LATITUDINAL VARIATION IN GROWTH RATES OF AMERICAN LOBSTER (Homarus americanus) AT THE SCALE OF THE COMMERCIAL RANGE

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Latitudinal variation in growth rates of American lobster (*Homarus americanus*) at the scale of the commercial range

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Abstract

Accurate life history information is essential for stock assessment and management of the American lobster (*Homarus americanus*) fishery in the Northwest Atlantic. To evaluate conservation measures adopted by lobster harvesters, a growth model is required to provide estimates of egg production and reproductive value. This study examines inconsistencies among previous estimates of growth rates and combines historical data with current tag-recapture studies to develop a general model to estimate growth rates. Growth rates calculated using multiple techniques differed substantially in a single dataset; therefore, a single technique must be used consistently in all locations. A general von Bertalanffy growth model for the entire species' range was developed and growth rates showed a steady decrease with increasing latitude within the range of 41.543600° and 50.722915° N. The decrease in growth rate per degree of latitude was approximately 0.3% for both male and female lobsters when using a regression weighted by the inverse variance. Growth parameters for American lobster can now be estimated on a site-specific basis using latitude, reducing the need for resource-intensive tag-recapture field studies.

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Chapter 1: Introduction and Goals

1.1 Background

The American lobster, *Homarus americanus,* supports one of the most profitable inshore commercial fisheries in North America. The export value in Canada alone reached $805 million in 2009. There are over 6500 lobster fishing licenses held in Atlantic Canada and approximately 12000 in the north-eastern United States, making the fishery an important economic resource for coastal communities.

Exploitation rates, defined as the proportion of harvestable lobsters removed from the population annually by the fishery, meet or exceed 75% in almost all Canadian stocks, and are in excess of 95% in some cases (FRCC, 2005). There is concern about the future of the stocks if they continue to be harvested at such high levels. To conserve the resource, various management regimes are used in different geographic regions throughout Canada and the US. These include minimum and maximum size limits, no-take reserves, voluntary v-notching of ovigerous females, and limitations on fishing licences, seasons, and trap numbers. Accurate estimates of growth rates and other life history information can aid in evaluating the effectiveness of these management methods.

One way of measuring the success of these management methods is to compare reproductive value to the economic value of the lobster (Xu & Schneider, in prep.). Reproductive value is the reproductive contribution of an individual organism to its population (Fisher, 1930). It takes into account both present and future fecundity and mortality of that individual. Reproductive value generally increases to a maximum where the animal is at its reproductive peak, and then declines as the animal continues to age. Economic value is the dollar worth of the animal. In the case of the lobster, this is based purely on its body mass and so increases throughout its lifespan. The American lobster is a good candidate for the comparison between reproductive and economic value. It is long-lived and unlike animals with determinate growth, has a positive relationship between fecundity and size. Reproductive value of this species, as with economic value, will not necessarily decline with age. Accurate life history information (i.e. life tables) is required to estimate reproductive value, specifically age-specific growth information to produce mortality estimates as demonstrated by French McKay et al. (2003).

In addition to estimating reproductive value, growth information can be employed toward a variety of goals. Establishing a minimum legal size for harvesting based on egg-per-recruit models (FRCC, 1995) or maximum yield (Wilder, 1953) requires estimates of growth. Growth rates can be used to compare lobster stocks (Cooper & Uzmann, 1971) or evaluate enhancement measures (Chandrapavan et al., 2010). Growth parameters are also necessary in models that predict future yields (Fogarty, 1995). These could incorporate effects such as changes in fishing regulations or environmental conditions due to climate change.

1.2 Lobster Growth

Like all crustaceans, lobsters exhibit discontinuous growth. They increase in size only during discrete molting periods (ecdysis) throughout their life cycle. Juvenile lobsters will molt multiple times during the warmest months of the year. In mature lobsters, molting will occur once annually or every other year, during a synchronous molting period (Ennis et al., 1986). This can take place from mid to late summer or early fall, depending on the location. Mature females especially exhibit alternate-year molting, as they must delay ecdysis to brood their eggs. In large lobsters, as molting events become rarer, individuals may go three or more years without molting (Waddy et al., 1995).

One challenge to the study of age-specific growth in lobster is the absence of a reliable method to determine age in the wild (Wahle & Fogarty, 2006). All hard tissues are shed and replaced through regular ecdysis, leaving no record of age in the body like the otolith in fish. Following the life cycle of lobster larvae in a laboratory setting will give precise length-at-age information for an individual; however, there is no certainty that growth in laboratory conditions can be used to infer growth in the wild. Two possible methods of estimating size-at-age are length frequency analysis (Hudon & Fradette, 1988) and the measurement of lipofuscin or "age pigments" found in the brain tissue of crustaceans (Wahle et al., 1996). Length frequency analysis is complicated by variability in the number of molts during early life stages, which causes large variations in length at age for adults. Lipofuscin, a fluorescent pigment that accumulates with age in the brain tissue of crustaceans, can potentially be quantified to estimate the age of the specimen. This method cannot be applied to large sample sizes because lobsters have to be sacrificed for the pigments to be quantified. In addition, it depends on environmental conditions and must therefore be calibrated separately for each location.

Lobster growth depends on environmental factors, with temperature having the strongest impact (Aiken & Waddy, 1986). Lobsters are more likely to molt annually in warmer waters, and they will molt earlier in the season when temperatures are mild. Water temperatures below 5°C inhibit molting altogether. Other influences on growth include photoperiod, food availability, and salinity (Templeman, 1936). The American lobster is exposed to a wide variety of these conditions throughout its range, which extends from North Carolina, USA to the south coast of Labrador, Canada (Pezzack, 1992), including depths from shallow intertidal zones to offshore areas several hundred metres deep (Cooper & Uzmann, 1971).

1.3 Previous Work

Lobster growth is measured by tag-recapture studies. These studies became possible in the 1960s when tags were introduced that could be embedded into the muscle of the animal and would not be shed during the molt. Numerous tagging studies on growth have been conducted throughout the range of the American lobster, from Maine (Krouse, 1977), to the Maritimes (Campbell, 1983; Comeau & Savoie, 2001) and Newfoundland (Ennis, 1972); however, growth has only been estimated within parts of the range. Growth data have never been combined and analyzed to cover the full geographic extent of the species. This results in the problem of choosing the most appropriate parameter estimates for locations where estimates are not available. Quantifying the variation in growth throughout the species' geographic range would resolve this by providing an equation that could produce an estimate at any location within the range of the species. It will also eliminate the need for new tagging studies on growth, which are labour intensive and costly due to low return rates in a species with a high exploitation rate.

In a US report, Russell (1980) summarized the growth studies conducted along the east coast of the United States. He described a north-south trend in growth rates (Fig.1) and maximum size (Fig.2). These indicated that a general growth model based on latitude could potentially be applied to all lobster stocks.

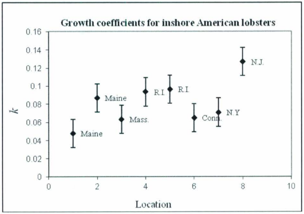

Figure 1. Growth parameter, *k* (yr^{-1}), reproduced from Russell (1980), with 95% confidence limits calculated from Location 1 (Maine) and applied to all points.

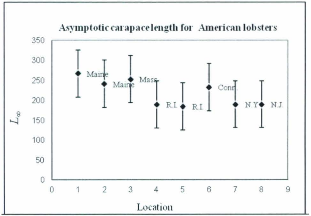

Figure 2. Maximum size, L_∞ (mm), reproduced from Russell (1980), with 95% confidence limits calculated from Location 1 (Maine) and applied to all points.

1.4 Goals

The goal of this study is to construct a general growth model for American lobster that will provide important life history information for fisheries management, including a means to estimate mortality rates necessary for determining reproductive value, at any location in the commercial range of the species. Preliminary findings led to an additional goal which will be discussed in section 1.5.

This research addresses the following objectives:

1. Use tag-recapture data to construct a growth model for American lobster applicable to any location.
2. Develop predictive equations for the growth parameters based on latitude and/or environmental factors to make the model geographically flexible.

1.5 Von Bertalanffy Growth Model and an Additional Goal

The von Bertalanffy growth function is the most commonly used model to describe growth in lobsters. *H. americanus* growth has been described by this model throughout its range along the east coast of the United States (Russell, 1980), as well as in the Bay of Fundy (Campbell, 1983), the Gulf of St. Lawrence (Dubé, 1986) and Newfoundland (Ennis, 1980; Ennis et al., 1982).

The von Bertalanffy growth curve in its general form is

$$L_t = L_\infty\left[1 - e^{-k(t-t_0)}\right] \tag{1.1a}$$

where L_t is the length of the animal at time t, L_∞ is the asymptotic maximum length, k is the proportional growth rate, and t_0 represents time (age) at size 0. This results in a curve describing size in relation to age, with t_0 shifting the curve to the left of the origin so that an organism at age 0 has a positive initial size (Fig. 3).

