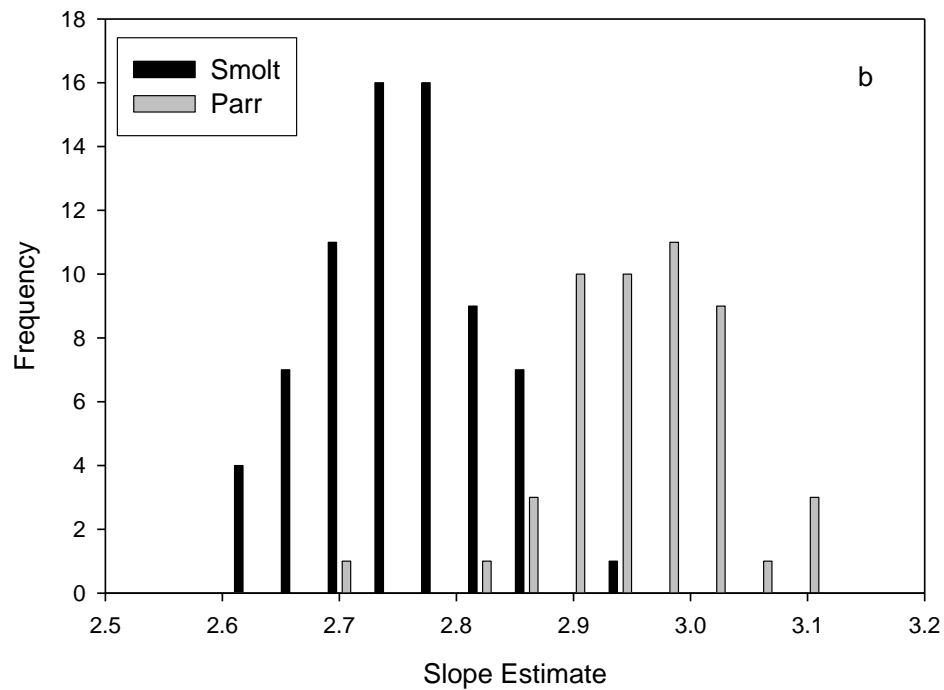
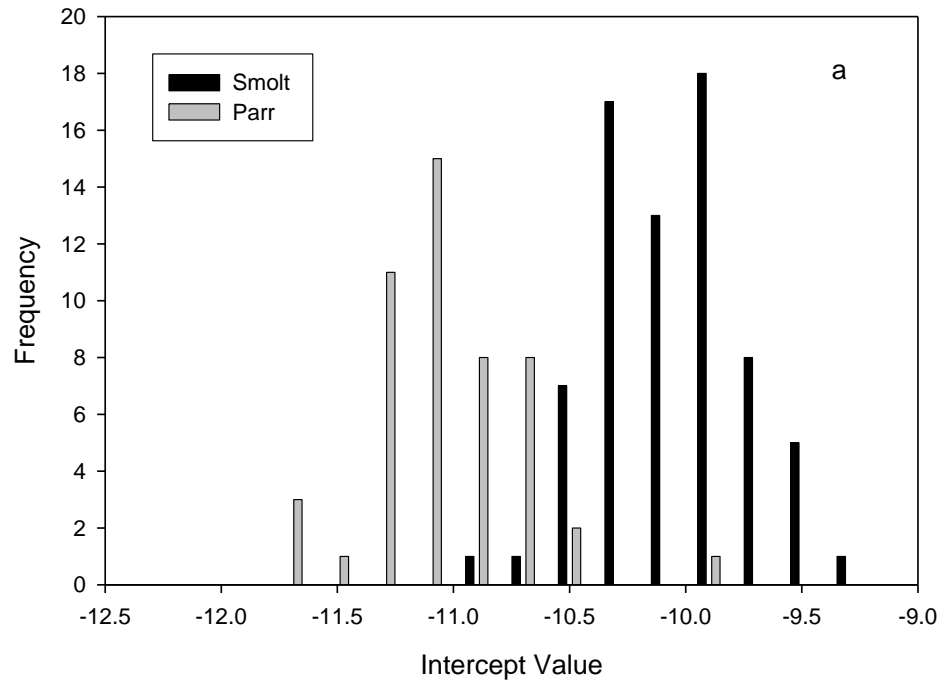


Figure 2.3: Individual intercept values (a) and slope values (b) estimated from separate regressions of log length on log weight performed on repeated measurements of individual juvenile Atlantic salmon grown in a laboratory.

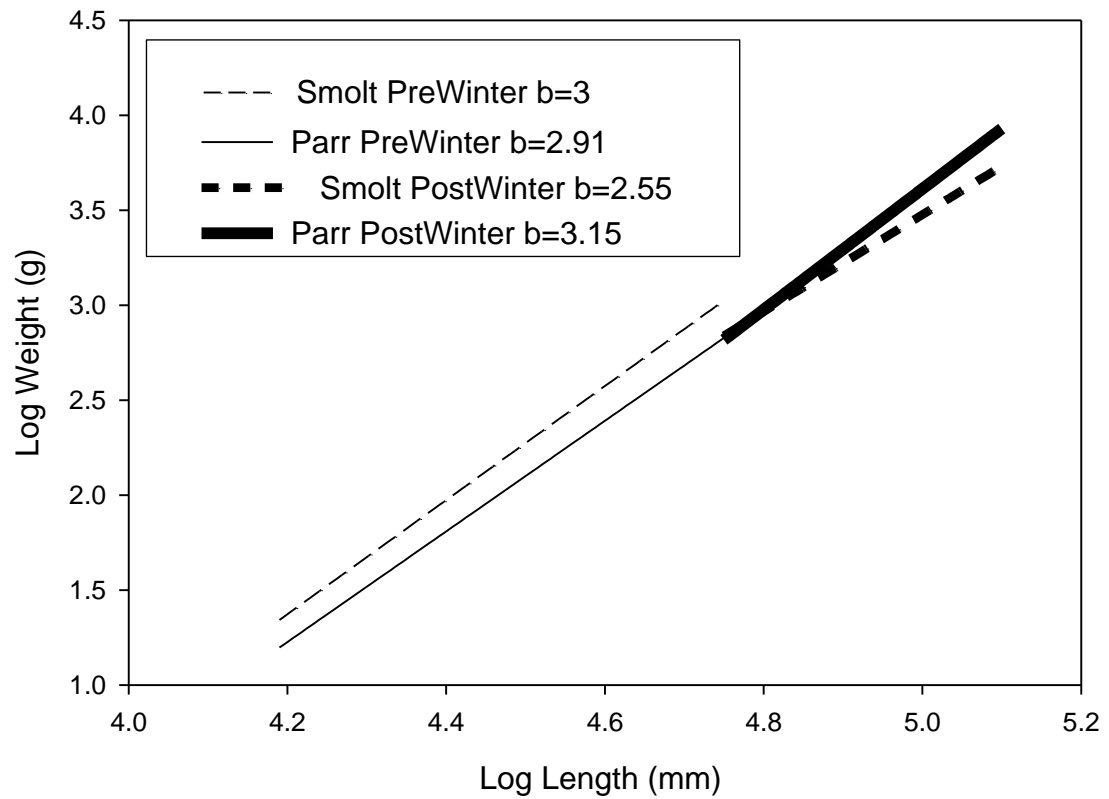


Figure 2.4: Length-weight relationships estimated from combined data of individually marked juvenile Atlantic salmon measured before winter and after winter. Allometric slopes (b) for each life history group (smolt or parr) are provided in figure legend.

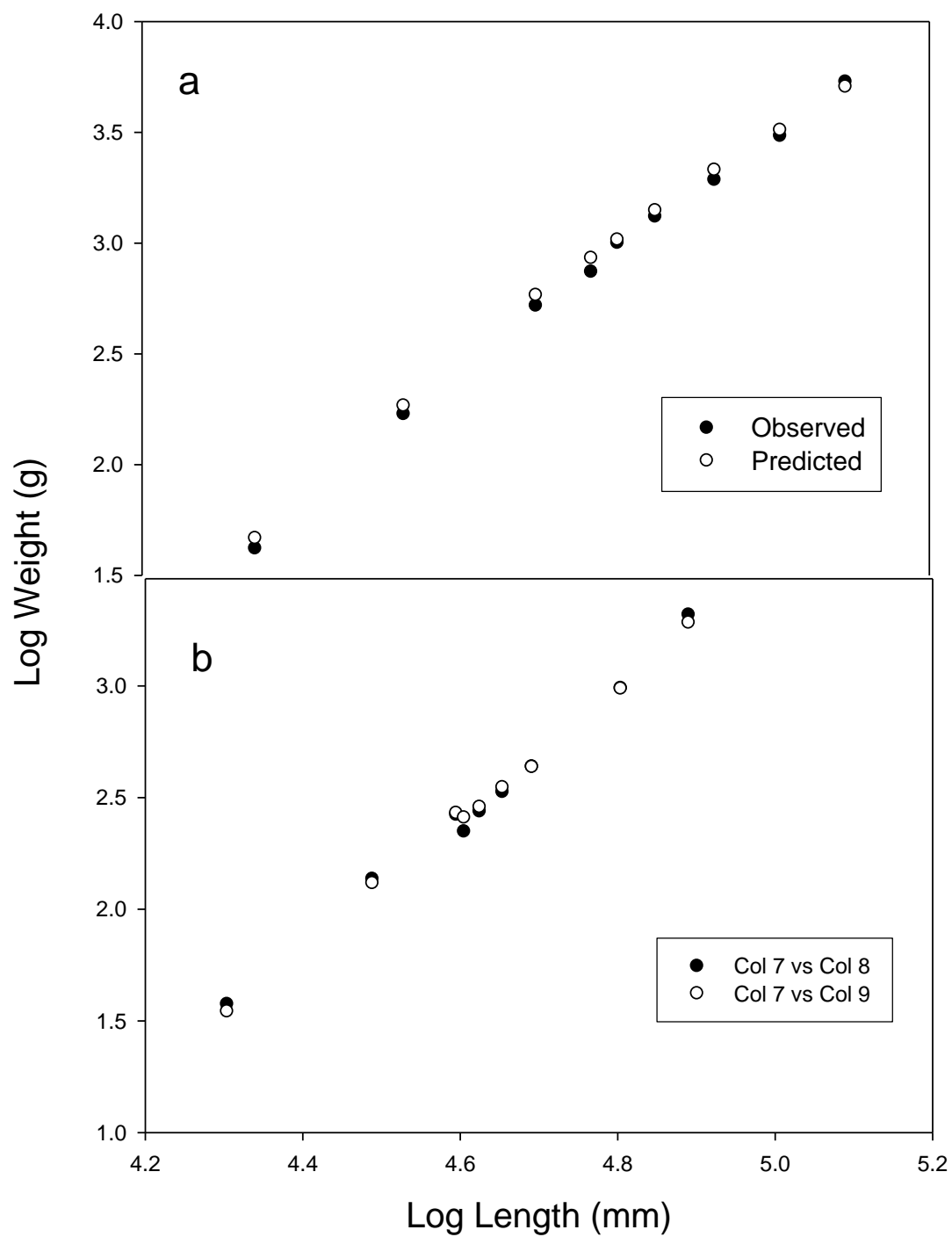


Figure 2.5: Predicted log weights from a linear mixed effects model vs observed log weights of an individually tagged juvenile Atlantic salmon which (a) transformed into a smolt in the spring and (b) remained as a parr in the spring.

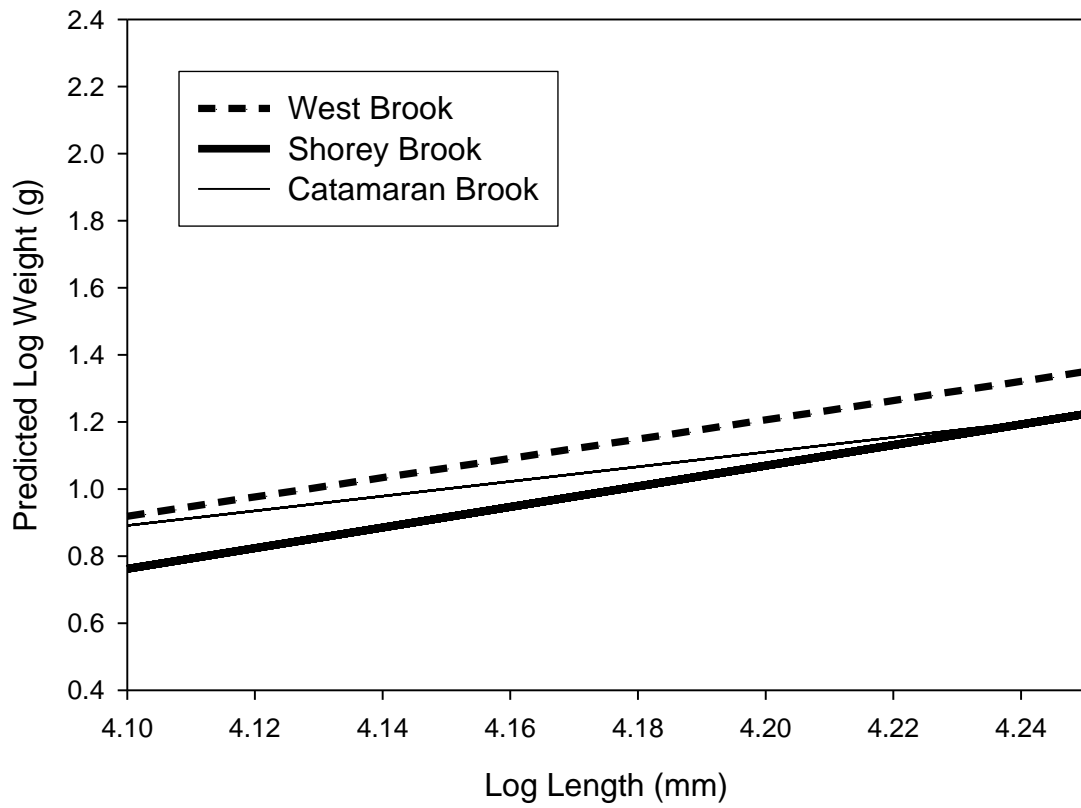


Figure 2.6: Spring length-weight relationships for three separate rivers estimated from a linear mixed effects model for juvenile Atlantic salmon.

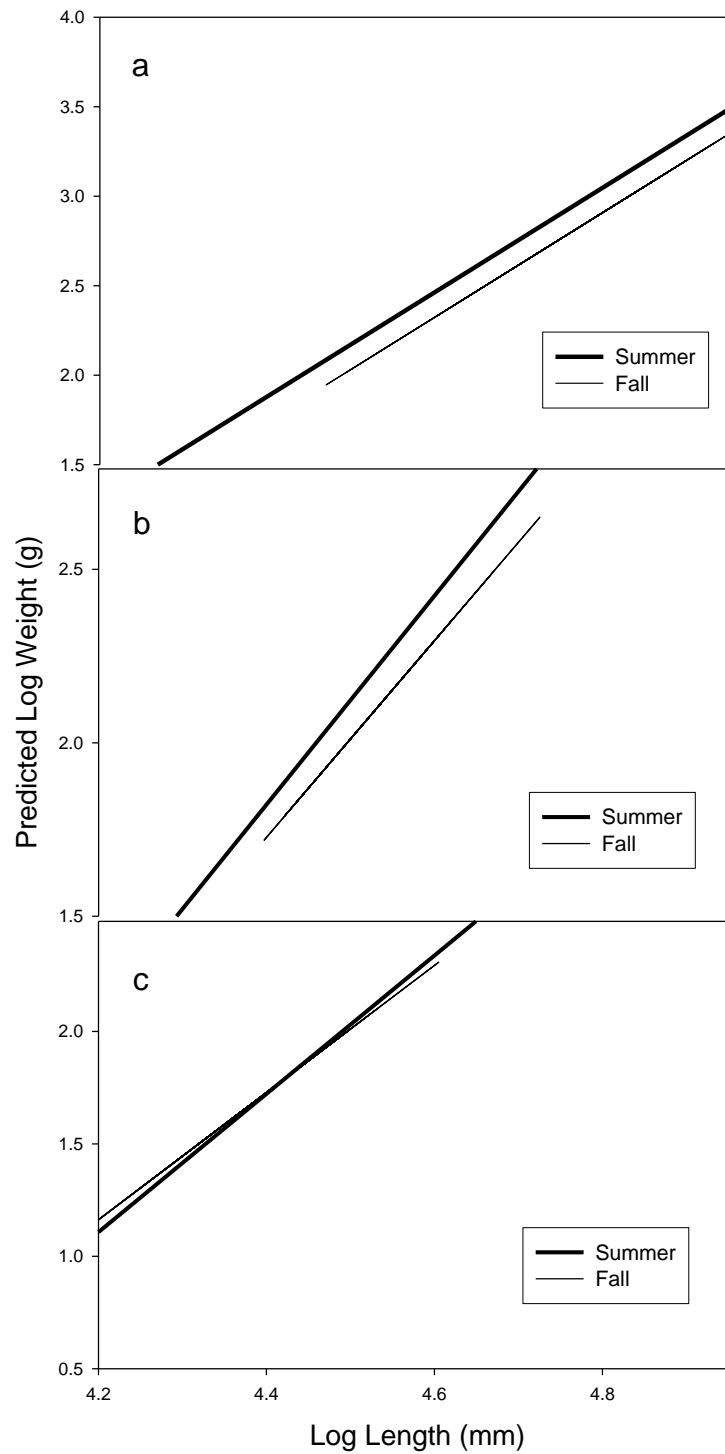


Figure 2.7: Estimated differences in log weight as a function of log length between summer and subsequent fall for juvenile Atlantic salmon captured in 2001 in (a) West Brook (b) Shorey Brook and (c) Catamaran Brook as predicted from a linear mixed effects model.