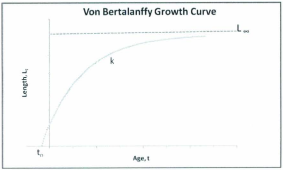

Figure. 3. Illustration of the von Bertalanffy growth function. Where L_∞ is the asymptotic maximum length, k is the proportional growth rate, and t_0 represents time (age) at size 0.

This model can be fitted to mark-recapture data (Fabens, 1965) by expressing the equation as:

$$\Delta L = (L_\infty - L_1)(1 - e^{-k\Delta t}) \tag{1.1b}$$

where ΔL is the change in length between captures (L_2-L_1), L_1 is the initial length at first capture, and Δt is the time between captures.

The von Bertalanffy model was chosen for this analysis over other possible models (e.g. Logistic, Gompertz, Richards) because of its physiological basis, developed from the difference between anabolic and catabolic reactions for a particular taxon. The parameters can therefore be interpreted biologically. L_∞ is the maximum size the organism can obtain, and k is the proportion of increase towards that maximum size for each time interval. It also has a form (Eq. 1.1b) that can be used for tag-recapture data without knowledge of age, since two of the three parameters, L_∞ and k, are independent of the age of the animal. There is a bias associated with this method described by Sainsbury (1980) and Maller & DeBoer (1988) in which applying a model intended for individual growth to describe average growth in a population tends to overestimate size-at-age values (discussed further in Chapter 3). Despite this, the von Bertalanffy function still produces curves that closely resemble: 1) curves based on indeterminate growth with an increase of energy allocated towards reproduction with age (Kozlowski, 1996), and 2) stepwise growth increments based on crustacean molt intervals (Caddy, 2003). Its parameters can also be used to produce mortality estimates required for determining reproductive value, and its prevalence in the primary literature makes it useful for management and

Chapter 2: Comparison of von Bertalanffy Growth Parameters for American Lobster throughout the Species Range.

2.1 Introduction

Tag-recapture studies on American lobsters have been conducted throughout the species range, from Virginia to Newfoundland (Campbell, 1983; Ennis, 1980; Ennis et al., 1982; Russell, 1980). The majority of these studies report von Bertalanffy growth parameters. These have been calculated using several methods. To determine whether these published parameters could be used to develop a general growth model, it was necessary to establish whether the method of estimation had a substantial effect on the resulting values. If estimates reported in different studies are not comparable, the parameters must be recalculated from original data using a consistent methodology.

Previous estimates of von Bertalanffy growth parameters are summarized in Table 1. When attempting to interpret them biologically, several problems are evident. Many of the maximum sizes are too small compared to actual sizes of large lobsters observed in the field. For example, lobsters with a carapace length greater than 127 mm are regularly found off the coast of Grand Manan Island in the Bay of Fundy (Campbell, 1992). Here, L_∞ values as low as 99mm are reported (Ennis, 1992). The growth rates, k, range from 0.04785 to 0.389. It is unlikely that lobsters at different sites would have growth rates that differ by an order of magnitude, even if they are found in different geographic regions. For t_o to be biologically meaningful, it must be a negative number. Several of these conservation, since it allows for comparison of life history and population information in different regions.

The data analysis for this project uncovered several problems. The first attempt to use published von Bertalanffy growth parameters to compare sites failed, because different studies used different methods of estimation. Since this affects the parameter estimates, results are not comparable between sites. Consequently, new parameter estimates were calculated from original data using a nonlinear least squares approach (Fabens' method). This resulted in unrealistic values for L_∞ and t_o, as had been reported in previous studies. It also produced extreme variation in both the estimates of the growth rate, k, and the error associated with them, as well as occasional negative growth rates. These difficulties in utilizing conventional methods to describe lobster growth led to the development of an additional objective for this project: to search for a more reliable method of obtaining von Bertalanffy growth parameter estimates from lobster tag-recapture data.

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studies report a positive t_o value. This implies that a newly hatched lobster has a negative size.

Table 1: Published von Bertalanffy growth parameters for American lobster, where L_∞ is the asymptotic maximum length, k is a proportional growth rate, and t_0 is time (age) at size 0.

Location	**Sex**	L_∞ **(mm)**	k **(yr^{-1})**	t_0 **(yr)**	**Reference**
Newfoundland	M	105	0.39	-0.8	Ennis (1980)
	F	112	0.24	-0.69	
Comfort Cove, NL	M	102.1	0.3701	3.6113	Ennis et al. (1982)
	F	99	0.3417	4.2504	
Magdalen Islands	M	129.84	0.192	1.46	Dubé (1986)
	F	105.86	0.228	2.89	
Bay of Fundy	M	281	0.065	0.76	Campbell (1983a)
	F	207	0.089	0.42	
Port Maitland, NS	M	165	0.11	-0.122	Campbell (1983b)
	F	103	0.389	2.064	
	M	119	0.242	1.247	
	F	109	0.288	1.303	
	M	118	0.229	0.963	
	F	109	0.288	1.303	
	M	135	0.193	1.224	
	F	108	0.372	2.262	
Maine	combined	266.77	0.04785	-0.7725	Thomas (1973)
Maine	combined	241	0.087	-0.096	Krouse (1977)
Massachusetts	combined	253	0.0634	-0.5485	Fair (1976)
Southern New England (offshore)	M	253	0.115	-0.14	Uzmann et al. (1977)
	F	230	0.08	-0.36	
Rhode Island	M	189.55	0.09361	-0.29012	Russell et al. (1978)
	F	184.59	0.09664	-0.19756	
Rhode Island (offshore)	M	281	0.081	0.179	Russell and Borden (1975)
	F	240	0.071	-0.134	
Connecticut	combined	233	0.065	-0.98	Smith (1977)
New Jersey	combined	190	0.127	0.653	Halgren (1976)
Virginia (offshore)	combined	287	0.087	-0.3	Harris & Van Engel (1978)

The most commonly reported methods of estimating von Bertalanffy parameters are those of Ford-Walford (Walford, 1946), Gulland-Holt (Gulland, 1969), and Fabens (1965). The first two involve graphical estimation of parameter values. They are considered obsolete, but are included here because they are the most recent, and sometimes the only published growth parameters for lobster from these regions.

Each of these methods will be applied to three different sets of lobster tag-recapture data. If these methods give substantially different parameter values for the same datasets, then the values previously reported are not comparable, and cannot be used to develop a general growth model. The parameters will have to be re-estimated from raw data for all locations using the same methodology.

2.2 Methods

2.2.1 Field Tagging

Data were provided by Jennifer Janes, Oceans Division, Fisheries and Oceans Canada (DFO), and Roanne Collins, Science Division, DFO. They were obtained from DFO tag-recapture studies carried out in the Duck Islands, Round Island, and Leading Tickles, Newfoundland. Tagging was conducted from July to October in 1997 and 2004 - 2008 in Duck Islands (n = 285) and Round Islands (n = 275), and June to October from 2004 - 2006 in Leading Tickles (n = 121). Lobsters were captured using commercial traps and released soon after tagging with a polyethylene streamer tag. These tags are inserted through the dorsal musculature between the carapace and abdomen and are usually retained through the molt. The tag number of each lobster was recorded, along with the carapace length, sex, location, date, and condition of females (ovigerous or v-notched). Measurements of carapace length were taken with Vernier callipers and recorded to the nearest millimetre. Carapace length is the standard metric of body size in lobster, and is measured from the eye socket to the posterior edge of the carapace, parallel to the dorsal midline. Lobsters were recaptured between 1 and 2565 days after tagging and the same set of information was recorded.

2.2.2 Data Analysis

To focus the model on average growth per molt, all lobsters that demonstrated zero growth were removed from the dataset. This ensures that only lobsters that had molted at least once between captures were considered for the analysis, assuming that all lobsters increase in size during molting. In addition, growth increments of $\leq$3mm were removed to account for measurement error. Male and female lobsters from the same tagging location were pooled for analysis. Von Bertalanffy growth parameters were calculated for each location using the three common methods of estimation as follows:

i) Ford-Walford

This is used for describing growth of mature animals, after the inflection point of most growth curves. Average L_1 is plotted against L_2 at equal time intervals. The growth rate, k, can then be calculated from the slope:

$$slope = e^{-k} \tag{2.1}$$

This produces a constant k that is < 1 since the annual increase in length will become progressively smaller as the animal ages. Maximum size, L_∞, is where the regression line intersects a 45 degree line from the origin, or where length at age n equals the length at n+1.

ii) Gulland-Holt

In this method, the annual change in length ($\Delta L/\Delta t$) is plotted against initial length. Growth is again calculated from the slope:

$$slope = 1 - e^{-k} \tag{2.2}$$

The line produced by this regression intersects the x-axis at L_∞, where the annual increase in length is equal to zero.

iii) Fabens

Here the modified version of the von Bertalanffy function for tag-recapture data is used:

$$\Delta L = (L_\infty - L_1)(1 - e^{-k\Delta t}) \tag{2.3a}$$

The parameters k and L_∞ are estimated by nonlinear least squares. Non-linear regression analysis was conducted using S-PLUS software. This iterative process requires initial values to be assigned to the parameters. For this, I used the average of published parameter estimates ($k = 0.18\text{yr}^{-1}$, $L_\infty = 177\text{mm}$).

For the graphical methods (Ford-Walford & Gulland-Holt), there were no means of estimating error associated with the parameters. The nonlinear least squares used for Fabens' method produced standard errors for both k and L_∞. In all cases the t_o parameter is calculated by rearranging the original von Bertalanffy equation:

$$L_t = L_\infty\left[1 - e^{-k(t-t_0)}\right] \tag{2.3b}$$

Arbitrary values of length at age of 81mm and 6 years were used to solve for t_o (Campbell, 1983).

2.3 Results

The results from each method are summarized in Tables 2, 3, & 4.

Table 2: Estimates of growth rate, *k*, for three sites in Newfoundland using Ford-Walford, Gulland-Holt, and Fabens methods.

	Duck Islands		**Round Island**		**Leading Tickles**	
Method	*k*	SE	*k*	SE	*k*	SE
Ford-Walford	-0.0377		0.0154		0.024	
Gulland-Holt	-0.0906		-0.0484		-0.0528	
Fabens	0.0448	0.0412	0.0432	0.013	0.113	0.0436

Table 3: Estimates of maximum size, L_∞, for three sites in Newfoundland using Ford-Walford, Gulland-Holt, and Fabens methods.

	Duck Islands		**Round Island**		**Leading Tickles**	
Method	L_∞	SE	L_∞	SE	L_∞	SE
Ford-Walford	-233		853		558	
Gulland-Holt	210		352		296	
Fabens	234	42	229	39.3	161	25.42

Table 4: Estimates of shift parameter, $t_{o,}$ for three sites in Newfoundland using Ford-Walford, Gulland-Holt, and Fabens methods.

	Duck Islands	**Round Island**	**Leading Tickles**
Method	t_o	t_o	t_o
Ford-Walford	13.6	-12.5	-5.90
Gulland-Holt	9.15	11.9	11.4
Fabens	-0.376	-0.612	3.47

The estimated growth rates were all positive for Fabens' method, but not so for the two other methods. The estimates of growth parameter *k* ranged from 0.0488 yr^{-1} to -0.0377 yr^{-1} in Duck Islands, 0.0432 yr^{-1} to -0.0484 yr^{-1} in Round Island, and 0.113 yr^{-1} to -0.0528 yr^{-1} in Leading Tickles. Maximum size ranges from -233 mm to 234 mm, 229 mm to 853 mm, and 161 mm to 558 mm in Duck Islands, Round Island, and Leading Tickles, respectively. Both positive and negative values were obtained for the t_o parameter, which ranged from -0.376 to 13.6 in Duck Islands, -12.5 to 11.9 in Round Island, and -5.90 to 11.4 in Leading Tickles.

2.4 Discussion

Parameter values not only varied within sites, but were physiologically unrealistic in some cases. For instance, attempts at applying the Ford-Walford method gave negative values for L_∞ and k. Since the slope of the regression was > 1, the 45° line intersects it at a negative x value. The fact that the slope was > 1 also resulted in a negative estimate of the growth rate, k. The Ford-Walford plot would only give positive results for k and L_∞ when the slope of L_2 vs. L_1 is < 1. However, the estimate of the slope from this study was within the normal range found in the literature. Published values of premolt-postmolt regressions, known as the Hiatt equation, (Hiatt, 1948) rarely stray far from a slope = 1 (Fogarty, 1995). This indicates the American lobster is not a suitable organism for this method of estimating growth parameters.

Both Ford-Walford and Gulland-Holt gave negative values for k (-0.0377, -0.0463, -0.0528 and -0.0906) and also L_∞ (-233mm) in the case of Ford-Walford. It is impossible for these parameters to be negative as lobsters clearly exhibit a positive growth rate and a maximum size above zero. Similar outcomes have been reported using the Ford-Walford method (Krouse, 1977).

The t_0 parameter was consistently positive for the Gulland-Holt method. Ford-Walford and Fabens methods also produced positive values in some cases. As previously stated, t_0 must be negative so that a lobster at age zero will have a positive size. However, since it is calculated directly from estimates of k and L_∞, finding a method that provides reasonable estimates of the latter two parameters should provide realistic t_0 values as well. In this case the positive t_0 values indicate that these methods are not producing reliable estimates of the growth parameters.

Fabens' non-linear least squares provided reasonable parameter estimates for k and L_∞ at all locations, but were still inconsistent with the other two methods. The variation in parameters estimated from the same data set indicate that these are not comparable between studies if different methods were used to calculate them. Therefore the growth model, which is the primary objective of this study, must be based on new, consistent parameter estimates from original tagging data.

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Chapter 3: A Latitudinal Growth Model for American Lobster

3.1 Introduction

There are numerous growth models available in fisheries research to describe size-at-age. The simplest is a two-parameter power function describing allometric growth. This is best suited for species that do not approach an asymptotic size as they age, such as Pacific halibut (Quinn & Deriso, 1999). The three-parameter Gompertz model (Ratkowsky, 1990) has been used to describe the growth of numerous taxa from mussels (Akiyama & Iwakuma, 2009) to cetaceans (Stolen et al, 2002), but in general it has been suggested that the Gompertz model is better suited to describe juvenile growth in fishes (Gamito, 1998). The von Bertalanffy growth function is a mechanistic equation and is the most widely used growth model in fisheries research (Quinn & Deriso, 1999). The Richards model (Ratkowsky , 1990) is a four-parameter curve that has been successfully used to describe the growth of abalone (Rogers-Bennett et al., 2007) and tuna (Griffiths, et al. 2010). However, Ratkowsky (1990) advised against its use because it fails to exhibit close-to-linear behaviour and does not reduce skewness of parameter estimates when examined in a comparison study (Hernandez-Llamas & Ratkowsky, 2004).

Growth model parameters have been shown to vary geographically in various taxa. This can be due to average annual temperature or latitude (Jensen, et al., 2000), habitat area (Durham et al., 2005) or the duration of the growing season (Durham et al., 2005; Houston & Belk, 2006). In lobster, growth is dependent on several environmental factors

(Templeman, 1936), but is primarily influenced by temperature (Aiken & Waddy, 1986). Lobsters are more likely to molt in a given year if the water temperature is warmer (Ennis, 1983). Also, since they cannot molt in water temperatures below 5⁰C (Aiken, 1980), growth may depend on the length of the season during which the water temperature is above this threshold. Russell (1980) indicated that a latitudinal trend in growth parameters may exist for American lobster. This would be consistent with what is known about how temperature influences growth in this species, and could provide a general growth model that allows site-specific estimation of growth parameters based on latitude. This would reduce the need for resource-intensive tag-recapture studies and also prevent growth parameters estimated at one specific site from being arbitrarily applied to other locations.

In contrast with the heuristic models mentioned above (Gompertz and Richards), the von Bertalanffy growth model is mechanistic; it is derived from the difference between the physiological processes of catabolism and anabolism within an organism (Fabens, 1965). It is the most widely used growth model to describe size-at-age in crustaceans, and its parameters can be interpreted biologically. There are several methods of von Bertalanffy parameter estimation. The graphical methods of Ford-Walford and Gulland-Holt, as discussed in Chapter 2, are considered obsolete, as they were developed before modern computing methods made nonlinear least squares analysis manageable and do not provide estimates of error associated with the growth parameters. Fabens' straightforward method involves determining the k and L_∞ parameters (from Eq.2.3b, Chapter 2) via non-linear least squares analysis. This has come under scrutiny by several researchers in the past few decades due to an inherent bias in the procedure. Both Sainsbury (1980) and Maller & deBoer (1988) demonstrated by simulation that the method presented by Fabens for tag-recapture data tends to underestimate k and overestimate L_∞. This stems from the fact that the original von Bertalanffy equation was derived to describe the growth of an individual and cannot necessarily be used to describe mean population growth. The argument was presented by Sainsbury (1980), who instead considered individuals in a population to possess their own pair of von Bertalanffy parameters, and assigned frequency distributions to k and L_∞ for the population. This method of assigning a distribution to one or both von Bertalanffy parameters is carried out by several other authors (e.g. James, 1991; Maller & Deboer, 1988; Wang, 1998), each with their own assumptions regarding the type of distributions. Another approach is the expected value parameter models of Ratkowsky (1986) and Hernandez-Llamas & Ratkowsky (2004). They favour reparameterizing the von Bertalanffy equation so the parameters exhibit close-to-linear behaviour. Francis' (1988) expected-value parameter model involves calculating mean annual growth directly from the data for two arbitrary carapace lengths; the growth parameters come directly from the dataset and are not estimated by least squares methods. This type of analysis would require datasets with enough records of growth to produce trustworthy annual growth rates for specific sizes. For the type of data used in this project, Fabens' method of estimating von Bertalanffy parameters, including an examination of the extent of the bias, is appropriate.