CHAPTER 3

MODELING SEASONAL GROWTH TRAJECTORIES OF INDIVIDUALS USING A BAYESIAN HIERARCHICAL APPROACH

3.1. Abstract

Modeling physiological growth is an important component to understanding ecological dynamics, but in practice can prove difficult for a number of reasons. For example, in many temperate environments growth can be highly seasonal, growth performance often differs among individuals, and measurement error can contribute to parameter uncertainty. We derive a simple first order autoregressive growth model from von Bertalanffy growth dynamics which includes a nonparametric seasonal growth function. To estimate parameters we adopt a Bayesian state space framework that directly incorporates auxiliary information of the food environment and measurement error to derive informative priors. In addition, our model is hierarchical allowing for variation among individuals. We demonstrate the model's flexibility by applying it to two distinct life history groups of age 1+ Atlantic salmon, mature residents (parr) and immature emigrants (smolts) that are known to exhibit differences in their seasonal growth trajectories. We did not detect any differences in consumption or maintenance parameters but we did find subtle differences in their seasonal growth functions. The ability of the model to recover these life history patterns adds credence to its flexibility. Although we apply the model to a particular species as an example, the model is widely applicable across species because it is based on first principles of growth and does not assume species specific parameter values.

3.2. Introduction

Modeling physiological growth has remained a crucial endeavor in studies of both animal (Elliot and Hurley 1997) and plant populations (Schneider et al. 2006, Clark et al. 2007). Knowledge of the factors influencing growth is important for assessing the health of populations (Clark and Clark 1999, Bjorndal et al. 2000), biomass production (Ricker 1975, Quinn and Derisio 1999), and population dynamics (Clark and Clark 1999, Nisbet et al. 2000, Gurney et al. 2008). Because growth is a complex combination of physiological functions influenced by an array of intrinsic and extrinsic factors, it is often best understood by first reducing the process into its basic components. One way in which this task is achieved is through the development of growth models.

Informative growth models can aid managers directly and serve as an important component of more complex population or production models. There are a number of approaches to modeling growth, each with certain advantages and disadvantages. For example, the use of bioenergetic models has experienced considerable success in determining consumption rates and growth (Kitchell et al. 1977, Rice and Cochran 1984). However, they are difficult to parameterize, can require great effort to construct and due to local physiological adaptation are often only applicable to the species and population for which they were developed (Ney 1993, Munch et al. 2002, Chipps and Wahl 2008). Linear statistical models allow the researcher to identify factors that may influence growth (e.g. Vollestad et al. 2002, Bacon et al. 2005), but their lack of mechanistic underpinnings makes them prone to bias especially as growth tends to be a

nonlinear process. A more general modeling approach is to use ontogenetic growth models such as the von Bertalanffy model (von Bertalanffy 1938). This model lacks the detail that is included in more realistic bioenergetic models; however, it is derived from first principles of growth and its generality allows it to be fit to a wide range of organisms as it tends to capture the essential elements of the growth process (West et al. 2001).

Traditional applications of the von Bertalanffy model usually involve fitting the model to size-at-age information of a particular species or population (Ricker, 1975). However, more recent modifications have attempted to account for temporal variability in the growth dynamics as growth is highly sensitive to changes in the environment (Szalai et al. 2003). For example, organisms living in temperate environments will often exhibit strong seasonality in their growth dynamics (Baba et al. 2004, Bacon et al. 2005, Strothotte et al. 2005). This seasonality can reflect a mixture of fluctuations in temperature and food availability as well as other factors that affect the growth process (Vollestad et al. 2002, Letcher and Gries 2003). A model that can inform this dynamical process is potentially useful in contributing to more complex models of seasonal changes in ecosystems.

Because individuals will often vary in their performance, growth not only varies temporally but also varies among individuals within a population (Letcher et al 1997, Pfister and Stevens 2002, Pfister and Peacor, 2003). Traditional studies may ignore individual variation due to lack of information at the individual level. With the growing number of capture-mark-recapture (CMC) studies, longitudinal (i.e. repeated measures) data are becoming increasingly common suggesting the need for more sophisticated

approaches that address individual-level variation (Fujiwara et al. 2005). Such data are advantageous because they provide information on how changes in individual size vary among individuals over time. This variation adds a level of stochasticity to models that will generate inaccurate estimates if it is ignored (Clark 2003). A Bayesian hierarchical framework offers a tractable and informative method to understand and account for the magnitude of individual variability in growth in a population (Clark 2003, Clark et al. 2005). For example, accounting for individual heterogeneity in capture probabilities and survival can be a difficult task in mark-recapture studies, but this is easily accomplished in a Bayesian framework by implementing Markov chain Monte Carlo (MCMC) methods which allow for integration over the random effects (Zheng et al. 2007). Additionally, understanding effects of individual variability can provide key insights into the underlying mechanisms driving population dynamics (Letcher et al. 1996, Nisbet et al. 2000, Pfister and Stevens 2002, Fujiwara et al. 2004, Fujiwara et al. 2005).

Another source of variation that can influence parameter uncertainty is measurement error. Because all models are simple abstractions of some underlying process, a certain degree of process error must be assumed, however, when measurement error is also a factor parameter bias and uncertainty can be considerable (Hilborn and Mangel 1997, de Valpine and Hastings 2002, Paulsen et al. 2007). With growth models, measurement error can result in predicted growth trajectories that are unrealistic (Clark et al. 2007). For example, error in tree growth measurement can result in estimates that suggest negative growth even though such estimates are generally unrealistic biologically (Clark and Clark 1999, Clark et al. 2007). A state space modeling framework offers one approach to separate measurement error from process error (de Valpine and Hastings

2002). State-space models define the observation process explicitly making it independent from the underlying dynamics process. The ecological literature has recently undergone a steady increase in the number of studies employing a state-space approach (de Valpine 2003, Royle and Kerry 2007, Calvert et al. 2009, Rich et al 2009).

Until recently, models that could estimate parameters from complex data sets of repeated observations were rare in the ecological literature as statistical methods were not available or commonly employed (but see Jones et al. 2002). The advent of hierarchical Bayesian techniques such as MCMC provides an opportunity to fit relatively complex models to datasets even when some of the data are sparse all within a unified probabilistic framework (de Valpine 2009). In addition, a hierarchical model can be embedded within a state-space framework and thus models can simultaneously address individual variability and observational uncertainty. With the increase in computer power and availability of software packages to perform MCMC integration, the application of these techniques has become increasingly common in the ecological literature (Cressie et al. 2009).

In this paper we derive a discrete time growth model based on von Bertalanffy growth dynamics. We apply our model to CMC data of age-1 juvenile Atlantic salmon (*Salmo salar*). Atlantic salmon offer an ideal species to test the utility of our model because they exhibit a high degree of individual and seasonal variation in growth as well as tremendous plasticity generating two distinct life histories which include fish that remain immature during their second year of growth and emigrate in the following spring (smolts) and fish that mature during the fall of their second year of growth but remain as residents the following year (parr). Using modern statistical methods, our model

provides a comprehensive framework to estimate both seasonal variation and individual variation in growth in the face of measurement uncertainty.

3.3. Methods

3.3.1. Data Collection

Our study was conducted in the West Brook, a second-order tributary of the Connecticut River located in western Massachusetts, U.S.A. (42°25' N; 72°40' W). The study site is *c.* 1 km long and consists of 47 contiguous sections that average 20.3 m in length and 101.7 m² in area. Further details of the study site and data collection can be found elsewhere in the literature (Letcher et al. 2002, Letcher and Gries 2003) so we will provide only relevant details here. To capture individuals, electrofishing was conducted in an upstream direction using a two pass removal approach. Sampling occurred on six occasions throughout the course of the year from March through December. Each sampling occasion took approximately ten days. Captured salmon were placed in buckets before tagging. Each fish that was large enough for tagging (>60 mm and > 2.0 g) was placed in a solution of MS-222 that was buffered with sodium bicarbonate. Once a fish was sufficiently anaesthetized, it was scanned for a PIT tag, measured for total length and fork length and weighed. If a PIT tag was not present, the fish was tagged by making a small incision just below the pectoral fins and inserting a tag into the peritoneal cavity. In addition, all fish were lightly squeezed around the abdomen to check for milt, indicating a mature parr. All fish were returned to the section of capture.

In addition, during each fish sampling occasion, one benthic sample of invertebrates and one invertebrate drift sample were conducted during three different days at three different locations within the study site prior to electrofishing. Information

gained from the invertebrate sampling was used to help inform seasonal fluctuations in food availability. Details of collection and sorting can be found in Grader and Letcher (2006).

A picket weir was constructed each year to capture migrating smolts following the design of Anderson and McDonald (1978). The picket weir was placed in the brook early in the season and kept in the brook throughout the course of smolt emigration (March – June). The trap was located *c.* 3 km downstream of the study site. All fish captured in the trap were measured for fork length and weighed. All fish captured in the weir were processed at the trap.

3.3.2. Model Development

To derive our model we start by assuming growth in weight follows basic von Bertalanffy dynamics where assimilation is a product of consumption rate and food availability. If we assume that random noise in the growth scales with consumption, then the underlying dynamic can be written as the following stochastic differential equation (SDE):

$$\frac{dW}{dt} = \alpha W^{\frac{2}{3}} F(t) - mW + zW^{\frac{2}{3}} \quad (1)$$

where $F(t)$ represents a seasonal growth function (SGF), α is consumption, m is maintenance and z represents correlated Gaussian noise. To derive an equation for growth in length we assume length is related to weight through the allometric relationship:

$$L = \phi W^{\frac{1}{3}} \quad (2)$$

We can then write the equation for growth in length as

$$\frac{dL}{dt} = \frac{\phi}{3} \alpha F(t) - \frac{m}{3} L + \frac{\phi}{3} z \quad (3)$$

which we can re-arrange to show

$$\frac{dL}{dt} + \frac{m}{3} L = \frac{\phi}{3} \alpha F(t) + \frac{\phi}{3} z \quad (4)$$

To perform the integration we make a Stratonovich interpretation of the SDE (Socha 2008). This interpretation is appropriate in this modelling framework because growth represents a continuous process where noise in the dynamics is likely to be highly correlated due to the complexity of physiological feedback mechanisms. By assuming that z is weakly correlated instead of representing uncorrelated white noise, we can integrate both sides using standard calculus. As such, we can use the integrating factor method to integrate both sides of the equation as follows

$$\int_t^{t+1} \left(\frac{dL}{dt} + \frac{m}{3} L \right) e^{\frac{m}{3}t} = \int_t^{t+1} \left(\frac{\phi}{3} \alpha F(t) + z \frac{\phi}{3} \right) e^{\frac{m}{3}t} \quad (5)$$

After performing the integration and substituting in dummy variables we can show

$$L_{i,t+1} = L_{i,t} \delta + b_i f(t) + \varepsilon_{i,t} \quad (6)$$

where

$$\begin{cases} \delta = e^{\frac{m}{3}} \\ b_i = \frac{\phi \alpha_i}{3} \\ f(t) = \int_t^{t+1} e^{\frac{m}{3}} F(t) dt \\ \varepsilon_{i,t} = \frac{\phi}{3} \int_t^{t+1} e^{\frac{m}{3}} z dt \end{cases} \quad (7)$$

As a result, the underlying assumptions are that consumption varies among individuals, but not as a function of body size, and the SGF and maintenance rate are constant among individuals.

3.3.3. Bayesian State-Space Estimation

To estimate parameter uncertainty we adopted a Bayesian state space framework. This framework allows us to include both process error in the state dynamics and observation error in the observed states. In addition, because the model assumes individual variability in consumption within this hierarchical framework the consumption parameters can be modeled as random effects with hyperparameters defining the distribution of the individual random effects. We consider the true length of an individual as unobservable and the observed length as a Gaussian process dependent on measurement error.

For our likelihood we assume a normal distribution given the unobserved states

$$L_{i,t}^O / L_{i,t} \sim N(0, V_e) \quad (8)$$

where $L_{i,t}^O$ is the observed length of individual i at time t , and V_e represents measurement error in length.

For the growth process we also assume a normal distribution given the model such that

$$L_{i,t+1}|L_{i,t}, \delta, b_i, f(t), V_P \sim N(0, V_P) \quad (9)$$

where V_P represents process error in the growth dynamics and b_i represents the random effect for individual i . The full posterior can be written as:

$$\begin{aligned} P(\theta, \vec{b}_i, \vec{L}_{i,t} | L_{i,t}^O) &\propto \prod_{t=2}^T \prod_{n=1}^n P(L_{i,t}^O | L_{i,t}, V_e) \prod_{n=1}^N P(L_{i,t=1}^O | L_{i,t=1}, V_e) && \text{Likelihood} \\ &\times \prod_{t=2}^T \prod_{i=1}^n P(L_{i,t+1} | L_{i,t}, \delta, b_i, f(t), V_P) && \text{Process model} \quad (10) \\ &\times \prod_{i=1}^n P(b_i | \mu_b, V_b) && \text{Random Effects} \\ &\times P(\theta) && \text{Priors.} \end{aligned}$$

The likelihood, the process model, and the prior distribution for the random effects are all assumed to follow a normal distribution. $P(\theta)$ represents the prior distribution for the hyperparameters for the random effects μ_b and V_b , the SGF $f(t)$, the unobserved initial states $L_{i,t=1}$ and the variances V_P and V_e . Prior distributions are listed in Figure 3.1. For most parameters, conjugate uninformative priors were used (e.g. inverse gamma priors for variances, (Gelman et al. 2004)). However, for the SGF and measurement error, we took advantage of the Bayesian framework to develop general methods that use auxiliary information to develop informative priors that reduce posterior uncertainty.

3.3.3.1. Seasonal Growth Function

To approximate the seasonal growth function in discrete time we use a flexible, nonparametric step function of the form

$$f(t) = \sum_{i=1}^n \partial_i 1_{A_i}(t) \quad (11)$$

for all $t \in \mathfrak{R}$ where \mathfrak{R} represents the set of real numbers and 1_A is an indicator function such that $1_A(t) = 1$ if $t \in A$ and 0 otherwise.

To specify a prior distribution in the seasonal growth function (SGF) we collect the coefficients ∂_i in the vector \vec{f} and assume a multivariate normal distribution such that

$$\vec{f} \sim \text{MVN}(\mu_f, C_f) \quad (12)$$

where the vector \vec{f} represents a vector of the coefficients defining the food function.

To specify the covariance function we assume C_f decays over time. Therefore, we specify C_f as

$$C_f(f(t), f(t + \tau)) = \nu e^{-\phi(t - (t + \tau))^2} \quad (13)$$

where ν is the variance in the food function, τ is the time lag and ϕ represents the rate of decay in covariance with the time lag. An intuitive description of the covariance function can be found in Munch et al. (2005). We assume a value of 0.5 for ϕ and 10 for ν .

One issue with the SGF is that it is confounded with mean consumption (μ_b). To minimize the confounding between these two parameters we can make use of multivariate conditioning where we can specify the prior for the food given a specified condition. To do so we can use the inverse of partitioned matrices to introduce a constraint. This constraint yields a multivariate distribution for \vec{f} , with updated mean $\tilde{\mu}_f$ and covariance \tilde{C}_f , given the condition that for any time t the expectation of $f(t)$ is constrained to be one (details are described in Appendix A).

Now that we have specified a prior food function that is conditioned such that $f(t)$ must sum to one, we can incorporate prior information on the food environment. If we assume the likelihood of the observed food data (F_O) given the food function can be written as

$$P(\vec{F}_O \mid \vec{f}, V_f) \sim N(0, V_f) \quad (14)$$

where V_f is the variance in the food, then we can use Baye's rule to derive a multivariate normal distribution for \vec{f} such that

$$P(\vec{f} \mid \vec{F}_O, V_f) \propto P(\vec{F}_O \mid \vec{f}, V_f) \cdot P(\vec{f} \mid \tilde{M}u_f, \tilde{C}_f) \sim MVN(\mu_f, \Sigma_f) \quad (15)$$

Where the mean and covariance of the informative prior are

$$\mu_f = \Sigma_f (\tilde{C}_f \tilde{M}u_f + \vec{F}_O / V_f) \quad (16)$$

$$\Sigma_f = (\tilde{C}_f^{-1} + \frac{1}{V_f})^{-1} \quad (17)$$

Because invertebrate biovolume was measured three times per sample, we could calculate a variance in food availability for each sample. For V_f we substituted a value of 0.781 which represents the highest observed value in variance among all samples. For all fixed values ϕ , v , and V_f we assessed sensitivity to prior choices with a sensitivity analysis.