The von Bertalanffy growth function has been used to estimate growth rates in lobster in over 15 studies throughout its range, including Newfoundland (Ennis, et al. 1982, 1986, 1989), the Bay of Fundy (Campbell, 1983), Maine (Krouse, 1977), and Massachusetts (Fair, 1976). To examine growth throughout the range, historical tagging data were combined with current field studies. Field work was conducted on the west coast of Newfoundland to ensure that data were available from the northern limit of the lobster's range. The von Bertalanffy function was used to estimate growth parameters from each site, and the relationship between growth rate and latitude was then determined and used to develop an equation that estimates the growth rate for *H. americanus* at any desired location.

3.2 Methods

3.2.1 Field Tagging

Tag-recapture studies were carried out in two sites in Newfoundland (Fig. 4). The sites were chosen to represent the latitudinal range of the coastline: Port-aux-Basques (47.570431°N, 59.135724°W) at the southern tip of the west coast and Port-au-Choix (50.722915°N, 57.328927°W) close to the northern boundary of the American lobster's range at the Strait of Belle Isle, NL.

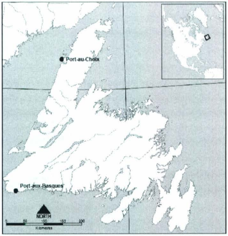


Fig. 4: Location of field sites in Newfoundland.

Lobsters were captured by professional fish harvesters using commercial lobster traps. Each lobster was tagged with a polyethylene streamer tag bearing a unique ID number. These tags are inserted through the dorsal musculature between the carapace and abdomen, and are usually retained through the molt. Detrimental effects of streamer tags (increased mortality and low growth) are primarily found in lobsters tagged shortly before molting (Comeau & Savoie, 2001), so care was taken when planning field work to avoid months just prior to molting. The carapace length was measured from the posterior edge of the eye-socket to the edge of the carapace, parallel to the dorsal midline, to the nearest mm with Vernier callipers. Shortly after tagging, lobsters were released as close as possible to their capture site.

Tagging was first conducted during September-October of 2009, beginning late in September to target post-molt lobsters. Since lobsters would then be subjected to a spring fishing season before their next molting period, there was concern that many of the tagged lobsters would be removed from the population before exhibiting any change in size. To increase the sample size for recaptures, a second tagging session was conducted from May-June 2010, during the commercial fishing season. All lobsters that were ineligible for harvest (i.e. undersized, ovigerous or V-notched) were tagged. Recaptures were conducted from September-October 2010 to increase the likelihood of measuring individuals that molted only once

3.2.2 Historical Tagging Data

In addition to the field efforts from this project, 51 historical tagging datasets were compiled from various locations throughout the species' range. Any tag-recapture study carried out over at least one molt cycle, with records of carapace length, was included. Tagging datasets collected are summarized in Table 5. The locations of all tagging sites are shown in Figure 5.

Table 5: Historical tagging data compiled for growth analysis.

Region	Site	Dates	Records of Growth (n)	Size Range (Carapace length, mm)	Source
Newfoundland	Arnolds Cove, NL	1970-1989	205	42-125	Roanne Collins & Gerry Ennis, DFO
Newfoundland	Bellburns, NL	1976-1981	300	62-127	Roanne Collins & Gerry Ennis, DFO
Newfoundland	Boswarlos, NL	1974-1981	92	69-132	Roanne Collins & Gerry Ennis, DFO
Newfoundland	Comfort Cove, NL	1971-1975	176	46-105	Roanne Collins & Gerry Ennis, DFO
Newfoundland	Duck Islands, NL	1997-2008	284	69-135	Jennifer Janes, DFO Oceans (2004-2008) & Roanne Collins, DFO Science (1997)
Newfoundland	Leading Tickles, NL	2004-2006	103	68-132	Jennifer Janes, DFO Oceans (2004-2008) & Roanne Collins, DFO Science (1997)
Newfoundland	Round Island, NL	1997-2008	275	54-139	Jennifer Janes, DFO Oceans (2004-2008) & Roanne Collins, DFO Science (1997)
Newfoundland	Shag Rocks, NL	1976-1984	1034	69-144	Roanne Collins, DFO
Newfoundland	St Chads, NL	1968-1976	157	49-145	Roanne Collins, DFO
Gulf of St Lawrence	Anse-Bleu, NB	1994-1997	55	54-89	Michel Comeau, DFO

Table 5 (continued)

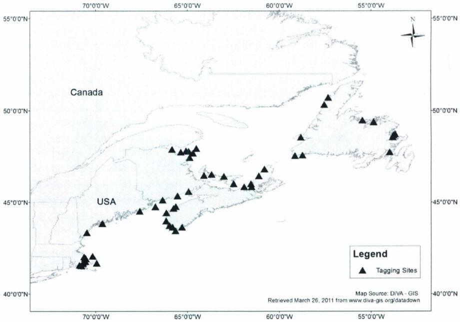
Region	**Site**	**Dates**	**Records of Growth (n)**	**Size Range (Carapace length, mm)**	**Source**
Gulf of St Lawrence	Baxter's Cove, NS	2000-2001	2	71-102	Michel Comeau, DFO
Gulf of St Lawrence	Beach Point, PE	1982-1983	51	61-120	Michel Comeau, DFO
Gulf of St Lawrence	Belledune, NB	1980-1983	563	52-138	Michel Comeau, DFO
Gulf of St Lawrence	Caraquet, NB	1993-1999	343	53-133	Michel Comeau, DFO
Gulf of St Lawrence	Egmont Bay, PE	1982-1983	248	48-97	Michel Comeau, DFO
Gulf of St Lawrence	Le Goulet, NB	1996-1998	7	59-98	Michel Comeau, DFO
Gulf of St Lawrence	Malpeque, PE	1989-1990	401	50-101	Michel Comeau, DFO
Gulf of St Lawrence	Margaree, NS	1984-1993	375	53-117	Michel Comeau, DFO
Gulf of St Lawrence	Miscou, NB	1994-1998	73	54-117	Michel Comeau, DFO
Gulf of St Lawrence	Pleasant Bay, NS	1988-1993	262	54-128	Michel Comeau, DFO
Gulf of St Lawrence	Port Hood, NS	1988-1993	867	54-143	Michel Comeau, DFO
Gulf of St Lawrence	Stonehaven, NB	1994-2000	52	53-111	Michel Comeau, DFO
Gulf of St Lawrence	Tracadie Bay, PE	1984-1985	11	56-111	Michel Comeau, DFO

Table 5 (continued)

Region	**Site**	**Dates**	**Records of Growth (n)**	**Size Range (Carapace length, mm)**	**Source**
Bay of Fundy	Alma, NB	1979-1986	251	66-187	Peter Lawton, DFO
Bay of Fundy	Chance Harbour, NB	1979-1986	793	61-186	Peter Lawton, DFO
Bay of Fundy	Delaps Cove, NS	1979-1983	17	79-122	Peter Lawton, DFO
Bay of Fundy	Flagg Cove, NB	1990-1993	6	106-158	Peter Lawton, DFO
Bay of Fundy	Little River Harbour, NS	1986-1988	6	81-128	Peter Lawton, DFO
Bay of Fundy	McNutts Island, NS	1982-1987	72	21-149	Peter Lawton, DFO
Bay of Fundy	North Head, NB	1977-1988	739	60-198	Peter Lawton, DFO
Bay of Fundy	St Martins, NB	1979-1994	133	63-182	Peter Lawton, DFO
Bay of Fundy	Victoria Beach, NS	1993-1995	9	78-128	Peter Lawton, DFO
Nova Scotia (SW)	Port Maitland, NS	1978-1987	84	67-127	Peter Lawton, DFO
Nova Scotia (SW)	Lower Wedgeport, NS	1983-1986	29	95-152	Peter Lawton, DFO
Nova Scotia (SW)	Lower West Pubnico, NS	1984-1987	5	36-80	Peter Lawton, DFO
Nova Scotia (SW)	Clarks Harbour, NS	1979-1982	16	79-118	Peter Lawton, DFO

Table 5 (continued)

Region	**Site**	**Dates**	**Records of Growth (n)**	**Size Range (Carapace length, mm)**	**Source**
Maine	Jonesport, ME	1975-1976	23	81-113	Krouse, 1977
Maine	Kennebunkport, ME	1975-1977	10	81-102	Krouse, 1977
Cape Cod	Cape Cod Canal, MA	1979-1981	9	68-90	Robert Glenn, Massachusetts Division of Marine Fisheries (MADMF)
Cape Cod	Chatham, MA	1984-1989	3	91-129	Robert Glenn, MADMF
Cape Cod	Cole`s Hole, MA	1971-1974	15	77-103	Robert Glenn, MADMF
Cape Cod	Manomet, MA	1970-1977	240	64-95	Robert Glenn, MADMF
Cape Cod	Provincetown, MA	1969-1972	14	55-162	Robert Glenn, MADMF
Cape Cod	Rocky Point, MA	1971-1977	154	64-107	Robert Glenn, MADMF
Cape Cod	White Horse, MA	1973-1977	111	52-99	Robert Glenn, MADMF
Buzzards Bay	Lower Buzzards Bay, MA	1971-1972	7	70-105	Robert Glenn, MADMF
Buzzards Bay	North Ledge, MA	1969-1972	103	70-101	Robert Glenn, MADMF
Buzzards Bay	Upper Buzzards Bay, MA	1982-1984	24	67-92	Robert Glenn, MADMF



Map Source: DIVA - GIS
Retrieved March 26, 2011 from www.diva-gis.org/datadown

Figure 5: Tagging locations in the Northwest Atlantic.

3.2.3 Quantitative Analysis

Separate analyses were carried out for males and females. To exclude the individuals that did not molt between captures, only lobsters that exhibited an increase in carapace length >3mm were considered for analysis. A 3 mm measurement error was assumed based on lobsters that were captured and measured multiple times over a single tagging period. Molt frequency is not considered in this analysis as it requires differentiation between zero growth during a time of year when lobsters have the opportunity to molt, and zero growth during a time period where no molting occurs in the population (Campbell, 1983).

Molting seasons are difficult to define for historical data as they vary within and between locations and with annual variability in temperature (see Comeau & Savoie, 2001).

The von Bertalanffy parameters k and L_∞ were estimated for males and females at each site using non-linear least squares analysis on two versions of the Fabens tag-recapture equation. The first gives the change in carapace length, ΔL, as a function of the initial length, L_1, and time at large, Δt.

$$\Delta L = (L_\infty - L_1)(1 - e^{-k\Delta t}) \tag{3.1a}$$

The second is a modification by Quinn & Deriso (1999), which reorganizes the equation in terms of post-molt length, L_2.

$$L_2 = L_\infty(1 - e^{-k\Delta t}) + L_1 e^{-k\Delta t} \tag{3.1b}$$

Residual vs. fit plots were examined to determine which model was most appropriate for these data. Starting values for the parameters were k=0.2yr^{-1} and L_∞=177mm. These were the mean values of published parameter estimates for American lobster.

Next, nonlinear least squares was carried out on equation (3.1b) for each site, with L_∞ assigned a fixed value. Three different methods were used to fix L_∞ at a reasonable value, and the resulting k values were examined in each case:

1. L_∞ for each location was fixed at the maximum carapace length recorded in their respective data set.
2. L_∞ was determined for each location from a regression of the maximum carapace lengths and latitude, weighted by sample size.

3. L_∞ was fixed across all locations, using the value of the largest carapace length recorded for American lobster in the primary literature, $L_\infty = 326$mm (Wolff, 1978).

In regression modelling it is generally assumed that the error associated with the dependent variable is much larger than the error associated with the independent variable, otherwise the regression produces biased estimates of error, confidence intervals and p-values. This assumption is not met in this analysis, as both variables are carapace lengths measured with the same error. To address the problem of having the response variable measured with the same error as the dependent, the analysis was carried out by fixing the independent variable, $L_{1,}$ as the midpoint of bins, and then using the mean L_2 from each bin, weighted by the number of values (Allen, 1939: Frost & Thompson, 2000). This was done for four representative data sets of various sample sizes: Leading Tickles, North Head, Rocky Point, and Upper Buzzards Bay.

To test the sensitivity of starting value for the parameter, *k*, the starting value was varied by orders of magnitude from 0.002 to 20 on four representative datasets. To determine if sample size had any potential biasing effect on the parameter estimates, *n* was plotted against maximum carapace length, *k*, and latitude.

Estimates of von Bertalanffy growth rates were regressed against latitude. These estimates were weighted by sample size, weighted by the inverse of the variance, and unweighted. Unweighted results give equal weight to estimates from small and large sample sizes, while weighting by sample size gives more importance to larger sample sizes. Inverse-variance weighting assigns more importance to estimates with the lowest variance, thus reducing the influence of less reliable estimates. A general equation for estimating k from latitude was determined for males and females.

The bias in length-at-age estimates described above (Sainsbury, 1980) was calculated for males and females from ages 1-30. The relationship between this bias and latitude was determined through visual examination of the plotted data and nonlinear least squares analysis to estimate regression coefficients.

3.3 Results

3.3.1 Newfoundland Field Tagging

In Port-au-Choix, 62 of the 1518 tagged lobsters were recaptured the following year; 35 were from the fall sampling period and 27 from the spring sampling period. In Port-aux-Basques, 50 of the 1252 tagged lobsters were recaptured; 37 were from the fall sampling period and 13 from the spring. These recaptures resulted in 20 records of growth for Port-au-Choix and 36 records of growth from Port-aux-Basques.

3.3.2. VBGF: Two-Parameter Estimation

Upon examination of the residual versus fit plots for both equations (3.1a) and (3.1b) for all 53 locations, it was determined that the model with L_2 as the dependent variable (equation 3.1b) was most appropriate for this situation. Patterns observed in the plots that indicated non-homogenous errors were removed or diminished in the majority of sites when comparing 3.1b to 3.1a. The error associated with recapture size (L_2) was close to constant, while the error associated with the growth increment increases with increasing pre-molt size (L_1) and time at large (Δt).

When performing the nonlinear least squares analysis with SPLUS, the program failed to converge on a parameter estimate for several sites despite numerous adjustments of the parameter starting values. For the locations that did produce estimates, parameter values for both k and L_∞ were inconsistent and unrealistic in some cases, with large standard errors (Table 6). Values for k ranged from -0.182yr^{-1} to 17.1yr^{-1} for males, and from -0.242yr^{-1} to 100yr^{-1} for females. Several of the growth rates were negative or had standard errors that exceeded the magnitude of the estimates.

Table 6: Estimates of k and L_∞ growth parameters with standard errors for male and female American lobsters. Dashes denote situations in which non-linear least squares analysis failed to converge on parameter estimates.

Location	**Latitude**	**Males**				**Females**			
		k (yr^{-1})	**SE**	**L_∞(mm)**	**SE**	**k (yr^{-1})**	**SE**	**L_∞(mm)**	**SE**
Lower Buzzards Bay	41.5436	-	-	-	-	-0.242	0.399	30.3	89.7
North Ledge	41.568073	-	-	-	-	100	60.9	88.43	0.483
Upper Buzzards Bay	41.659203	1.05	1.15	105	22.9	24.8	14.4	84.7	0.861
Chatham	41.679603	*No data*	*No data*	*No data*	*No data*	-0.222	0.394	78.9	24.8
Canal	41.768156	*No data*	*No data*	*No data*	*No data*	6.25	4.73	88.1	1.22
Manomet	41.926761	17.1	4.27	89	0.439	12.3	2.15	88.3	0.312
White Horse	41.931732	-	-	-	-	-	-	-	-
Rocky Point	41.949826	5.04	0.74	90.1	0.587	5.39	1.11	88.7	0.704
Cole's Hole	42.026216	2.87	2.86	92.3	3.68	5.59	2.74	89.8	0.888
Provincetown	42.052547	0.0465	0.243	345	1375	0.18	0.193	203	70.5
Kennebunkport	43.34343	3.87	1.09	96.1	1.46	-	-	-	-
Clark's Harbour	43.446345	3.15	4.07	110	6	1.36	0.535	114	4.17
McNutt Island	43.636226	-0.182	0.0441	-4.39	11.1	-	-	-	-
Lower West Pubnico	43.638609	-	-	-	-	*No data*	*No data*	*No data*	*No data*
Lower Wedgeport	43.717035	-	-	-	-	0.983	0.88	126	8.63
Boothbay Harbor	43.844597	0.0833	0.311	221	467	0.461	0.864	111	22.4
Port Maitland	43.984837	0.251	0.0457	143	7.75	0.396	0.0775	121	5.33
Little River	44.442056	-	-	-	-	-	-	-	-
Jonesport	44.524502	4.22	2.34	103	4.18	6.11	4.39	99.7	2.5
Victoria Beach	44.67914	-	-	-	-	-	-	-	-
Flagg Cove	44.762532	*No data*	*No data*	*No data*	*No data*	-	-	-	-
North Head	44.76311	0.0411	0.0194	406	126	0.0934	0.0113	212	9.72
Delaps Cove	44.769971	-	-	-	-	0.126	0.152	209	121
Chance Harbour	45.12223	0.0847	0.0144	291	29.1	0.2	0.0138	167	4.27