3.3.3.2. Measurement error

In this state-space framework it can be difficult to obtain estimates of both measurement and process uncertainty simultaneously. We therefore developed a straightforward approach to generating an informed prior of measurement error uncertainty. We first assume that the observed size of fish is equal to its true size plus some degree of error. From this relationship we can use Baye's rule to derive the

probability of the measurement error and the true sizes of the fish given the observed sizes as

$$P(V_e, \vec{X}_T | \vec{X}_O) \propto P(V_e, \vec{X}_T) \prod_{i=1}^N P(\vec{X}_O | \vec{X}_T, V_e) \quad (18)$$

where \vec{X}_O is the vector of observed fish sizes, \vec{X}_T is a vector of true fish sizes and V_e represents measurement error. Using this relationship, we can again employ Baye's rule to show,

$$P(\vec{X}_T | \vec{X}_O, V_e) = \frac{P(\vec{X}_T, V_e | \vec{X}_O)}{P(V_e | \vec{X}_O)}. \quad (19)$$

We can rearrange this equation to show

$$P(V_e | \vec{X}_O) = \frac{P(\vec{X}_T, V_e | \vec{X}_O)}{P(\vec{X}_T | \vec{X}_O, V_e)}. \quad (20)$$

Our goal is to derive a probability distribution for V_e that minimizes our uncertainty in V_e .

We first assume our likelihood function $P(\vec{X}_O | \vec{X}_T, V_e)$ is normally distributed. Next,

we need to define a prior distribution for V_e . We chose $P(V_e)$ to be distributed as an

inverse gamma function with shape parameters α and β where we set β equal to an initial

guess of the measurement error. Based on previous field work we found measurement

error in length to be approximately 1 mm. We then set $\alpha = 2$ so that our prior distribution

in V_e is sufficiently vague.

Because the inverse gamma distribution is conjugate to the normal likelihood the

posterior distribution for V_e will also be in the form of an inverse gamma pdf with a

defined expectation and variance such that

$$P(V_e | data) \sim IG(\alpha', \beta') \quad (21)$$

With some algebra, it can be shown that the shape parameter B' is equal to B (our initial guess at the measurement error) plus the sum of squares (SS) of repeatedly sampling N fish n times. We can also define our uncertainty in V_e as the variance of this distribution. By substituting different values for the sum of squares for length that were in the range of what we expect the measurement error might be we calculated this variance for different sample sizes of N and n . We found that even with a fairly large measurement error we could minimize the uncertainty in V_e by setting $N=10$ and $n=10$. Thus, we sampled fish under field conditions and repeatedly measured 10 salmon parr each for a total of 10 times. In order to minimize observer bias, fish were randomly chosen for each measurement so the observer was not aware of which fish was being measured. We used these data to then quantify the SS which we used to estimate expected values of V_e .

3.3.3.3. Gibbs Sampling

Because full conditional distributions could be defined for all growth parameters and the latent states we could make use of the efficient Gibbs algorithm to sample from the posterior (Appendix B). We assessed convergence by examining trace plots and using standard diagnostics (Gelman et al. 2004)

3.4. Results

3.4.1. Parameter Estimates

We found reasonable estimates of marginal posterior uncertainty for the parameters of interest (Table 3.2). Posterior medians and high overlap of 95% Bayesian confidence intervals suggested little difference between the two life history groups in

both the mean consumption and maintenance growth parameters. Bayesian credible intervals were wider for the smolt group than the parr group most likely as a result of fewer salmon that could be classified as smolts ($n=26$) vs parr ($n=66$). Low sample sizes occur because many individuals are not captured during critical periods of life history expression (fall for mature parr and spring for migrating smolts) therefore they cannot be assigned to a life history group. Another issue contributing to uncertainty is missing observations among individuals. Fortunately, salmon tend to have high capture rates ($p = 0.6 - 0.8$, Letcher et al. 2002) yielding a high number of recaptures for each fish. Sensitivity analysis verified that marginal posterior distributions of all parameters were insensitive to choices made in the prior. The random effects seemed to add an important component of variation for both smolts and parr as evidenced by posterior estimates of the variance component (V_b) and Bayesian CIs that did not cover zero (Table 3.2).

3.4.2. Seasonal Growth Function

The SGF revealed subtle difference between the two life history groups in terms of their seasonal growth trajectories (Figure 3.1). Both parr and smolts exhibited high growth during the spring interval. Although there was high overlap in confidence envelopes, the mean posterior distribution suggested some subtle differences in summer and fall growth. During summer months it appeared that the smolt life history may have experienced slower growth than the parr life history. By fall however, this pattern reversed where smolts began to exhibit a slight increase in their SGF but the SGF of parr remained low.

3.4.3. Model Predictions

We found very close agreement between observed growth sizes and model predictions for both parr (Figure 3.2a) and smolts (Figure 3.2b) despite the fact that there were many more observations for length (Nobs) for parr (Figure 3.2a) than smolts (Figure 3.2a) . Posterior predictive growth trajectories suggested our model was able to capture the seasonal shape of individual growth trajectories as well as the variability among individuals (Figure 3.3a-f). The close agreement between observations and prediction is not all that surprising as the individual variation and seasonal parameters add a high degree of flexibility. We found close model fit for individuals with many observations (Figure 3.2a and d, parr and smolt respectively). Also, information about an individual's size at the end and beginning of the growth seemed to help pin down uncertainty where observations were missing (Figure 3b and e, parr and smolt respectively). Uncertainty around unobserved sizes tended to be substantial if there were only a few observations towards the end or beginning of the growth trajectory (Figures 3c and f, parr and smolt respectively).

3.5. Discussion

A primary goal of model development is finding the interface between realism expressed as model complexity and tractability that allows estimation of model parameters from data. We took a mechanistic modeling approach to derive a relatively simple first order autoregressive model from von Bertalanffy growth dynamics. The von Bertalanffy model offers a general ontogenetic growth model that captures the basic shape of animal growth trajectories without relying on a complex set of parameters. By the

same token, complexity can be added to the baseline model to develop more informative growth models. One advantage of our current model is that the dynamics are linear which allows for efficient estimation of parameters in a Bayesian framework. Also, the generality of this model allows it to be applied to other populations or species without needing to assume parameter values as is often the case with more complex bioenergetic models. Although this model lacks the detail of more realistic bioenergetic models, this framework allowed us to incorporate two key components of growth variation, temporal and individual, while separating process uncertainty from measurement uncertainty.

3.5.1. Seasonal Growth Function

Posterior predictions for the seasonal growth function indicated large seasonal differences in growth as well as subtle differences among life history groups in growth depending on the season. Seasonal variation in growth is well documented in stream salmonids as warming temperatures and the emergence of invertebrate prey tend to promote fast growth in spring followed by a decrease in summer as conditions generally become unfavorable for growth (Letcher and Gries 2003, Strothotte et al. 2005). To account for this predictable spring growth spurt we could take a parametric approach and try and fit a specific growth function that allows for this rise and fall (see Jones et al. 2002). However, this approach does not allow for flexibility in seasonal growth that may occur among life histories, populations or species. By including a nonparametric function we added flexibility which allows the growth function to vary independent of Julian date. Nonparametric Bayesian approaches are becoming increasingly popular as they allow the data to define the shape of the function of interest without having to assume an underlying parametric form (Munch et al. 2005). Because salmon exhibit

wide plasticity in their growth dynamics, a flexible approach is necessary to delineate life history differences.

Previous attempts at modeling growth in salmonids involved the development of laboratory derived models based on temperature with the idea that temperature is the major factor contributing to growth variation (Elliott and Hurley 1997, Forseth et al. 2001). Although these models experienced some success when applied to field data, they also have a tendency to underestimate the high spring growth and overestimate summer growth (Bacon et al. 2005). We found our model was able to predict interesting seasonal patterns in the growth trajectories of smolts and resident parr that corroborate previous studies on growth dynamics (Letcher and Gries 2003, Bacon et al. 2005). For example, feeding was highest in the spring but there was essentially no difference between life history groups in either the SGF or the other growth parameters. This lack of difference suggests that life history differences in growth dynamics are not manifest during this spring growth stage. During the early summer growth phase, parr seemed to gain a slight growth advantage over smolts. This difference may be a function of size disparity between these two groups. Smolts are on average larger than parr during the summer (Letcher and Gries, 2003). During stream residency, larger individuals tend to require deeper pool like habitats to attain positive growth which is limited in summer due to a decrease in flow (Hutchings 1986, Halvorsen and Svenning 2000, Sigourney et al. 2006). In addition, average size of invertebrate prey decreases in the summer (Grader and Letcher, 2006). Byström and Andersson (2005) showed that capture success can decrease with size depending on the size of the prey which may explain summer differences between life history groups. In contrast to this early summer period, the

growth function suggested a slight increase in late summer/early fall for migrating smolts. This pattern is consistent with the idea that smolt need to reach a threshold size for seaward migration and that there is a sensitive “window” occurring in the fall (Metcalf 1998, Thorpe et al. 1998). The ability of the model to recover these patterns indicates its ability to capture important biological aspects of the growth process.

3.5.2. Parameter Estimates and Random Effects

Posterior estimates and Bayesian confidence intervals of metabolism and mean consumption suggested little difference among life history groups. This result is not too surprising as size differences between these two groups tend to be established during their first year of growth (Letcher and Gries 2003). It is important to note, however, that although we made use of multivariate conditioning to reduce confounding between mean consumption (μ_b) and the seasonal growth function, some caution is required when making direct biological interpretations of these parameters. For example, one possible interpretation is that all the variation in growth between these two groups is due to seasonal changes in the growth environments that they experience. As discussed above, this interpretation may be partly valid as differences in size can influence food availability and habitat availability. However, there are also likely behavioral and physiological differences (Metcalf et al. 1986, Rowe and Thorpe 1990). For example, during fall smolts are motivated to feed to gain a threshold size for migration (Metcalf 1998) where as maturing parr are allocating energy into gonadal growth and reproduction and not into growth in length (Metcalf 1998, Thorpe et al. 1998).

Estimates of scale hyperparameters of the random effects suggested significant variation among individuals. By allowing for individual variation in performance

through the consumption parameter our model is flexible enough to allow for change in the size rank among individuals. Because our model makes no assumptions about the relationship between size and consumption (b_i) individuals with different initial sizes can grow at rates that allow smaller fish to eventually surpass larger fish in size. The mechanism that allows for rank change is variation in consumption, thus, an individual that is initially at a smaller size may have a higher consumption parameter and eventually exceed another individual in size. An interesting extension of our model would be to apply it to the quantitative genetics framework. There is much interest in the heritability of size trajectories and growth from natural populations (Wilson et al. 2003, Wilson et al. 2005, DiBattista et al. 2009). Because of the hierarchical nature of our model, information from pedigree analysis could be added as another level in the hierarchy and additive genetic variance could be quantified. This approach could be advantageous in highly seasonal environments.

3.5.3. Measurement Error

We offer an objective method to directly incorporate information on measurement error into a Bayesian state-space model. Application of the general state-space method has proven successful in overcoming the problem of imperfect detection in a variety of situations including analyzing population dynamics (Meyer and Millar 1999, de Valpine 2003, Lindley 2003), survival estimation (Gimenez et al. 2007), animal movements (Barraquand and Benhamou 2008, Jonsen et al. 2005), and growth (Fujiwara et al. 2005). Our method of assessing measurement error has a number of applications beyond our specific growth model. For example, many studies use otoliths or scales to reconstruct the growth history of individuals (Li et al. 2008, McCarthy et al. 2008). Another

promising approach to measuring individual size is through the use of underwater video (Harvey et al. 2002, Harvey et al. 2003). These techniques, however, are all subject to measurement error. Using our method, this error can be quantified in a probabilistic framework and used to derive informative priors to minimize parameter bias and posterior uncertainty. We found the measurement error for length was quite low as salmon were anesthetized and we were able to make careful measurements. Therefore, we felt comfortable simply fixing our prior to our empirical estimate of measurement error as sensitivity analysis revealed that the posterior was insensitive to different values. However, under more compromising conditions such as sampling at sea, careful measurement may be difficult. With minimal effort our approach can be applied to reduce uncertainty arising from this source of error.

3.5.4. Limitations

Our present model lacks two potentially important factors regulating salmon growth: density and temperature (Forseth et al. 2001, Elliott and Hurley 2003, Imre et al. 2005, Lobon-Cervia 2007). Because the relationship between growth and temperature is well defined for salmonids and there is substantial prior information in the literature regarding parameter values this function could be easily added to the model. Density may also be added as a covariate. However, when adding covariates a difficult task is to avoid identifiability issues among parameters resulting from parameter confounding. A more vexing problem is that our model may not perform well in a stochastic environment where autocorrelation in growth among individuals is low. By allowing for individual differences in consumption rates we are essentially constraining growth to be autocorrelated in time. It is important to realize, however, that in a natural setting other

environmental factors may be contributing to rank change, but the degree of growth autocorrelation may depend on the level of environmental stochasticity. For example, in some environments changes in food availability, temperature regime, the presence or absence of predators and a number of other variables may lead to substantial temporal variability in the quality of the growth environment among individuals (Pfister and Peacor 2003). When applying this model the degree of autocorrelation in growth should be considered.

3.5.5. Summary

Our goal in this paper was to develop a general growth model that can be applied to longitudinal data. Model derivation is similar to one derived by Gurney et al. (2007) as it is based on von Bertalanffy growth dynamics and incorporates a seasonal function; however, their model was fit to length-at-age statistics where we aimed to derive a model that could be fit directly to mark-recapture data while making limited assumptions. To this end, we adopted a Bayesian estimation framework more similar to the one described by Clark et al. (2007) where we used a hierarchical approach to incorporate uncertainty arising from individual variability and a state-space framework to address measurement error. Unlike Clark et al. (2007), we've also included a seasonality function to assess within-year temporal variation. Although our model has advantages over previous growth models it is still subject to limitations. We reiterate Elliott and Hurley (1997) who state "growth model development is an iterative process". Because there are a number of potential biotic and abiotic factors that also play important roles in the growth process it would be ideal to be able to integrate them within the modeling framework to be able to understand yearly variation in growth and variation among tributaries, rivers or

populations. We feel this model offers a good basis that can be built upon in future growth modeling projects.

Table 3.1. Prior distributions on model parameters. All distributions were centered on prior guesses of parameter values where c indicates constant (vague) priors for μ_b and $\vec{L}_{i,t=1}$. Scale parameters were set as follows $V_\delta=1000$, $a'_b=2$, and $a'_p=2$ to insure that priors were sufficiently vague to admit high prior uncertainty in parameter values.

Parameter	Prior
δ	$\sim N(\mu_\delta V_\delta)$
μ_b	$\sim c$
V_b	$\sim IG(a'_b, b'_b)$
V_p	$\sim IG(a'_p, b'_p)$
\vec{f}	<i>See text</i>
$\vec{L}_{i,t=1}$	$\sim c$

Table 3.2. Posterior median values and 95% Bayesian credible intervals for hyperparameters on consumption (μ_k and V_k) and maintenance (δ).

Life History	Parameter	Posterior median	Credible Interval	
			2.5%	97.5%
Parr	δ	0.9354	0.8792	0.9716
	μ_b	4.5605	3.4874	6.4812
	V_b	0.1985	0.1181	0.3218
Smolt	δ	0.9589	0.8769	1.0041
	μ_b	4.5224	3.0931	7.1159
	V_b	0.1543	0.0684	0.3435

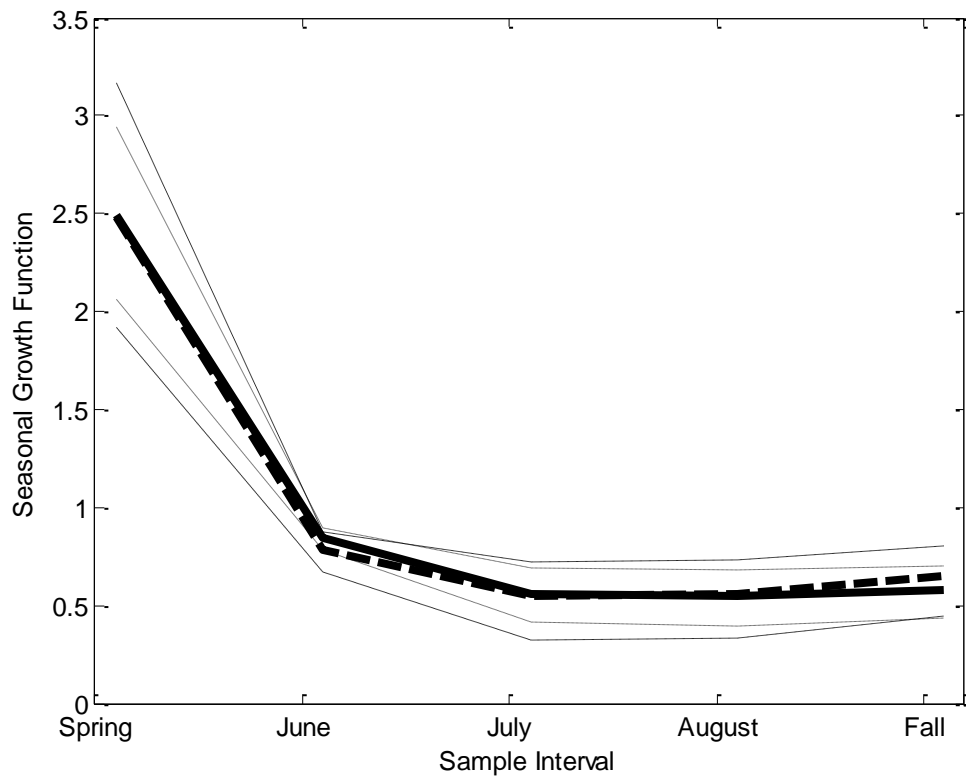


Figure 3.1: Predicted mean values for the seasonal growth function for juvenile Atlantic salmon parr (—) and smolts (---) including 95% Bayesian credible intervals for parr (----) and smolts (— —).