Table 6 (continued)

Location	Latitude	Males				Females			
		k(yr^{-1})	SE	L_∞(mm)	SE	k(yr^{-1})	SE	L_∞(mm)	SE
St Martins	45.35318	0.149	0.0485	232	33.1	0.268	0.0457	160	7.1
Alma	45.594959	0.081	0.0192	284	36.4	0.158	0.0247	175	8.26
Ballantynes Cove	45.857226	-	-	-	-	-	-	-	-
Baxter's Cove	45.858594	-	-	-	-	*No data*	*No data*	*No data*	*No data*
Port Hood	46.01467	0.131	0.0282	151	17.2	-	-	-	-
Beach Point	46.016531	-	-	-	-	0.22	0.0787	134	16.7
Tracadie Bay	46.422296	-	-	-	-	-	-	-	-
Margaree	46.453698	0.268	0.0583	109	8.29	0.03	0.0262	386	274
Egmont Bay	46.477751	0.103	0.126	194	153	0.0466	0.105	338	613
Malpeque	46.529085	-	-	-	-	0.0239	0.0282	459	462
Pleasant Bay	46.833619	-	-	-	-	-	-	-	-
Val Comeau	47.460812	-	-	-	-	-	-	-	-
Port-aux-Basques	47.570431	0.0397	0.117	503	1198	1.48	0.417	105	2.93
Shag Rocks	47.595604	0.181	0.0202	141	3.9	0.168	0.0172	132	2.16
Le Goulet	47.702856	-	-	-	-	*No data*	*No data*	*No data*	*No data*
Stonehaven	47.755567	0.0498	0.0313	207	81.5	0.133	0.0776	114	26.6
Arnolds Cove	47.759308	0.112	0.045	184	41.2	0.228	0.0298	120	5.01
Caraquet	47.799531	0.147	0.0223	133	9.02	0.233	0.0322	106	4.56
Anse-Bleu	47.831687	0.0398	0.0839	257	394	0.0841	0.0468	137	38.3
Belledune	47.909412	0.0965	0.0167	193	18.4	0.194	0.027	119	6.02
Miscou	47.960439	-	-	-	-	0.215	0.0993	108	16.2
Boswarlos	48.568732	0.141	0.0859	168	45.1	0.089	0.0531	187	56.4
Round Island	48.581713	0.0721	0.0238	190	29.6	0.0352	0.0127	238	51.4
St Chad's	48.694222	0.164	0.0298	122	6.77	0.111	0.0245	136	12.2
Duck Islands	48.7427	0.0629	0.0204	204	31.9	0.0328	0.0184	267	94.8

Table 6 (continued)

Location	**Latitude**	**Males**				**Females**			
		k(yr^{-1})	**SE**	L_∞(mm)	**SE**	k(yr^{-1})	**SE**	L_∞(mm)	**SE**
Comfort Cove	49.39443	0.541	0.149	98.9	4.95	0.424	0.0901	101	4.23
Leading Tickles	49.495531	0.0658	0.047	226	96.4	0.175	0.0738	133	15.9
Bellburns	50.335861	-	-	-	-	0.145	0.0331	120	8.27
Port-au-Choix	50.722915	0.1	0.273	216	350	0.151	0.311	155	132

3.3.3 VBGF: One-Parameter Estimation

Fixing L_∞ and estimating only k by least squares analysis produced much more consistent k values without errors in convergence or negative parameter estimates (Fig. 6). $L_\infty = 326$ mm, the maximum carapace length recorded for *H. americanus*, produced the smallest range of k values in comparison to $L_\infty =$ maximum carapace length recorded at each location and $L_\infty =$ a value generated by a regression of the largest carapace length recorded and latitude. $L_\infty = 326$ was chosen for the fixed parameter value of the subsequent growth model. Since neither the maximum recorded carapace length at each site, nor the maximum asymptotic size estimated by the initial analysis, were significantly related to latitude, L_∞ was kept constant across all sites.

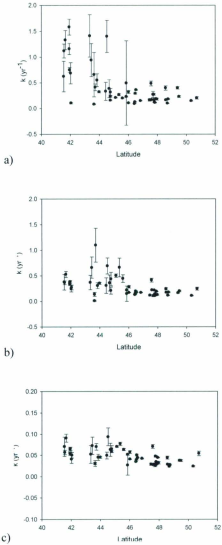


Figure 6: Growth parameter, *k,* for male lobsters estimated by fixing L_∞ at a) the maximum carapace length recorded at each location, b) a value generated by a regression of the largest carapace length recorded and latitude, and c) the largest carapace length recorded for *H. americanus* (326mm) across all sites.

Binning L_l and using the means from each bin weighted by the number of values in the bin resulted in the k values reported in Table 7.

Table 7: Growth rate and standard error estimates from non-binned and binned L_l to examine bias produced by equal error in dependent and independent variables

	Non-binned			**Binned**		
	k	SE	n	k	SE	n
Leading Tickles	0.032	0.00153	103	0.0152	0.0048	11
North Head	0.0498	0.00154	622	0.0498	0.00136	28
Upper Buzzards	0.0656	0.00804	24	0.0808	0.00377	6
Rocky Point	0.0609	0.00247	154	0.0659	0.0104	8

The estimates of SE increased in Leading Tickles and Rocky Point and decreased in North Head and Upper Buzzards Bay for the binned variables. The direction of the effect on the growth parameter k was inconsistent, decreasing the estimate of k in Leading Tickles and Upper Buzzard Bay, but increasing it in Rocky Point. Binning had no effect on estimates of k for North Head.

The chosen starting value of k had no effect on the parameter estimates. Altering the starting values by four orders of magnitude did not change the resulting k values for Leading Tickles, North Head, Upper Buzzards Bay, or Rocky Point locations.

3.3.4 Latitude-based Growth Model

No relationship was found between sample size and maximum carapace length, k, or latitude. When the von Bertalanffy growth rate, k, was estimated with a fixed L_∞ there was a significant relationship between k and latitude for both male and female lobsters. Regressions of k on latitude weighted by the inverse of the variance produced the following equations, and are illustrated in Figure 7:

Males: $k = -0.0031Lat + 0.177$ $r^2 = 0.21$, $p = 0.0008$ (3.2)

Females: $k = -0.0035Lat + 0.195$ $r^2 = 0.41$, $p < 0.0001$ (3.3)

Regressions of k on latitude weighted by sample size produced the following, and are illustrated in Figure 8:

Males: $k = -0.0051Lat + 0.283$ $r^2 = 0.45$, $p < 0.0001$ (3.4)

Females: $k = -0.0040Lat + 0.224$ $r^2 = 0.54$, $p < 0.0001$ (3.5)

The unweighted regressions between *k* and latitude produced the following, and are illustrated in Figure 9:

Males $k = -0.0036Lat + 0.213$ $r^2 = 0.26$, $p < 0.0001$ (3.6)

Females $k = -0.0027Lat + 0.165$ $r^2 = 0.20$, $p = 0.001$ (3.7)

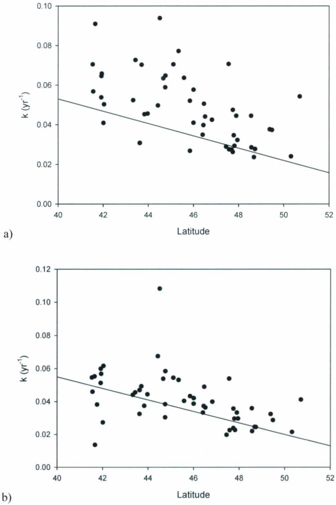


Figure 7: Relationship of von Bertalanffy growth parameter *k* to latitude for a) male and b) female American lobsters, with regression lines weighted by the inverse of the variance. r^2= 0.21 and 0.41, respectively.

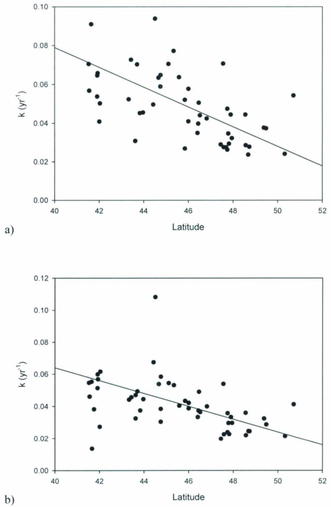


Figure 8: Relationship of von Bertalanffy growth parameter *k* to latitude for a) male and b) female American lobsters, with regression lines weighted by sample size. r^2= 0.45 and 0.54, respectively.

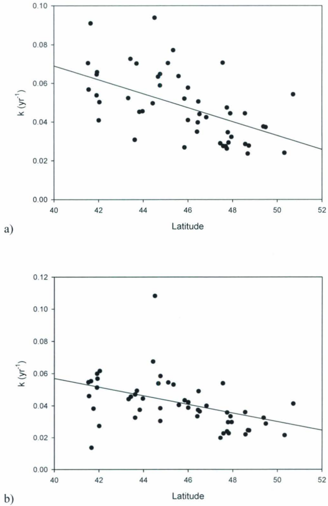


Figure 9: Relationship of von Bertalanffy growth parameter *k* to latitude for a) male and b) female American lobsters, with unweighted regression lines. r^2= 0.26 and 0.20, respectively.

Of the three different estimates, the regression weighted by sample size had the highest r^2 values, 0.45 and 0.54 for males and females, respectively. Weighting the regression by the inverse of the variance improved the r^2 over unweighted in females (0.20 to 0.41), but not in males (0.26 to 0.21). The largest slope magnitudes were produced by the regressions weighted by sample size (-0.0051 for males and -0.0040 for females), while the lowest came from the inverse variance weighting for males (-0.0036) and the unweighted regression for females (-0.0027). The magnitude of the slope was larger for males than females in two of the three cases (weighted by sample size and unweighted). The most conservative estimates of k were produced by the inverse variance weighted regression.

3.3.5 Bias in Estimation of Growth Rate

Tables 8 and 9 display the bias in length estimations for male and female lobsters at age 8 and 25, using the growth rates from the single-parameter estimation method (Sainsbury, 1980). Average bias for male lobsters was approximately 3% at age 8 and 6% at age 25. For females, the average bias was 4% at age 8 and 8% at age 25. Figure 10 shows the relationship between the bias and latitude for male and female lobsters at ages 8 and 25, weighted by sample size. In all four cases, there was a significant decrease in bias with increasing latitude.

Table 8: Bias in length at age estimation for male lobsters at ages 8 and 25.

Location	**Latitude**	***k***	***n***	**bias (age 8)**	**bias (age 25)**
Upper Buzzards Bay	41.659	0.0908	10	1.03	1.03
Manomet	41.927	0.0536	101	1.08	1.15
Rocky Pt	41.950	0.0656	73	1.05	1.07
Boothbay Harbor	43.845	0.0451	11	1.04	1.08
Jonesport	44.525	0.0937	12	1.14	1.18
Alma	45.595	0.0635	121	1.03	1.06

Table 8 (continued)

Location	Latitude	*k*	*n*	bias (age 8)	bias (age 25)
Margaree	46.454	0.0396	130	1.02	1.04
Egmont Bay	46.478	0.0504	114	1.03	1.06
Shag Rocks	47.596	0.0274	486	1.00	1.00
Arnolds Cove	47.759	0.0473	70	1.02	1.04
Boswarlos	48.569	0.0443	32	1.03	1.06
Round Island	48.582	0.0284	119	1.03	1.06
St Chad's	48.694	0.0235	71	1.02	1.05
Duck Islands	48.743	0.0276	170	1.03	1.06
Comfort Cove	49.394	0.0375	75	1.03	1.06
Leading Tickles	49.496	0.0372	46	1.02	1.04
Lower Buzzards Bay	41.544	0.0703	2	1.04	1.07
North Ledge	41.568	0.0566	44	1.06	1.11
White Horse	41.932	0.0644	49	1.05	1.08
Cole's Hole	42.026	0.0407	7	1.05	1.11
Provincetown	42.053	0.0501	7	1.02	1.04
Kennebunkport	43.343	0.0522	4	1.11	1.19
Clark's Harbour	43.446	0.0725	5	1.08	1.13
McNutt Island	43.636	0.0306	35	1.03	1.07
Lower West Pubnico	43.639	0.0307	3	1.02	1.04
Lower Wedgeport	43.717	0.0701	13	1.03	1.05
Port Maitland	43.985	0.0454	69	1.03	1.05
Little River Harbour	44.442	0.0495	2	1.01	1.02
Victoria Beach	44.679	0.0632	4	1.05	1.08
North Head	44.763	0.0587	117	1.04	1.07
Delaps Cove	44.770	0.0646	8	1.03	1.04
Chance Harbour	45.122	0.0703	342	1.03	1.05
St Martins	45.353	0.077	63	1.04	1.05
Ballantynes Cove	45.857	0.0519	62	1.01	1.01
Baxter's Cove	45.859	0.0267	2	1.14	1.32
Port Hood	46.015	0.0408	378	1.01	1.02
Beach Point	46.017	0.0575	22	1.01	1.02
Tracadie Bay	46.422	0.0348	2	1.00	1.00
Malpeque	46.529	0.0439	197	1.01	1.02
Pleasant Bay	46.834	0.0423	63	1.01	1.01
Val Comeau	47.461	0.0288	7	1.01	1.02
Port-aux-Basques	47.570	0.0705	25	1.02	1.03
Le Goulet	47.703	0.0273	6	1.02	1.04
Stonehaven	47.756	0.0261	34	1.01	1.02
Caraquet	47.800	0.0345	159	1.01	1.03

Table 8 (continued)

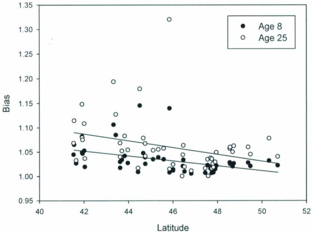
Location	Latitude	k	n	bias (age 8)	bias (age 25)
Anse-Bleu	47.832	0.0292	23	1.01	1.02
Belledune	47.909	0.0443	377	1.01	1.03
Miscou	47.960	0.0321	27	1.02	1.05
Bellburns	50.336	0.0239	93	1.03	1.08
Port-au-Choix	50.723	0.0541	12	1.02	1.04

Table 9: Bias in length at age estimation for female lobsters at ages 8 and 25.

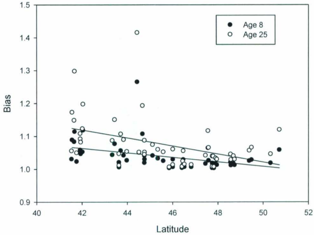
Location	Latitude	k	n	bias (age 8)	bias (age 25)
Lower Buzzards Bay	41.544	0.0544	5	1.03	1.05
North Ledge	41.568	0.0458	59	1.09	1.17
Upper Buzzards Bay	41.659	0.0551	14	1.08	1.15
Chatham	41.680	0.0134	3	1.11	1.30
Canal	41.768	0.038	9	1.02	1.05
Manomet	41.927	0.0511	140	1.06	1.11
White Horse	41.932	0.0597	62	1.05	1.09
Rocky Point	41.950	0.0566	81	1.05	1.08
Cole's Hole	42.026	0.0271	8	1.05	1.12
Provincetown	42.053	0.0614	7	1.12	1.20
Kennebunkport	43.343	0.0439	6	1.04	1.09
Clarks Harbour	43.446	0.0454	11	1.08	1.15
McNutt Island	43.636	0.0323	37	1.02	1.05
Lower West Pubnico	43.639	0.0468	2	1.01	1.01
Lower Wedgeport	43.717	0.0491	16	1.06	1.11
Boothbay Harbor	43.845	0.0372	14	1.04	1.09
Port Maitland	43.985	0.0442	65	1.03	1.05
Little River	44.442	0.0672	4	1.26	1.41
Jonesport	44.525	0.108	11	1.05	1.05
Victoria Beach	44.679	0.0536	6	1.11	1.19
Delaps Cove	44.770	0.0582	9	1.03	1.05
Flagg Cove	44.763	0.0302	6	1.02	1.04
North Head	44.763	0.0382	622	1.04	1.09
Chance Harbour	45.122	0.0542	440	1.04	1.07
St Martins	45.353	0.0529	70	1.03	1.06
Alma	45.595	0.0402	130	1.02	1.05
Ballantynes Cove	45.857	0.0431	62	1.00	1.01
Port Hood	46.015	0.0385	489	1.01	1.01
Beach Point	46.017	0.0419	29	1.03	1.06
Tracadie Bay	46.422	0.0331	9	1.00	1.01

Table 9 (continued)