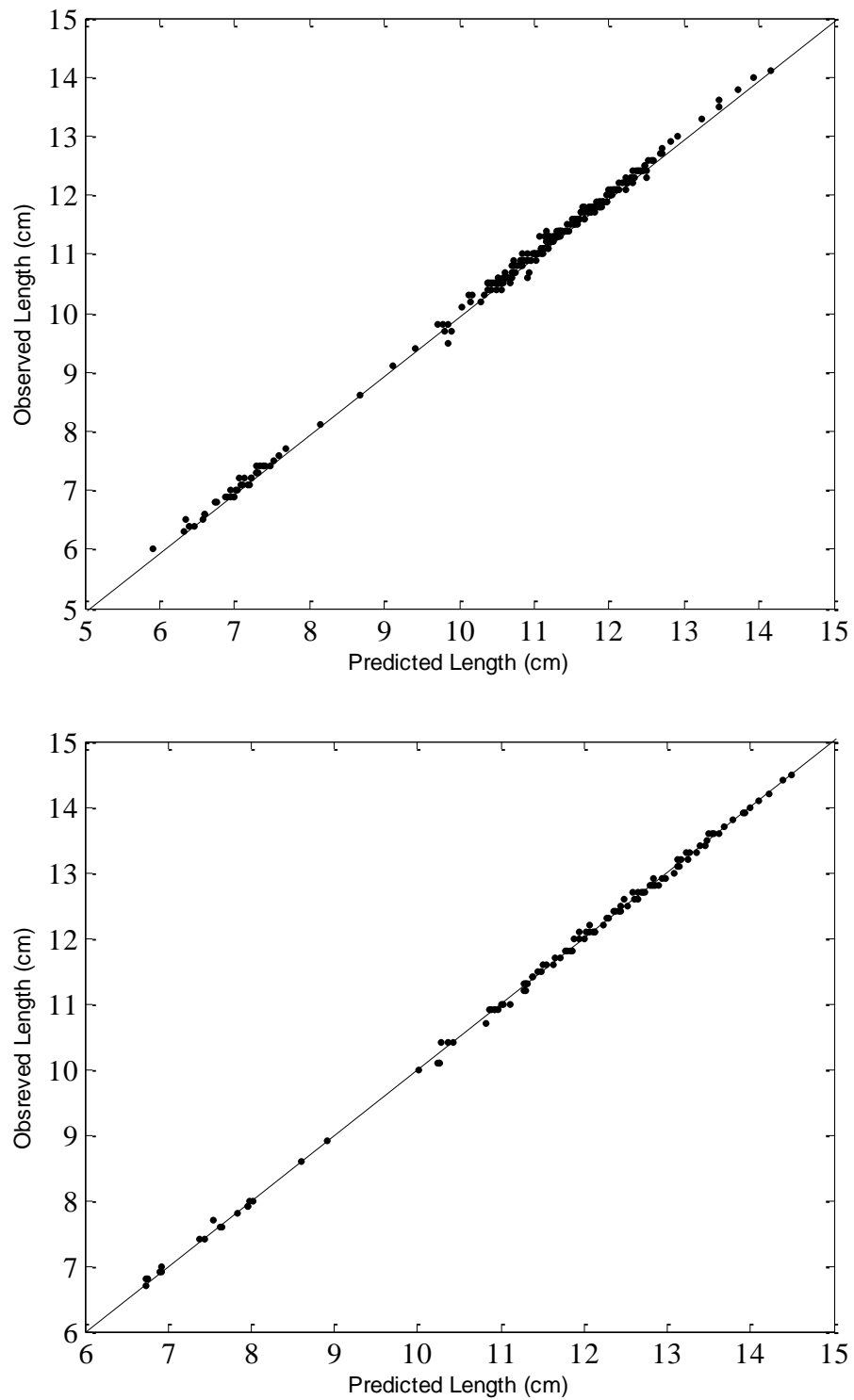


Figure 3.2: Predicted mean lengths vs observed lengths for all individual juvenile Atlantic salmon observed in (a) the parr dataset ($r^2=0.998$, $N_{\text{observations}}=264$) and (b) the smolt dataset ($r^2=0.999$, $N_{\text{observations}}=113$).

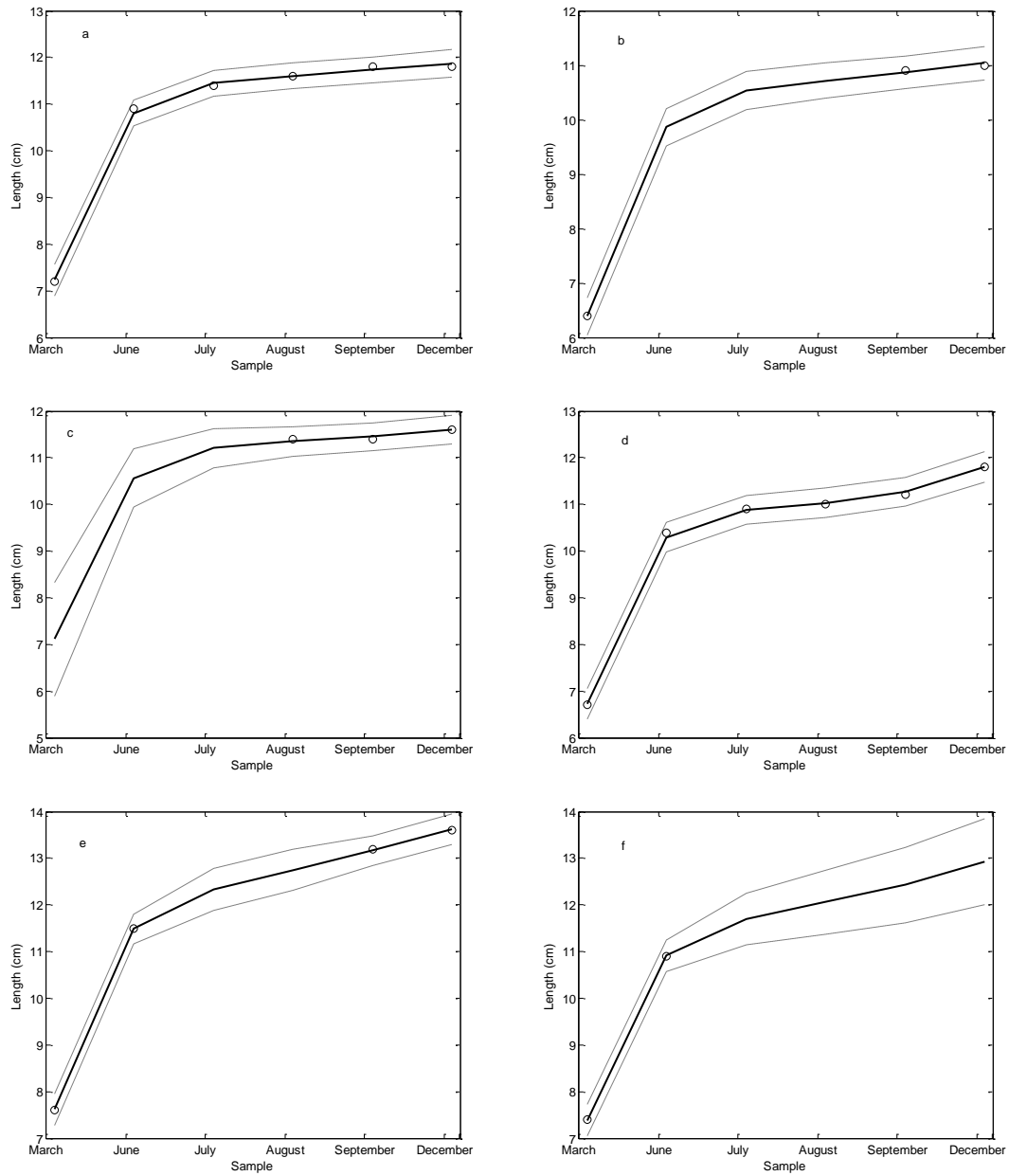


Figure 3.3: Representative growth trajectories of individual parr (a-c) and individual smolts (d-f). Open circles represent observed lengths. Predictive means and (—) and credible intervals are shown (---).

CHAPTER 4

INTERACTING EFFECTS OF SIZE, LIFE HISTORY AND SEASON ON GROWTH IN SALMONIDS: CAUSATION FOR COMPENSATORY AND FREQUENCY-DEPENDENT RESPONSES IN THE WILD?

4.1. Abstract

Size-dependent growth has long intrigued ecologists particularly because of its consequences on population dynamics. Compensatory growth, an important form of size-dependent growth, has been intensively studied in a number of taxa. Many studies have investigated this phenomenon by manipulating growth rates and comparing the responses of treatments to controls. Few studies have observed its presence in a natural environment, and therefore, the functional role of compensatory growth is still somewhat ambiguous. Because growth tends to have strong consequences on fitness, compensatory growth may be linked to life history strategies. In this study we use strictly observational data from both the laboratory and the field to study the interaction between life history and the presence and strength of compensatory growth in immature Atlantic salmon. Because we could not always assign individuals to a life history group we used piecewise quantile regression to analyze regression plots when there might be a mix of the two life history groups. We found that life history-dependent compensatory growth was evident in the laboratory and field depending on the season analyzed. In addition, we found some evidence of an interaction between season and density on growth rate in age 1 salmon but not in age 2 salmon. We hypothesize that this may be due to a conditional strategy where large age 1 salmon will accelerate fall growth in years of high density and smolt the following spring rather than try to survive an extra year in the stream where per capita mortality could be high. Our results indicate that life history and season can be important

determinants of compensatory growth responses and can lead to the maintenance of two growth strategies: 1) those that display compensatory growth to reach an adequate size before migration and 2) those who forgo compensatory growth and remain in the stream for another year before migration. This information could be useful in smolt production models that aim to predict the size and age structure of migrating smolts.

4.2. Introduction

Size-dependent growth has long interested ecologists both in terms of identifying the underlying causes and understanding the consequences in nature. Although it is important to consider underlying biological scaling relationships that result from the relationship between size and metabolism when studying size-dependent growth (Peters 1983, West et al. 2001), ecologists are often interested in understanding the eco-evolutionary context that influences the size-growth rate relationship. Changes in growth rate with size can determine key life history transitions such as the timing of ontogenetic habitat shifts (Altweg 2002, Tammaru et al. 2004, Vonesh and Bolker 2005, De Block et al. 2008). This connection to life history has both ecological and evolutionary implications as the biotic and abiotic environment may be a cause of size-dependent growth, but as a consequence different life histories may evolve to maximize fitness where there are trade-offs between growth rate and survival (Abrams et al. 1996)

One intriguing pattern of size dependent growth is compensatory growth. This pattern occurs when smaller individuals grow faster than larger individuals decreasing the variance in size (Ali et al. 2003). Compensatory growth has often been studied under laboratory conditions usually by subjecting one experimental unit to a reduction in food

or temperature (Ali et al. 2003). Although this phenomena has been well explored through manipulative studies (Johnsson and Bohlin 2005, Vonesh and Bolker 2005) and theoretical modeling (Gurney et al. 2003, Mangel and Munch 2005, Skalski et al. 2005), observational studies from the field are lacking (but see Bjorndal et al. 2003 and Carlson et al. 2004). Thus, the role of compensatory growth in nature is still somewhat ambiguous (Ali et al. 2003, Johnsson and Bohlin 2005)

The fact that compensatory growth acts to decrease size variation suggests that it may play an important role in ontogenetic development for organisms that undergo a migration or metamorphosis that depends on attaining some critical size. Indeed, many investigations into the causes and consequences have been conducted on the larvae of ephemeral pond breeding amphibians and insects that face strong selection pressure to reach a critical size (Altweg 2002, Vonesh and Bolker 2005, De Block et al. 2008). In addition, compensatory responses are often evident in migratory animals where large size often increases survival during migration (Fraser et al. 2007, Hegyi and Torok 2007, Dale et al. 2008). Empirical (Johnsson and Bohlin 2005) and theoretical studies (Mangel and Munch 2005, Mangel 2007) suggest that trade-offs exist between fast growth and current or future fitness (*for a review see* Metcalfe and Monaghan 2001). These trade-offs might give rise to the expression of several life histories that vary in the degree to which they will engage in compensatory growth in a given environment. Despite these implications there are few observational studies from the wild documenting the influence of life history on the strength of compensatory growth. Studies of this nature could help clarify the role of compensatory growth in the wild and illuminate the ecological context under

which compensatory growth may be expected to manifest itself without unnatural manipulations of the growth environment.

Atlantic salmon represent an ideal species to study in terms of the interaction of life history and size on growth rates. For example, they showcase flexible life histories that are strongly influenced by growth (Thorpe 1977, Myers et al. 1986, Letcher and Gries 2003), undergo a long migration which includes both a morphological and physiological metamorphosis and a distinct change in environments (McCormick et al. 1998), and they are relatively easy to mark and recapture in the wild (Juanes et al. 2000). In addition, this species is well studied so current investigations can be coupled with past research to establish common aspects of their population dynamics among geographical locations. In the context of life history, it is well established that members within a cohort segregate by size with members in the different size modes adopting different life history tactics (Thorpe 1977, Metcalfe et al. 1990, Nicieza et al. 1991). In addition, there are seasonal differences in feeding motivation (Metcalfe et al. 1986) and evidence that increased foraging incurs a cost (Nicieza and Metcalfe 1999). These characteristics set the stage for possible trade-offs in different growth strategies that allow the expression of different phenotypes depending on size and the environment experienced.

Previous laboratory studies on Atlantic salmon have established that they will undergo compensatory responses when subjected to a depression in growth (Nicieza and Metcalfe 1997, Metcalfe et al. 2002) and life history may play a role in determining the intensity of the response (Nicieza and Metcalfe, 1997). In addition, some field studies have provided some evidence of compensatory growth responses in migrating juveniles (Nicieza and Braña 1993, Utrilla and Lobón-Cerviá 1999), but it was not always clear if

smaller migrants grew faster or simply delayed migration to reach a critical size threshold. Thus, detailed studies into the timing of compensatory growth and the role of life history in natural environments are still lacking. In this study, we use both laboratory and field data to look at the interaction between size and life history on growth and whether or not there is a life history dependent compensatory growth response. Unlike other studies which unnaturally induce compensatory growth we use strictly observational data to isolate the effects of season and life history on the size-growth rate relationship.

4.3. Materials and Methods

4.3.1. Laboratory Data and Analysis

We used a detailed dataset of monthly growth rates of yearling Atlantic salmon from the fall of their age 0 year to the spring of their age 1 year. Growth trials were conducted at the Conte Anadromous Fish Research Center in Turners Falls, MA. All fish were fed ad libitum and temperatures followed ambient temperatures of the Connecticut River. Fish were anaesthetized with MS-222 (100 mg l⁻¹) and measured monthly for length (mm) and weight (g). To quantify growth we focused on absolute growth in length because it tends to be linear in salmonids during juvenile development (Sigourney et al. 2008, Nicieza and Alvarez 2009) and length measurements tend to be more accurate than weight measurements (Sigourney unpublished data). Therefore, growth was calculated as:

$$G_L = \frac{L_2 - L_1}{t_2 - t_1}$$

Where L_1 is size at the beginning of the interval L_2 is size at the end of the interval and the difference between t_2 and t_1 represents the length of the growth interval in number of days. Because we followed each individual until life history status was expressed in the spring we could retrospectively assign all fish to a life history group based on a combination of size and shape variables (see Pearlstein and Letcher 2008). Using a combination of shape, size and growth as criteria we categorized fish into two groups: 1) parr (i.e. fish that did not metamorphose into migrants in the spring) and 2) smolts (i.e. fish that did metamorphose in the spring).

Sigourney et al. (2008) presented some brief analysis of this dataset showing the tendency of smolts to maintain growth in the late fall while parr exhibited decreased growth late in the season as temperatures drop. In this analysis, we take a more detailed look at the monthly growth rates focusing on the interaction between size and life history on growth rates over four consecutive fall/early winter growth intervals. We limited our analysis to these first few intervals because differences in energy allocation among life history groups during later development may obfuscate growth patterns. We used general linear models (GLM) in which length was a covariate and life history was a grouping variable to test for an interaction between length and life history. We analyzed each monthly dataset separately to identify the time course of an interaction between size and life history on growth rate.

4.3.2. Field Sites and Data Collection

To examine the interaction between size and growth rate in the wild, we used an extensive dataset of field data collected from three different systems over multiple years. Field data were collected from the West Brook (WB) a 3rd order tributary to the Connecticut River located in Whately, Massachusetts USA (42°25'N 72°39'W), Shorey Brook (SB) a 2nd order tributary to the Narraguagus River located in Beddington, Maine USA (44°49'N 68°03'W) and Catamaran Brook (CB) a 3rd order tributary to the Little Southwest Miramichi River located in Renous, New Brunswick Canada (46°52'N 66°06'W) (Figure 4.1). CB is a completely natural system where populations are maintained through the natural reproduction of adults, populations in SB are maintained primarily through stocking fry in the spring although there is some limited natural spawning in this tributary and WB is solely maintained by the stocking of unfed fry in the spring (see Horton et al. 2009 for more details). Each study site was sampled a minimum of four times a year starting in the spring when conditions allowed sampling and ending in the late fall or early winter just before freeze up.

There are a number of papers that detail how data were collected in the field sites so we will only present the pertinent information here (Letcher and Gries 2003, Horton et al. 2009). Study sites were divided into 47 (WB), 37 (SB) or 22 (CB) continuous sections of approximately 100 m². Fish were captured using standard electroshocking techniques. Each section was closed off using block nets. All fish captured that were \geq 60 mm fork length and \geq 2.0 g in mass were individually tagged with an 11 mm passive integrated transponder (PIT) tag. Maturity was determined by applying gentle pressure to the abdomen and checking for the expression of milt. In addition, scales were collected for age determination.

In addition to the electroshocking samples, a picket weir was installed below each study site and was primarily used to collect migrating smolts in the spring. The modal age of migration is 2 for WB and 3 for both SB and CB. Similar to the laboratory data, we retrospectively assigned all individuals to the smolt life history group if it was captured during this time period and to the resident life history group if it was captured after the smolt run (*for more details see* Letcher and Gries 2003).

4.3.3. Analysis of Field Data

We only focused on known immature fish because the seasonal growth dynamics of mature parr differs substantially due to the allocation of energy to the development of gonads (Metcalf et al. 1986). Of the immature fish we could identify two life history groups, those that would emigrate in the spring (smolts) and those that would remain in the stream for an additional year (residents) (*see* Letcher and Gries 2003). Ideally, we would be able to repeat the analysis that we performed with the lab data by testing for an interaction between life history and size on fall growth. Unfortunately, it is difficult to assign large numbers of individuals to these groups because they have to survive and be captured at the right time (e.g. during the smolt migration) for a life history status to be assigned. For CB and SB limited information on the smolt life history group precluded any meaningful analysis. In WB; however, there were a number of year classes and sampling occasions where we could assign a reasonable number of individuals to the smolt life history group (Table 4.1). Therefore, we used linear regression to test for the effect of size on growth rate for these subsets of smolt data. Because the laboratory data suggested that the effect of life history on growth rate depended on season (*see Results*),

we looked at three different seasons leading up to the smolt migration which included fall, winter and spring.

For the other years and streams the data are mostly comprised of unknown immature individuals that likely represent a mix of smolts that will migrate in the spring and smaller residents that will delay migration. Because we know these two groups grow differently during this sensitive fall window and there is likely some overlap in size between those that smolt and those that remain as parr we developed two different hypotheses that should determine the shape of the bivariate relationship. Based on previous studies both in the lab and field detailing differences in growth between parr and smolts we restricted our hypotheses to two main predictions. Our main hypotheses are 1) only life history dependent growth is occurring with smolts growing faster than residents or 2) life history dependent compensatory growth is occurring with residents displaying no compensatory response and faster growing smolts displaying a compensatory response. Under the first hypothesis we might expect there to be an initial increase in the upper quantiles with size that represents the increase in growth rate as size increases from smaller residents to larger smolts followed by a flattening out of the upper residuals (see Figure 4.2a). Under the second hypothesis we would expect a triangular pattern in the upper quantiles with smaller smolts representing the fastest growing (compensating) individuals and then a general decrease in growth with size in the larger smolts (see Figure 4.2b). Applying linear models to such a dataset could be misleading because of the heterogeneity in growth rates. Therefore, to test these hypotheses we employed piecewise quantile regression. We apply two different constraints, an increasing constraint and a decreasing constraint, to the upper 95th quantile that restrict the shape of

the quantile and compare them to a regression with no constraint. The increasing constraint allows the quantile to increase and flatten out but not decrease. Similarly, the decreasing constraint allows the quantile to decrease and flatten out but not increase again. This pattern may occur if there is some sort of compensatory growth but is not restricted to the middle of the size distribution. For all quantile regressions we set the penalty parameter (λ) to 6 to minimize prediction error. We compare the different constraints with Akaike's Information Criterion (AIC) to evaluate which hypothesis the data support the most. To visualize the overall shape of the scatterplot cloud we also examined the 50th and 5th quantiles.

As previously mentioned, CB is a natural system in which yearly variation in densities is highly dependent on the spawning stock biomass. During the course of this study densities of parr fluctuated dramatically. To test if there was a detectable difference in growth rates between a high density year (2001) and a low density year (2003) and whether or not this variation might be seasonally dependent we used ANCOVA with G_L as the response variable, year and season as predictor variables, and length as a covariate. If we did not detect an effect of length, we used ANOVA instead of ANCOVA. We focused on CB because similar analyses of seasonal and yearly variation have already been conducted on WB and SB (Letcher and Gries 2003, Horton et al. 2009, Davidson et al. 2010). Because in CB the percentage of individuals that smoltify differs by age class, we analyzed age 1 and age 2 fish separately. For the age 2 class, the sample size was low for the 2003 summer, therefore, we restricted our analysis to a comparison of fall growth rates between 2001 and 2003 for this age class.

4.4. Results

4.4.1. Laboratory

Results from the laboratory data revealed that the effect of size on growth rate depended on the life history group and growth interval examined (Figure 4.3). In October, there was little size-dependent growth in the parr group and positive size dependent growth in the smolt group leading to a significant interaction between length and life history on growth rate ($F_{1,114} = 5.7$, $P=0.02$). This pattern was maintained over the November growth interval with a significant interaction between length and life history on growth rate ($F_{1,115} = 15.1$, $P<0.001$). By December however, we did not detect a significant interaction between size and life history ($F_{1,116} = 15.1$, $P=0.09$) as size-dependent growth appears to be weakly negative in the smolt group but remains weakly positive in immature parr (Figure 4.3c). By the January growth interval there is a significant interaction between size and life history on growth rate with negative size dependence in smolts and positive size dependence in parr ($F_{1,116} = 30.9$, $P<0.0001$).

4.4.2. Field

Results from the linear regressions on subsets of known smolts from different year classes of salmon in WB indicated the relationship between size and growth rate depended on the year class and season. For the 1996 year class there was no evidence of a strong compensatory response in the fall; however, by winter there was a significant negative relationship between size and growth rate which continued into the spring leading up to the smolt migration (Figure 4.4). For the 1997 year class evidence of compensatory growth was weak, and none of the relationships were statistically

significant. For the 1999 year class we found a negative relationship between size and growth rate in all three seasons analyzed; however, the relationship was not statistically significant until spring. For the 2001 year class there was no December sample so we could only look at the spring interval. The relationship was negative although not statistically significant (Figure 4.4)

We found results from the piecewise quantile regression analyses to be mostly consistent with our expectations under the life history dependent compensatory growth hypothesis in WB (Figure 4.5), SB (Figure 4.6) and CB (Figure 4.7) with the exception of the 1997 and 1998 growth season in WB and 2002 in SB. For these three datasets the quantile regression with the increasing constraint had the lowest AIC values although the delta AIC value for the regression with no constraint was 2 or less in all cases indicating little difference in support for the two hypotheses (Table 4.2). Piecewise linear regressions of the upper 95th quantile for 1997 and 1998 in WB suggested little change in G_L with size. The lower 5th quantile also seems to change little with size for 1997 but increase slightly for 1998 in WB (Figure 4.5). For SB in 2002 all quantiles increase with size and then reached a plateau (Figure 4.6).

For all other datasets analyzed the upper (95th) quantile generally increased with size and peaked somewhere in the middle of the size distribution after which there appeared to be a negative relationship between size and growth. This pattern suggests that the fastest growing fish are in the middle of the size distribution. Plots of the lower 5th quantile were either flat or generally increased with size with some variation. This relationship between size and growth rate resulted in a polygonal shape with the greatest variance in growth rate occurring in the middle of the size distribution. This pattern

seemed relatively consistent across years and systems with the few exceptions mentioned above.

Results from an ANCOVA showed no significant effect of length on G_L therefore we used a two factorial ANOVA to test for the effect of season and year and there interaction on age 1 growth. This analysis indicated a significant interaction between year and season (Figure 4.8). Overall, growth is higher in the summer consistent with seasonal growth from the other tributaries; however, we found that growth in the fall of 2001 was higher than in 2003 even though densities of parr were considerably higher in 2001. For age 2 we again found no effect of length so we used ANOVA to compare fall growth among the two years. Opposite to age 1 fish, we found significantly higher growth in 2003 than in 2001 (Figure 4.9)

4.5. Discussion

Our results from both the laboratory and field suggest that relatively small parr which adopt the smolt life history tactic may compensate for small size by increasing individual growth rates; however, the timing and intensity of the compensatory response may vary among years and among populations. Unlike the majority of compensatory growth studies which experimentally manipulate the growth environment to induce a compensatory response, we show that individual life history decisions can dictate whether or not an individual displays compensatory growth even when all individuals within a cohort are experiencing the same growth conditions. This distinction is important because if life history is ignored and data are pooled then the application of standard statistical techniques may lead to erroneous conclusions concerning the presence

and strength of size dependent growth. We addressed this problem by applying nonparametric quantile regression techniques to datasets where we could not confidently assign individuals to a life history group. Overall, the combination of detailed laboratory and field data as well as novel statistical techniques used in this study helped establish the prevalence of compensatory growth across spatial and temporal scales.

Our use of laboratory data allowed us to unambiguously assign a large number of fish to the correct life history group and observe their growth dynamics on a fine, monthly time/temporal scale. The form of size dependent growth seemed to depend both on life history group and season. Smolts initially seemed to display compensatory growth with the largest fish growing the fastest whereas the parr showed weak to no size dependent growth throughout the experiment. This pattern is consistent with many other studies that have shown that salmon establish strong dominance hierarchies in laboratory settings with larger fish gaining more access to food and growing faster (Thorpe 1977, Metcalfe et al. 1989, Metcalfe and Thorpe 1992). During subsequent growth intervals, smolts began to exhibit a compensatory response leading to an interaction between size and life history on growth rates. Our results complement previous compensatory growth studies on Atlantic salmon. Nieceza and Metcalfe (1997) showed that both parr and smolts will respond to changes in the growth environment by increasing their growth rates, but there is a life history effect where smolts display a stronger compensatory response. Unlike their study, we show that this response can occur in smolts without manipulating the growth environment, and therefore, it may be an evolved response to ensure adequate size before migrating to sea. In addition, Metcalfe et al. (1986) showed that smaller parr tend to exhibit a decrease in feeding motivation during the fall and

winter months which may explain the overall differences in growth rates between parr and smolts. These life history dependent growth strategies between the unwillingness of parr to grow and the strong compensatory response of smolts suggest tradeoffs in fitness depending on the life history tactic adopted.

Our analyses of field data paralleled our findings in the laboratory although compensatory growth responses were not as strong. Using a high quality dataset we were able to assign a reasonable number of individuals to the smolt life history group depending on the cohort analyzed. A general pattern of compensatory growth and greater ability to detect compensatory growth as the growth interval approached the smolt window was evident. We found a weak negative relationship between size and growth rate in the fall for two of the three intervals examined, but none of the regressions was statistically significant. However, all spring intervals were negative and half were statistically significant. Low sample sizes may have hampered our ability to detect statistically significant responses, but the general pattern appeared consistent with the laboratory data. Nicieza and Braña (1993) estimated size at migration from scales to present evidence of compensatory growth in Atlantic salmon smolts; however, it was not clear if this pattern was the result of faster growth rates or delayed time of migration. Utrilla and Lobón-Cerviá (1999) used a similar analysis and also concluded that that smaller smolts exhibited compensatory growth prior to migration; however, they used specific growth rate as a metric for growth rate which is itself negatively size dependent (Sigourney et al. 2008). Our study validates other studies and helps to establish a compensatory growth response in migrating smolts which may start as early as the fall before migration.

An inability to categorize immature fish into appropriate life history groups limited the number of datasets for which we could apply standard linear models to test for an interaction between life history and compensatory growth. To be able to analyze the majority of datasets for which we could not confidently assign a large sample size to the different life history groups we used a novel form of nonparametric regression. Our application of piecewise linear quantile regression to the analysis of scatter plots of fall size vs growth rate revealed that most years lead to a polygonal shape consistent with our hypothesis of life history-dependent compensatory growth. Quantile regression is well suited for the study of complex ecological relationships; however, its use is still relatively rare in the ecological literature (Sharf et al. 1998). Because many ecological relationships can result in scatterplots that have a polygonal shape (Sharf et al. 1998), nonparametric quantile regression may be particularly useful, yet we are not aware of any ecological studies that apply this technique. The laboratory data showed that there is overlap in size distributions and between parr and smolts with parr growing slower and displaying no compensatory response and smolts growing faster and potentially displaying compensatory growth depending on the season. This relationship leads bivariate plots of size vs growth rates that have a polygonal shape with both the fastest and slowest growth rates occurring in the middle of the size distribution. By using a nonparametric quantile technique we were able to expand the scope of our analysis across additional years and across populations to show that this life history dependent effect of growth can have a strong and consistent influence on the relationship between size and fall growth rates in immature juvenile salmon.

The negative relationship between density and growth rate has been well described by a negative power curve in stream salmonids including Atlantic salmon (Jenkins et al. 1999, Imre et al. 2005, Lobon-Cervia 2007). However, our analysis of seasonal growth rates in CB suggests that, depending on the age class, density-dependent responses may not be consistent across seasons. We found that variation in summer growth rates in CB was consistent with this negative relationship between density and growth but fall growth showed a weak positive relationship with density. One explanation for changes in fall growth could be that other abiotic factors are influencing fall growth rates. In an earlier study, Davidson et al. (2010) found that fall growth rates in WB correlated positively with fall discharge in age 1 salmon. In CB, however, average discharge was lower in 2001 when we observed higher growth rates and temperature profiles were roughly the same (Appendix C). Because fall growth rates seemed to be linked to life history, one possible explanation for this counterintuitive pattern is that it represents a frequency-dependent life history response. A number of studies on stream salmonids have demonstrated that at high densities per capita survival rates decrease (Elliot 1987, Marschall and Crowder 1995, Cattaneo et al. 2002). Therefore, the probability of surviving to a specific size and age before smolting is partly density-dependent. In addition, some studies suggest that size may actually be selected against in small stream environments likely due to the inability of larger fish to find adequate refuge such as deep pools (Carlson et al. 2008, Letcher and Horton 2008). Complicating matters, Atlantic salmon smolts are faced with opposing selection pressures because physiological constraints and size selective mortality at sea select for a relatively large size at smolting (Lundqvist et al. 1994). These opposing selection pressures may create dynamic fitness

surfaces that are conditionally dependent on the state of an individual (e.g. size), the environment (e.g. proportion of available refuges) and the life history tactic adopted (e.g. smolt or resident). This change in fitness with density may lead to a conditional strategy in which the switch point (i.e. the size at which is more beneficial to smolt) changes with density. In other words, in years of high density, the largest age 1 fish may actually gain higher fitness by accelerating growth and smolting at age 2 rather than trying to survive an extra year in the stream where competition for space may decrease survival. Thus, both size and density may play a role in an individual's decision to accelerate fall growth and smolt in the spring. Frequency-dependent responses are evident in other aspects of salmonid life histories particularly in regards to early maturation in males (Gross 1985, Hutchings and Myers 1994), but few studies have considered tradeoffs with early smolting. The potential for a shift in the costs and benefits of fast growth and early smolting may also explain some of the variation we observed in the field data in the apparent strength of compensatory growth. Regardless of the underlying mechanism, our results suggest that density-dependent growth may be seasonally dependent and could interact with life history in complex ways.

For age 2 salmon fall growth was more consistent with a negative relationship between density and growth rates. Unlike age 1 salmon, because age 2 salmon already have attained a critical size to smolt it may be that they do not increase their fitness by trying to undertake risky foraging in years of high density. A number of studies suggest that larger size can lead to greater mortality particularly in the fall (Letcher and Horton 2008, Carlson et al. 2008) and this mortality may be enhanced by risky foraging. Also, salmon generally need adequate refuge to forage effectively. Larger, older salmon

generally need deeper, pool like habitat (Hutchings 1986, O'Connell and Ash 1993, Sigourney et al. 2006) which was lacking in the study site. For age 2 fish in years with high density, competition for good foraging habitat may inhibit continued growth, and therefore, density continues to have a negative effect in the fall. It is important to also note that samples sizes were fairly low and the effect size was small so our results should be interpreted with caution.

Understanding the interactive effects of environment and growth on life history decisions play a critical role in conservation and management of anadromous salmonids particular as future environmental conditions become more variable and uncertain (Gross 1991). For example, anthropogenic forces can change size selective mortality through changes in fishing practices (Gross 1991). Also, changing predator fields and prey availability could alter the benefits gained from early migration (Mather 1998). In contrast, in stream survival and hence the relative fitness of delaying migration will depend on availability of appropriate refuges (Finstad and Einum 2009). Ecologists and evolutionary biologists are becoming increasingly aware of the need to apply evolutionary principles to management practices (Crozier et al. 2008, Hendry et al. 2010). Application of evolutionary principles combined with the development of proximate models (*see* Thorpe et al. 1998) may be necessary to aid conservation and predict future fitness.

In summary, we have demonstrated the role of life history in structuring the relationship between size and growth rates in Atlantic salmon. Our results provide a conceptual framework to understand the ecological context under which compensatory growth responses may be expected to evolve in nature. This information could be

integrated into more mechanistic models of population dynamics. In the case of Atlantic salmon, such models may help predict variation in smolt production and the size and age structure of migrating smolts, a key goal in management of this species (Power and Power 1994, Chaput et al. 1998). From the view point of basic science, Atlantic salmon may serve as an effective conceptual model to understand variation in the strength of compensatory growth across species with similar complex life histories that undergo environmental transitions or migrations.

Table 4.1. Number of known Atlantic salmon smolts (N) in each year class for regression analysis of length on growth rate for different growth intervals in West Brook, Massachusetts.

Year Class	Season	Median Date Start Sample	Median Date End Sample	N
1996	Fall	9/30/1997	12/15/1997	9
	Winter	12/15/1997	3/14/1998	9
	Spring	3/24/1998	4/23/1998	11
1997	Fall	9/18/1998	12/5/1998	28
	Winter	12/5/1998	3/17/1999	25
	Spring	3/17/1999	4/30/1999	30
1999	Fall	9/26/2000	12/7/2000	17
	Winter	12/7/2000	3/13/2001	16
	Spring	3/13/2001	5/9/2001	21
2001	Spring	4/9/2003	5/9/2003	16

Table 4.2. Sample sizes by age class for each dataset used for quantile regression on length vs fall growth rates for Westbrook (WB), Shorey Brook (SB) and Catamaran Brook. AIC and Δ AIC values are shown comparing three different constraints on the 95th quantile.

River	Year	N _{Age1}	N _{Age2}	Constraint	AIC	Δ AIC
WB	1997	93	3	Increasing	-383	0
				None	-382	1
				Decreasing	-372	11
WB	1998	77	0	Increasing	-225	0
				Decreasing	-225	0
				None	-224	1
WB	1999	148	2	None	-430	0
				Increasing	-422	8
				Decreasing	-408	22
WB	2000	104	5	None	-381	0
				Decreasing	-369	12
				Increasing	-353	28
WB	2001	65	5	None	-224	0
				Increasing	-214	10
				Decreasing	-210	14
WB	2003	56	17	None	-164	0
				Decreasing	-150	14
				Increasing	-149	15
SB	2000	49	23	None	-225	0
				Increasing	-214	11
				Decreasing	-169	56
SB	2001	42	14	None	-78	0
				Increasing	-71	7
				Decreasing	-50	28
SB	2002	67	3	Increasing	-127	0
				None	-125	2
				Decreasing	-107	20
SB	2003	107	23	None	-332	0
				Increasing	-318	14
				Decreasing	-291	41
CB	2001	61	19	None	-209	0
				Increasing	-188	21
				Decreasing	-179	30
CB	2003	16	13	None	-65	0
				Increasing	-57	8
				Decreasing	-57	8

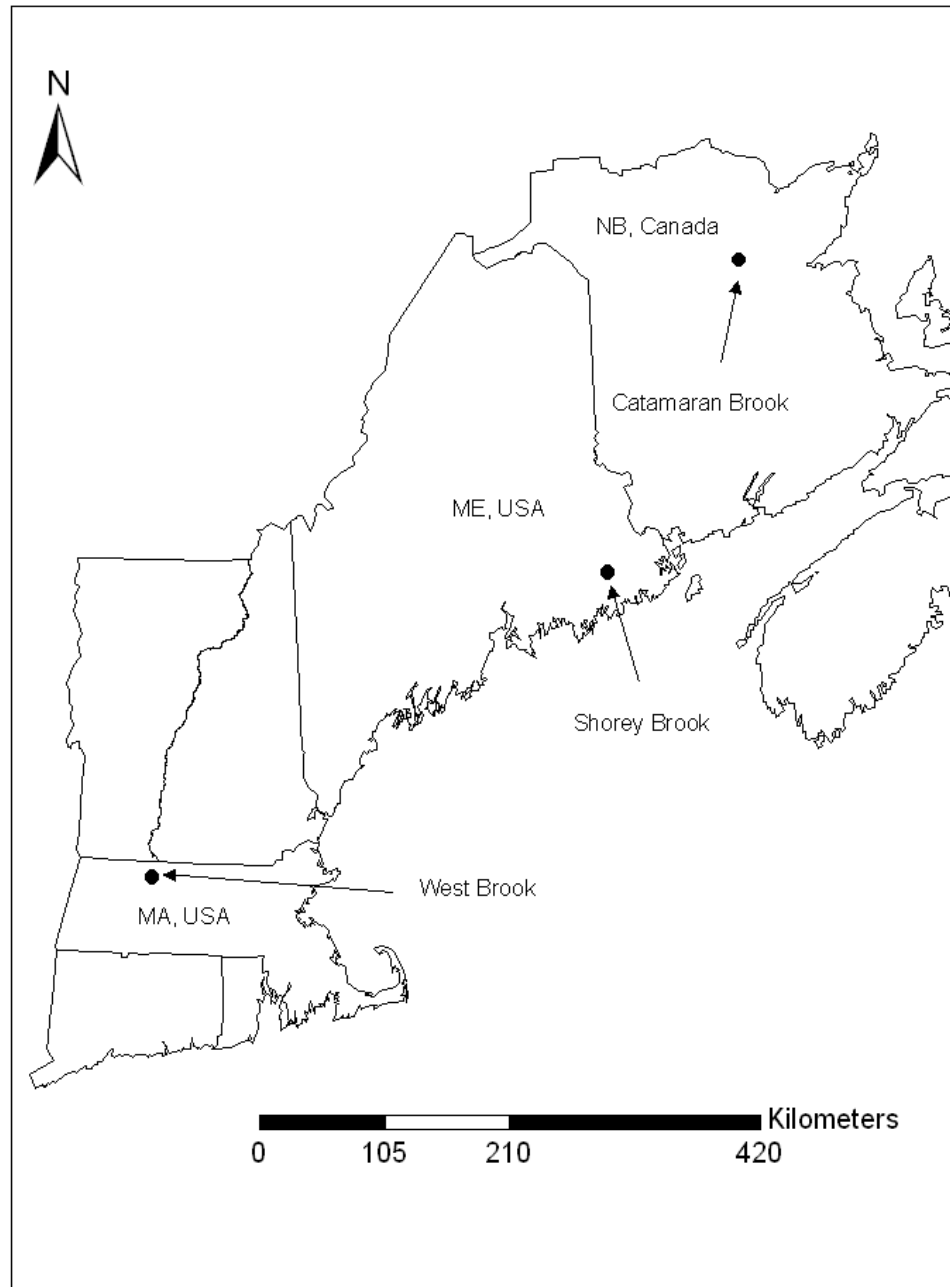


Figure 4.1: Map showing the geographical locations of the study streams in Massachusetts (MA), Maine (ME) and New Brunswick (NB).

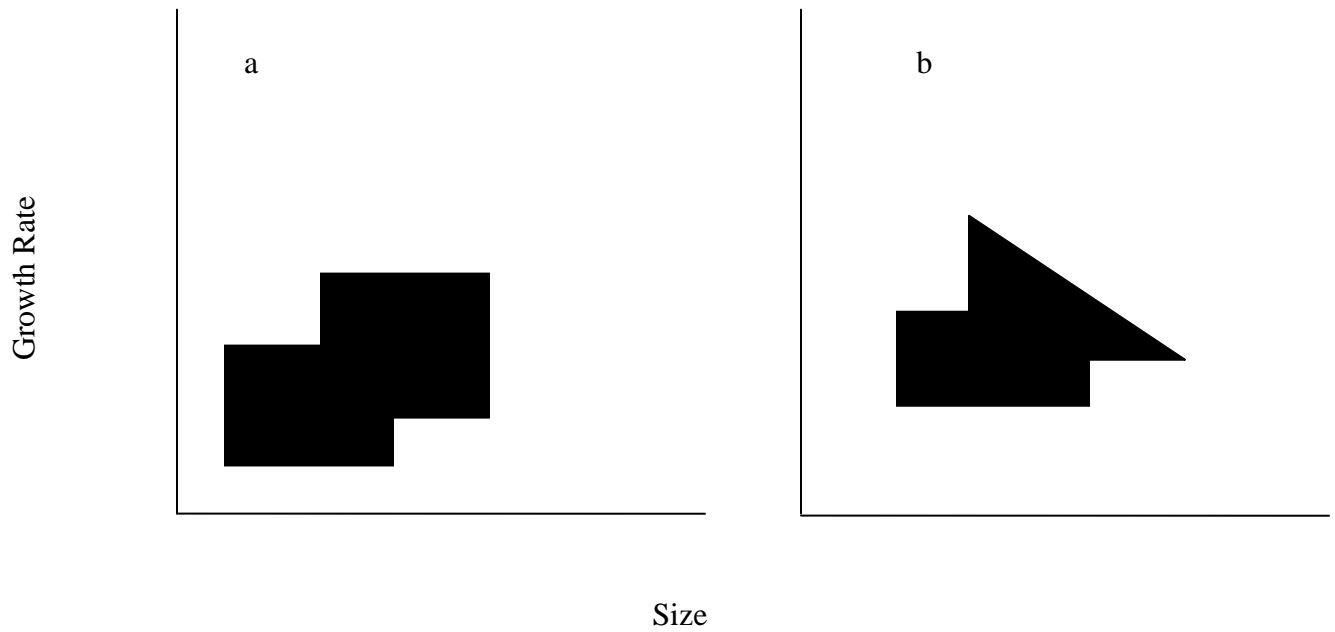


Figure 4.2: Hypothetical scatter plots expected under two different scenarios of size dependent growth where life histories are separated by size class including a) life history dependent growth and b) life history dependent compensatory growth.

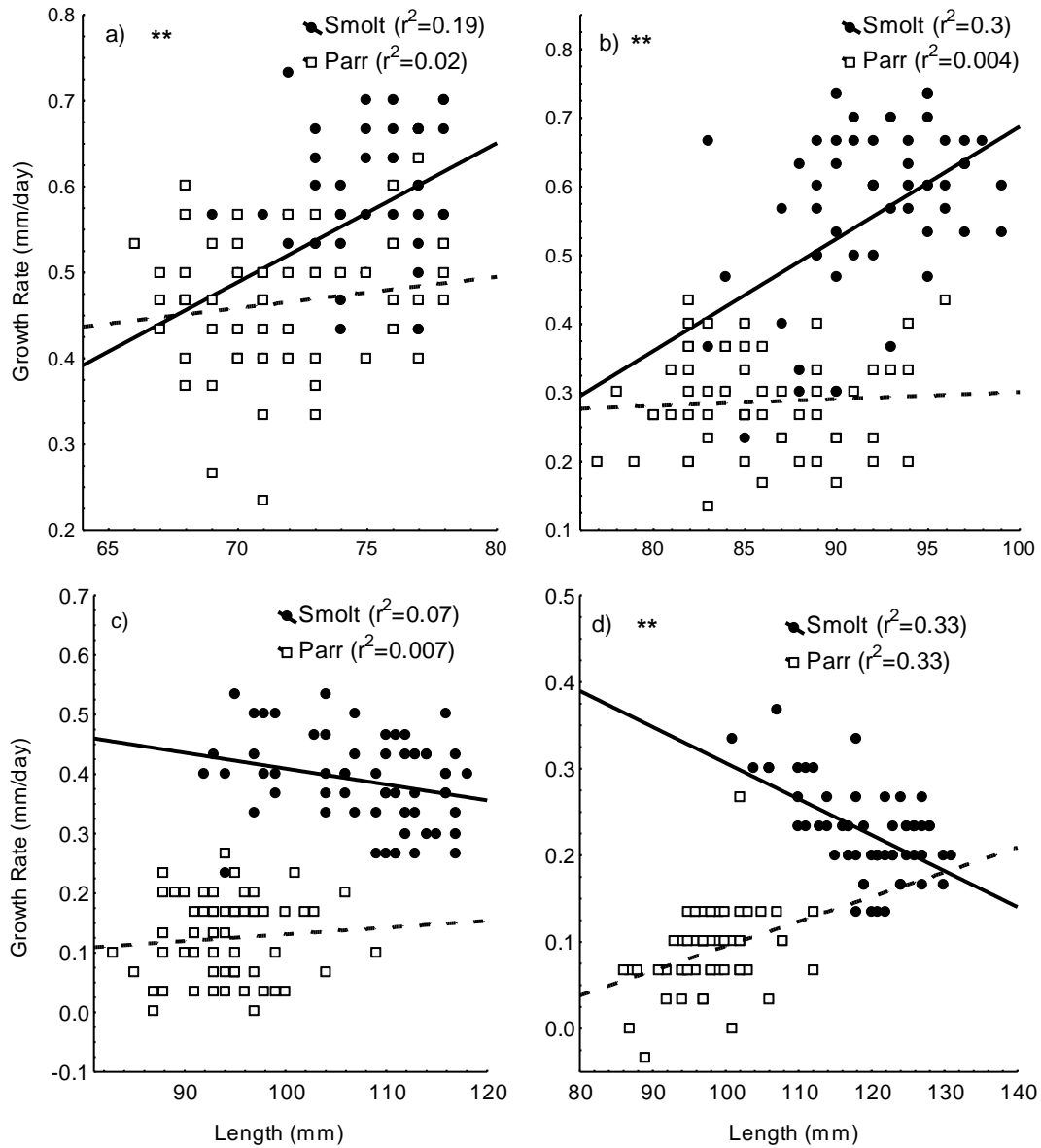


Figure 4.3: Plots of linear regressions describing the relationship between length and growth rate for both parr (□) and smolts (◆) grown under laboratory conditions during (a) October (b) November (c) December and (d) January growth intervals. Separate r^2 values for each life history group are shown in each figure.

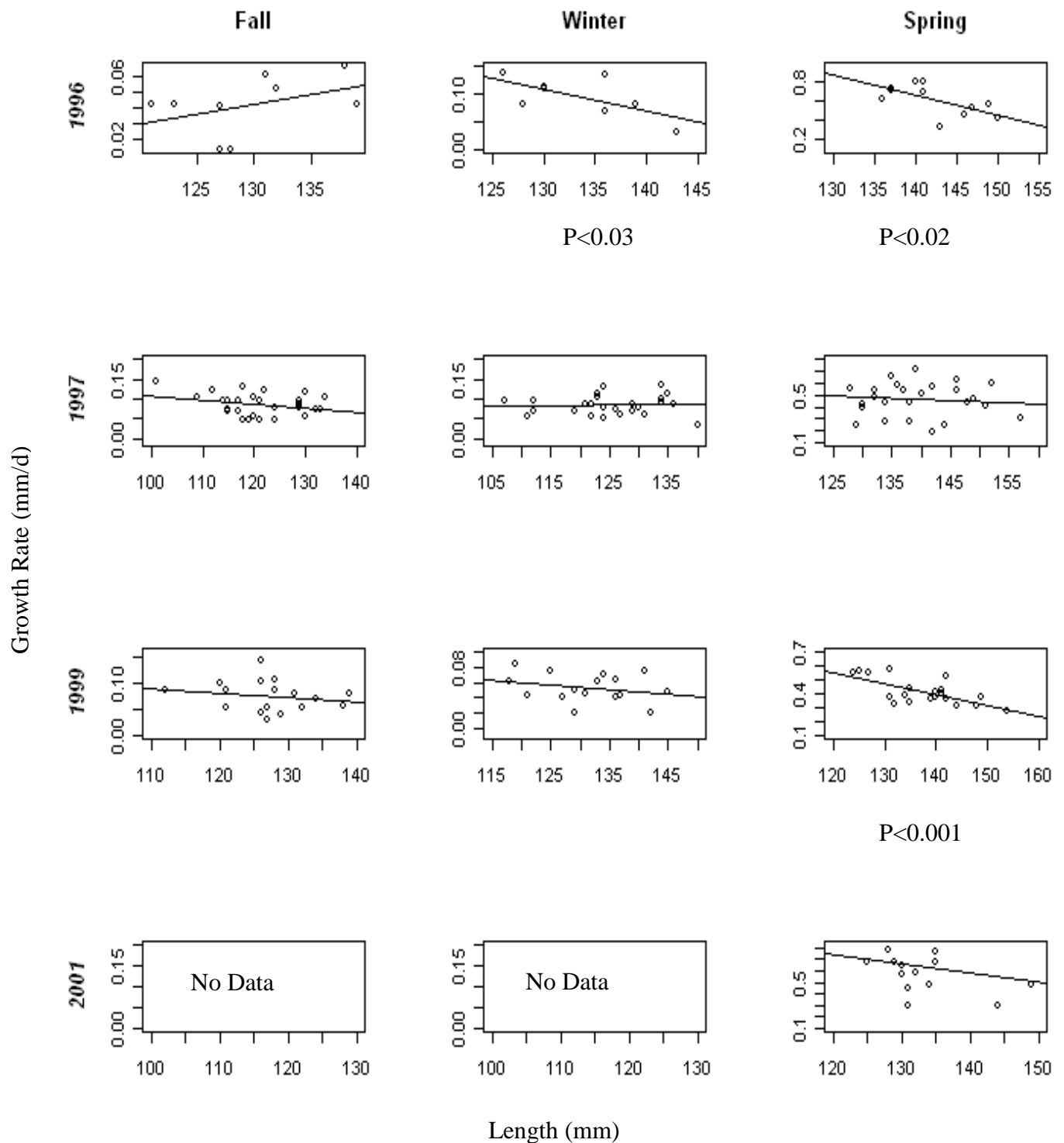


Figure 4.4: Linear regressions of length vs growth rate for subsets of known Atlantic salmon smolts for different year classes in WB. P-values for significant regressions are shown below scatter plots.

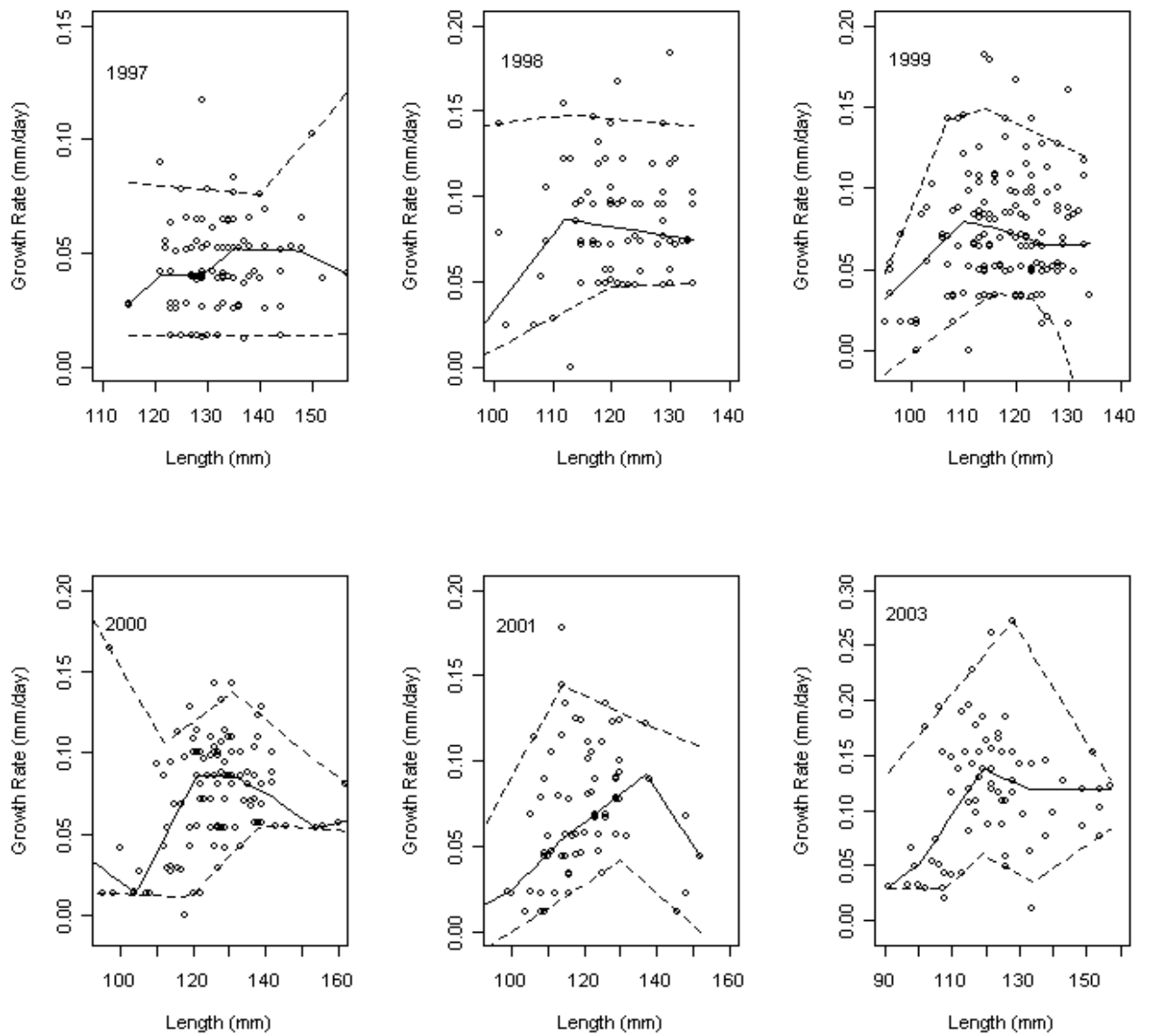


Figure 4.5: Piecewise quantile regressions on length vs growth rates for different fall growth intervals of Atlantic salmon parr in WB. The upper 95th (----), median 50th (—), and lower 5th (-.-) quantiles are shown.

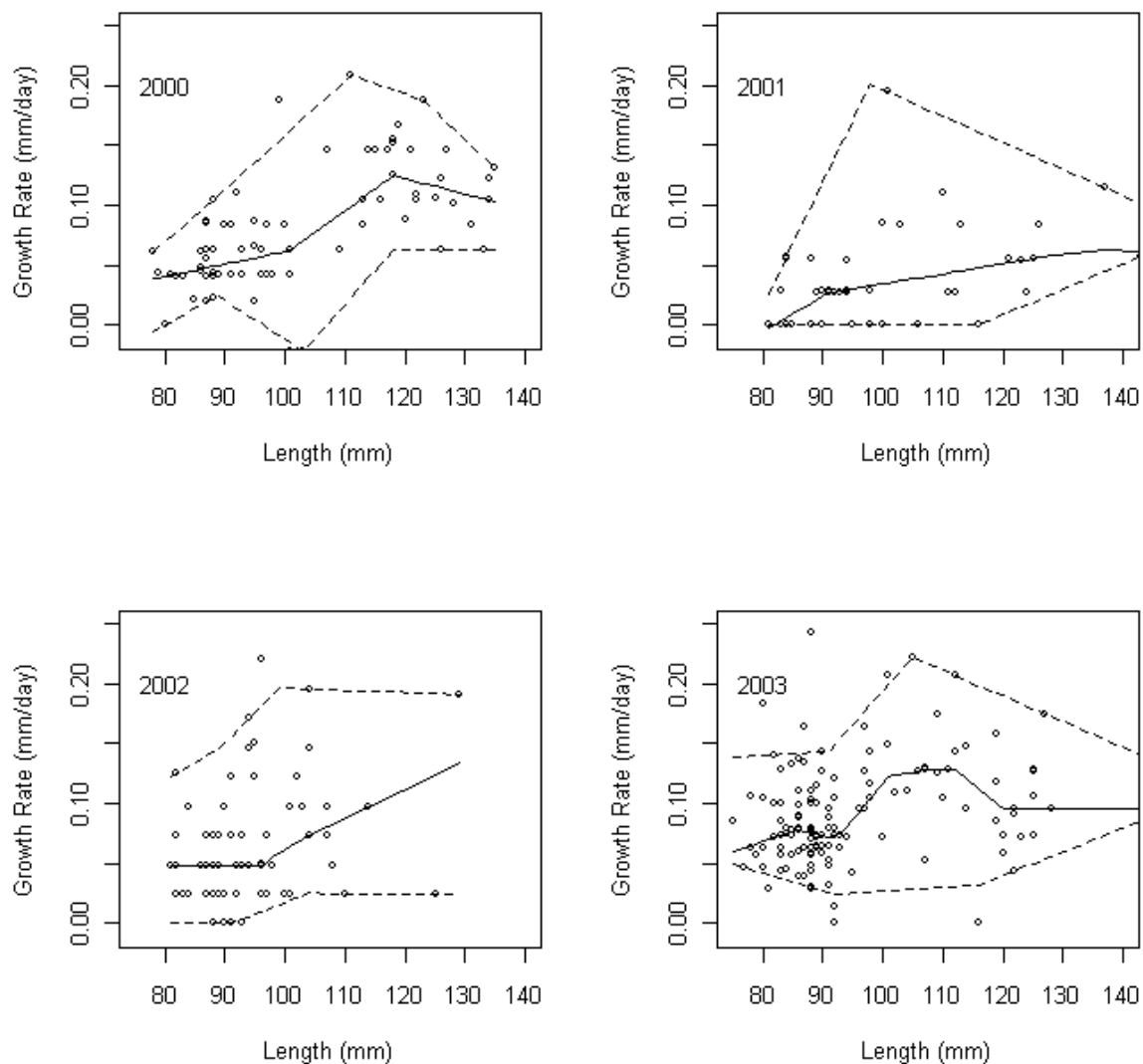


Figure 4.6: Piecewise quantile regressions on length vs growth rates for different fall growth intervals of Atlantic salmon parr in SB. The upper 95th (----), median 50th (—), and lower 5th (----) quantiles are shown.

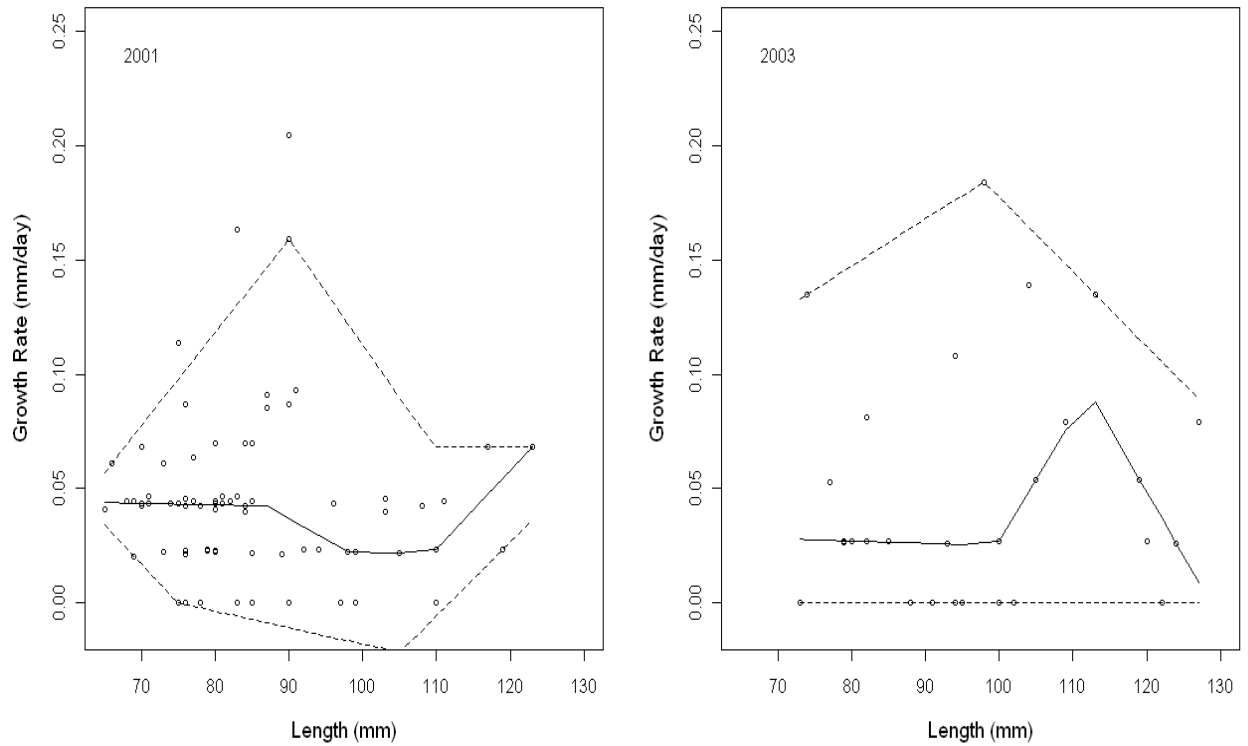


Figure 4.7: Piecewise quantile regressions on length vs growth rates for different fall growth intervals of Atlantic salmon parr in CB. The upper 95th (----), median 50th (—), and lower 5th (— · —) quantiles are shown.

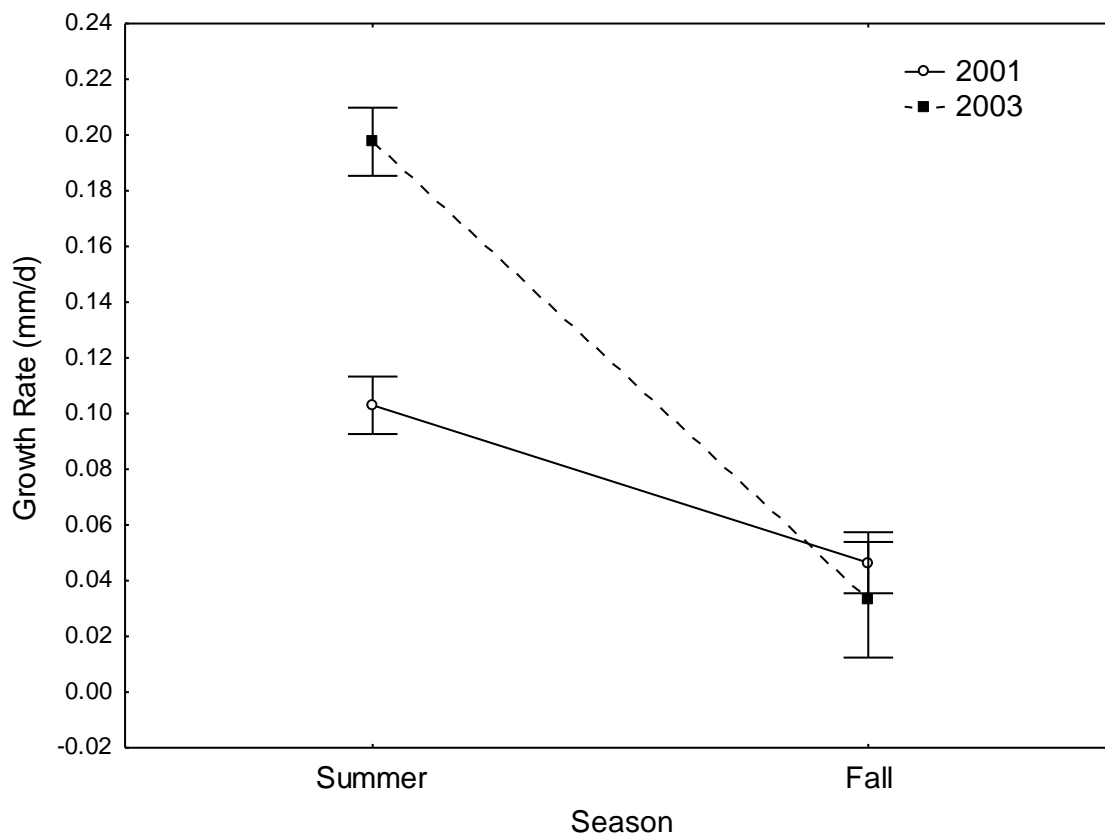


Figure 4.8: Comparison between summer and fall growth rates of age 1 immature Atlantic salmon sampled over a high density year (2001) and a low density year (2003) in CB. A 2-way ANOVA indicated a significant effect of season ($F_{1,192}=235.2$, $p<0.0001$), year ($F_{1,192}=31.8$, $p<0.0001$), and an interaction between season and year ($F_{1,192}=56.1$ $p<0.0001$).

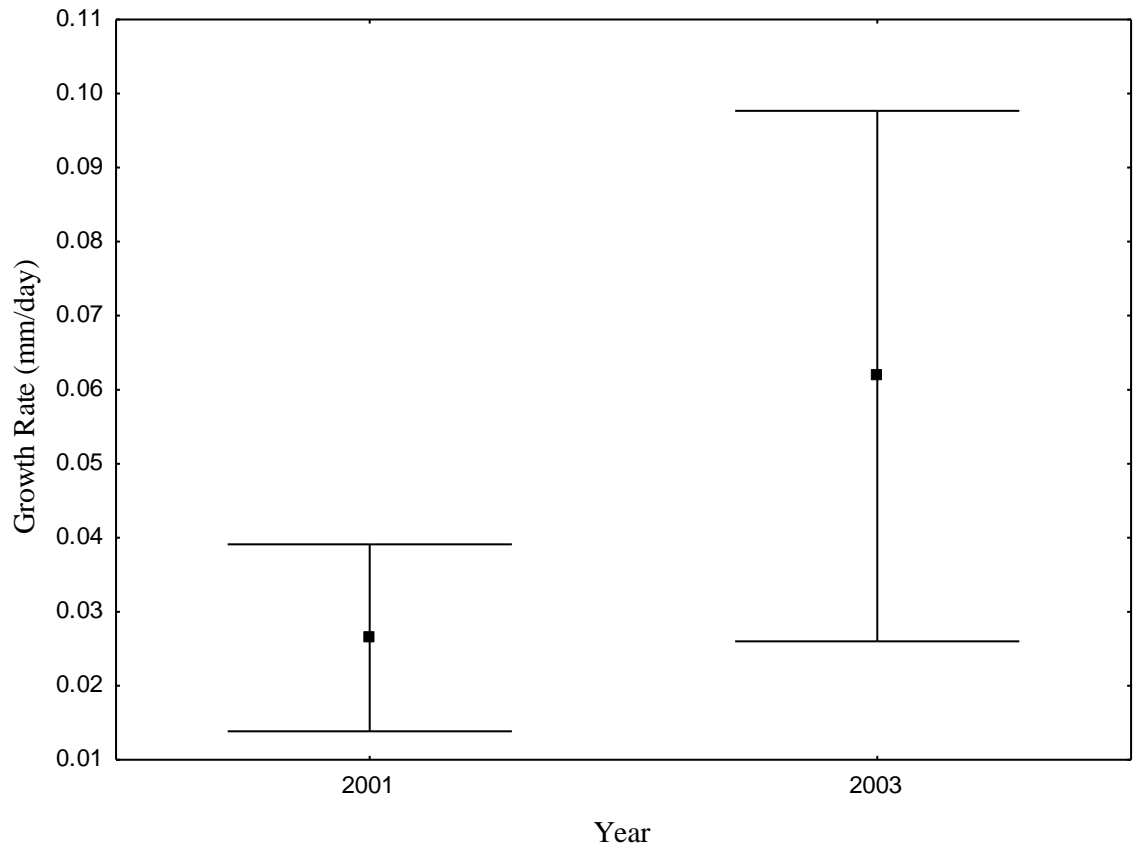


Figure 4.9: Comparison of fall growth rates of immature age 2 Atlantic salmon sampled in CB over two different years. One-way ANOVA indicated a significant difference ($F_{1,27}=4.8$, $p=0.04$).

APPENDIX A

MULTIVARIATE CONDITIONING OF THE SEASONAL GROWTH FUNCTION

As defined in the text the prior food function consists of a vector of coefficients that are distributed multivariate normal with a mean and a covariance $\vec{f} \sim \text{MVN}(Mu_f, C_f)$. We can constrain the function such that when it is multiplied by some linear operator L it will have a specified condition

$$f | Lf=k$$

where $k=t-1$ (i.e. the number of growth intervals). Next we define a matrix H that consist of L and an identity matrix I as follows

$$H = \begin{bmatrix} I \\ L \end{bmatrix}$$

Multiplying the matrix H by the original function f yields

$$Hf = \begin{bmatrix} f \\ Lf \end{bmatrix}$$

Which is distributed normally as

$$Hf \sim N \left(\begin{bmatrix} IM \\ LM \end{bmatrix} \begin{bmatrix} C & C & L^T \\ LC & LCL^T \end{bmatrix} \right)$$

Using the inverse of partitioned matrices we can derive a conditioned mean and covariance for f given the specification that the coefficients must sum to $t-1$. The conditional mean and covariance is now

$$\tilde{Mu}_f = Mu_f + C_f L^T (LC_f L^T)^{-1} (k - LMu_f)$$

$$\tilde{C}_f = C_f - C_f L^T (LC_f L^T)^{-1} LC_f$$

where $k=t-1$, and Mu_f and C_f are the prior mean and covariance for the n -variate normal distribution of f and L is a $1 \times k$ vector of ones. This conditioning yields a multivariate distribution for f given the condition that for any time t the expectation of $f(t)$ is constrained to be one. Because we are constraining the food function to sum to $t-1$, we need to transform the observed f_o by dividing by the mean (\bar{f}) such that

$$\sum f' = \frac{1}{\bar{f}} \sum f_o = t-1$$

APPENDIX B

GIBBS SAMPLING

To sample δ and b_i jointly we can derive a bivariate conditional distribution. We first re-write the process equation using vector notation as

$$\vec{L}_{t+1} = \vec{L}_t[\delta] + [1_n \otimes \vec{f}][\vec{b}] + \vec{\varepsilon}_L$$

where \vec{L}_{t+1} is a $(n \times t-1) \times 1$ column vector of all individual lengths from time $t=2$ to t , \vec{L}_t is a $(n \times t-1) \times 1$ column vector of all individuals from $t=1$ to $t-1$, \vec{k} is a $n \times 1$ column vector of individual consumption parameters, 1_n is an $n \times n$ identity matrix, \vec{f} is a $1 \times (t-1)$ vector of coefficients defining the food function, \otimes indicates the Kronecker product, and $\vec{\varepsilon}_L$ is a random error vector. We can derive a multivariate distribution for a and \vec{k} as

$$\delta, \vec{b} \mid \cdot \sim MVN(\mu_{\delta,b}, \Sigma_{\delta,b})$$

where

$$\Sigma_{\delta,b} = \left[\frac{F_{mat}' F_{mat}}{V_p} + C_{\delta,b}^{-1} \right]^{-1}$$

$$F_{mat} = [1_n \otimes f]$$

$$C_{\delta,b}^{-1} = \begin{bmatrix} V_{\delta} & 0 & 0 & \dots \\ 0 & V_b & 0 & \dots \\ 0 & 0 & V_b & \dots \\ \vdots & \vdots & \vdots & \ddots \end{bmatrix}$$

$$\mu_{\delta,b} = \sum_{\delta,b} \left[\frac{F_{mat} \vec{L}_{t+1}}{V_p} + C_{\delta,b}^{-1} \begin{bmatrix} \mu_{\delta} \\ \mu_b \mathbf{1}_n \end{bmatrix} \right]$$

To derive conditional distributions for the latent states and the food function, we again re-write the growth equation as:

$$\vec{L}_i S_1 = \delta \vec{L}_i S + b_i \vec{F} + \vec{\varepsilon}_i$$

where \vec{L}_i is a $tx1$ vector of lengths for individual i , S_1 and S represent identity matrices of the form

$$S_1 = \begin{bmatrix} 0 & 0 & \dots \\ 0 & 1 & \dots \\ \vdots & \vdots & \ddots \end{bmatrix} \text{ and } S = \begin{bmatrix} \ddots & \vdots & \vdots \\ \dots & 1 & 0 \\ \dots & 0 & 0 \end{bmatrix}$$

The conditional for the food function \vec{f} can be written as

$$\vec{f} | \cdot \sim MVN(\Phi_f, Z_f)$$

where

$$Z_f = \left[\Sigma_f^{-1} + I_f \frac{\sum_{i=1}^{i=n} \kappa_i^2}{V_p} \right]^{-1}$$

$$\Phi_f = Z_f \left[\Sigma_f^{-1} \mu_f + \frac{\sum_{i=1}^{i=n} b_i (S_1 - \delta S) \vec{L}_i}{V_p} \right]$$

where I_f is a $(t-1) \times (t-1)$ identity matrix.

We can also make use of the Gibbs algorithm to sample \vec{L}_i states where we can show that that \vec{L}_i is conditionally multivariate of the form

$$P(\vec{L}_i | \cdot) = P(\vec{L}_i^0 / \vec{L}_i) P(\vec{L}_i | \delta, b_i, \vec{f}) \sim MVN(\mu_{L,i}, \Sigma_{L,i})$$

where

$$\Sigma_{L,i} = \left[\frac{(S_1 - \delta S)'(S_1 - \delta S)}{V_P} + \frac{O_{L,i}}{V_e} \right]^{-1}$$

$$\mu_{L,i} = \Sigma_{L,i} \left[\frac{(S_1 - \delta S)^{-1} b_i F_{mat}}{V_P} + \frac{\tilde{L}_i^O}{V_e} \right]$$

where F_{mat} is the same as defined above and $O_{L,i}$ is an indicator matrix of 1s and 0s with 0s represent missing observations.

For all hyperparameters we use the same conditional distribution for location and scale parameters where N indicates a normal distribution and IG indicates an inverse gamma distribution

$$\theta_\mu \sim N\left(\bar{\theta}_i, \frac{\theta_v}{n}\right)$$

$$\theta_v \sim IG\left(\frac{n}{2} + \alpha_{\theta_v}, \frac{SS\theta_i}{2} + \beta_{\theta_v}\right)$$

where θ_μ and θ_v represent the location and scale hyperparameters respectively, $\bar{\theta}_i$ represents the mean of the individuals parameters, $SS\theta_i$ represents the sum of squares of individual parameters.

Similar to the scale of the parameters for the hypereparameters we can also sample the variances for the process error in the growth dynamics (V_P) from conditional inverse gamma distributions

$$V_P/\cdot \sim IG(A_p^{'}, B_p^{'})$$

where

$$A_p^{'} = \left(\frac{n^*(t-1)}{2} + a_p^{'} \right)$$

$$B_p^{'} = \left(\frac{\sum_{i=1}^n \sum_{t=1}^{t-1} (L_{i,t+1} - (aL_{it} + b_i f(t)))^2}{2} + b_p^{'} \right)$$

APPENDIX C

COMPARISON OF DISCHARGE AND TEMPERATURE IN CATAMARAN BROOK DURING THE FALL SEASON OF 2001 AND 2003

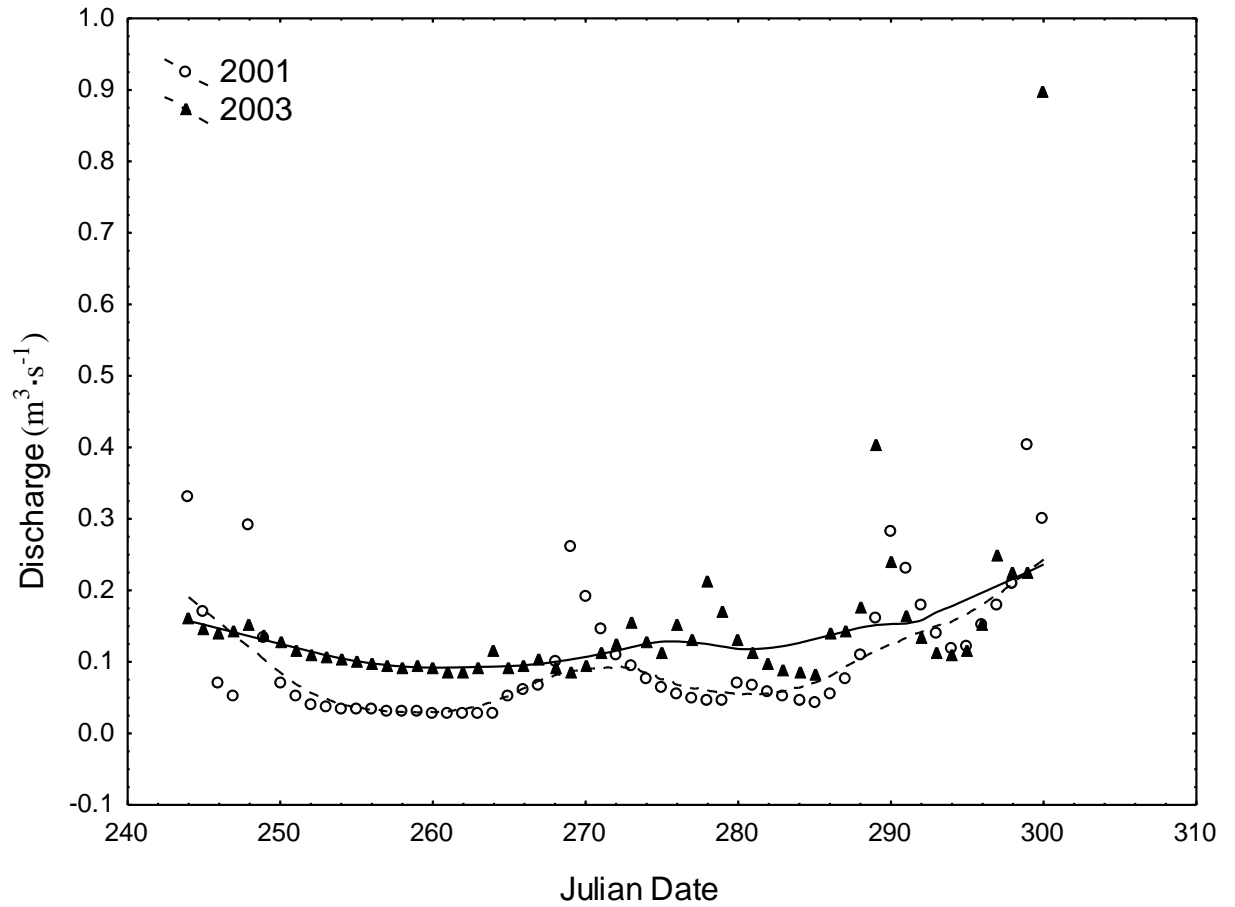


Figure C1. Comparison of average daily discharge measured at the mouth of Catamaran Brook in 2001 and 2003 during the fall growth intervals (September to October). Loess smoothing line are shown.

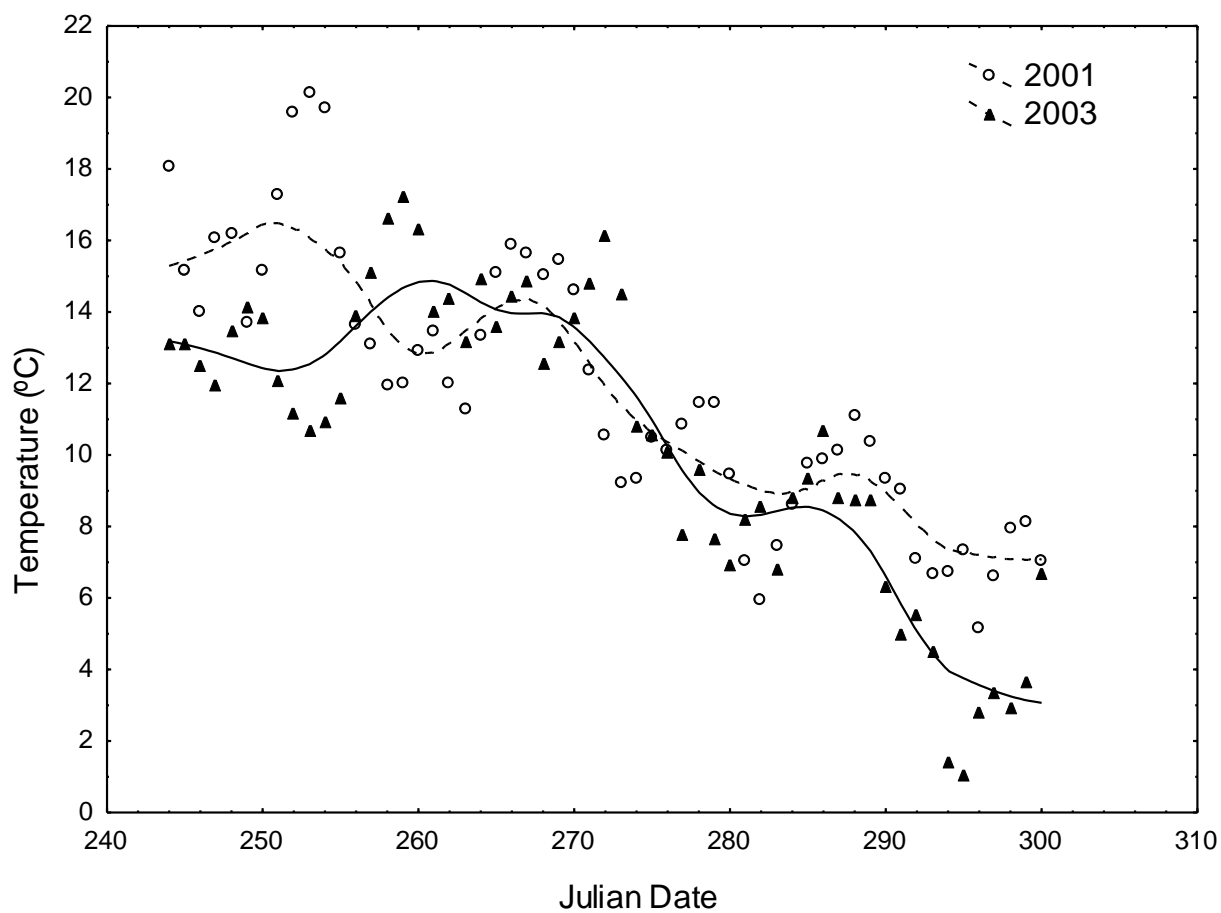


Figure C2. Comparison of average daily water temperatures in Catamaran Brook during the 2001 and 2003 fall growth interval. Loess lines are shown.

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