Location	**Latitude**	***k***	***n***	**bias (age 8)**	**bias (age 25)**
Margaree	46.454	0.0371	245	1.01	1.02
Egmont Bay	46.478	0.0488	134	1.03	1.05
Malpeque	46.529	0.0362	204	1.01	1.01
Pleasant Bay	46.834	0.0397	199	1.01	1.01
Val Comeau	47.461	0.0196	2	1.02	1.04
Port-aux-Basques	47.570	0.0537	11	1.06	1.12
Shag Rocks	47.596	0.0224	546	1.03	1.06
Stonehaven	47.756	0.0237	18	1.00	1.01
Arnolds Cove	47.759	0.0355	134	1.02	1.04
Caraquet	47.800	0.0294	184	1.02	1.04
Anse-Bleu	47.832	0.0225	32	1.00	1.01
Belledune	47.909	0.0331	186	1.01	1.03
Miscou	47.960	0.0295	46	1.01	1.03
Boswarlos	48.569	0.0357	60	1.02	1.04
Round Island	48.582	0.0218	156	1.01	1.03
St Chads	48.694	0.0244	86	1.02	1.04
Duck Islands	48.743	0.0243	114	1.01	1.03
Comfort Cove	49.394	0.0322	101	1.02	1.06
Leading Tickles	49.496	0.0285	57	1.03	1.07
Bellburns	50.336	0.0213	207	1.02	1.05
Port-au-Choix	50.723	0.041	8	1.06	1.12



a)



b)

Figure 10: Relationship between bias in length-at-age estimates and latitude for a) male lobsters ages 8 (*bias* = -0.0053*Lat* + 1.27, $r^2 = 0.32$, $p < 0.0001$) and 25 (*bias* = -0.0071*Lat* + 1.37, $r^2 = 0.19$, $p = 0.0016$ and b) female lobsters ages 8 (*bias* = -0.0055*Lat* + 1.28, $r^2 = 0.21$, $p = 0.0007$ and 25 (*bias* = -0.0089*Lat* + 1.46, $r^2 = 0.26$, $p = 0.0001$.

The bias-corrected estimate of *k* (*pop.k*) was determined by the product of the inverse variance weighted estimate of *k* as a function of latitude (the most conservative estimate of the relationship), and the estimate of bias as a function of latitude and age (Appendix 1). The result was the following equations to calculate corrected values of *k* using both latitude, *Lat*, and age, *A*:

Males

$$pop.k = (-0.003Lat + 0.177)[(-0.0077A^2 + 0.033A + 1.0) - (1.5 \times 10^{-5}A^2 - 0.0063A - 0.0072)Lat] \tag{3.8}$$

Females

$$pop.k = (-0.0035Lat + 0.195)[(-0.0014A^2 + 0.056A + 0.99) - (2.8 \times 10^{-5}A^2 - 0.0011A + 0.00016)Lat] \tag{3.9}$$

3.4 Discussion

The most reliable and biologically reasonable estimates of von Bertalanffy growth rates for lobster came from a one-parameter model in which the maximum asymptotic size is fixed at a constant value (the largest carapace length recorded for American lobster) across all locations. These estimates of the growth parameter *k* demonstrated a negative relationship with latitude for male and female lobsters. A known bias in this method of parameter estimation was examined and determined to be minor. Equations are now available to estimate von Bertalanffy growth rates for American lobster at any location based on latitude.

3.4.1 One-Parameter versus Two-Parameter Growth Models

The one-parameter model (L_∞ fixed across locations) produced more consistent k values than the two-parameter model, with no convergence errors. James (1991) produced similar results when he assigned a distribution to L_∞, obtaining more consistent parameter estimates. Here, L_∞ was fixed based on what is known about the biology of the species. 326 mm is the largest carapace length recorded in the primary literature for this species. It is reasonable to assume that American lobsters from any location are mechanically capable of reaching the same maximum size. This would be more reasonable than estimating L_∞ from trap data, since the largest lobsters may not fit into commercial lobster traps and are unlikely to be represented in the tagging data. Population density also affects the size of lobsters found in any given area (Steneck, 2006), and this would also influence the sizes recorded in trap data.

3.4.2 Binned versus Unbinned Estimates

Binning the explanatory variable L_1 to meet the assumption of fixed values of the dependent variable (fixed at the class midpoint, Sokal & Rohlf, 1995) did not consistently reduce the estimate of the standard error, compared to estimates from unbinned data. There was no consistent upward or downward bias in the estimates of k from the binned data compared to the unbinned data.

3.4.3 Latitudinal Variation in Growth Rates

The von Bertalanffy growth parameter, k, was found to have a significant negative relationship with latitude for both male and female lobsters. The most likely cause of the decrease in growth rate with increasing latitude is the change in temperature. Temperature has been shown to have a substantial effect on lobster growth, and latitude is a good approximation of ocean temperatures in the range of *H. americanus*; according to Singer (2011), the coast of the Northwest Atlantic has the most pronounced latitudinal temperature gradient in the world. Growth rates are higher in the warmer waters of the southern part of the species range and decrease along a gradient from south to north. Here, using the regression equations weighted by the inverse of the variance, growth rates decrease by approximately 0.3% for each degree of latitude. The large scatter around the regression lines in Figure 7 may be attributable to environmental factors within and among sites, including temperature deviation from the latitudinal average. Latitude is an approximation for general ocean temperatures, but local coastal conditions can have a significant impact on the conditions that might affect lobster growth. The difference in average temperatures between secluded bays and areas of open coastline can be pronounced, even when neighbouring geographically. Much of the tag-recapture data used in this study provides only general location descriptions, but to fully examine the relationship between temperature and growth rate, temperature data would be required at a small scale for the sites of the tag-recapture studies during the appropriate years.

The latitudinal trend in growth rates can be obscured by the fact that size-at-maturity in lobsters decreases with temperature. Once lobsters, especially females, reach maturity, they allocate more resources to reproduction instead of growth, and the growth rate slows. Since lobsters reach maturity at smaller sizes in warmer waters (Fogarty, 1995), the slowing of growth occurs sooner. This is a possible reason why the latitudinal differences in *k* were not more pronounced.

The bias in growth estimates caused by the von Bertalanffy model failing to account for individual variability in growth parameters was minor. The magnitude of the bias is less than the average standard error associated with the estimates of the growth rate, *k*, and so is considered negligible. However, since the estimate of bias is not constant across latitudes the correction equations were developed (Eq. 3.8 & 3.9).

These models will be useful for management of the American lobster fishery in North America, as growth parameters can now be estimated in a site-specific manner. It will no longer be necessary to arbitrarily choose growth parameter estimates from one area to apply to a new location. It will also reduce the need for new tag-recapture studies, which are time and resource intensive. The cost of such programs is especially high when recapture rates are low, as found in the current Newfoundland field studies where only 4% of tagged lobsters were recaptured, with only half of those providing indices of growth.

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Chapter 4:Oceanographic Factors Affecting Growth Rates of American Lobster in the Northwest Atlantic.

4.1 Introduction

Growth rates are a key life history parameter in determining age-specific survivorship for use in fisheries management models. Growth in lobster has been shown to be affected by environmental conditions, with temperature having the strongest effect (Aiken & Waddy, 1986). Photoperiod, food availability, and salinity can also influence growth at some life stages (Templeman, 1936). Due to the physical extent of habitat occupied by the lobster, it is exposed to a variety of these conditions throughout its range, which extends from northern Newfoundland to coastal waters east of North Carolina (Pezzack, 1992), and from shallow coastal waters to offshore locations up to 700m deep (Cooper & Uzmann, 1971).

In Chapter 3, work with tag-recapture data demonstrated a significant relationship between growth rates and latitude. Growth coefficients were estimated using the von Bertalanffy growth function modified for tag-recapture data (Fabens, 1965; Quinn & Deriso). For both male and female lobsters, a significant negative relationship between growth rates and latitude was found.

In this chapter it will be determined if this trend in growth rates can be explained by environmental variables. This will be accomplished using GIS to map oceanographic factors (depth, temperature, salinity) throughout the range of the species and determine if there is a relationship between growth rates and any of these variables. This will provide insight into which of these factors, if any, are driving the latitudinal gradient in growth rates observed in the lobster.

4.2 Methods

4.2.1 Tag-Recapture Studies to Determine Growth Rates

Field studies were carried out in two locations in Port-au-Choix and Port-aux Basques, Newfoundland, as described in Chapter 3. Additional data was acquired from tagging studies throughout the Northwest Atlantic, ranging from northern Newfoundland to Buzzard's Bay off the coast of Massachusetts. A von Bertalanffy growth rate has been determined for males and females at each site (Chapter 3, Fig. 7 & 8.).

4.2.2 GIS Analysis

Environmental data (bathymetry, temperature, and salinity) were obtained from the General Bathymetric Chart of the Oceans (BODC, 2010) and the World Ocean Atlas. Both of these databases combine data from various sources using different types of sampling and measurement to produce datasets on a global scale. Temperature (Locarnini et al, 2010) and salinity (Antonov et al, 2010) were available for multiple depths at each sample point, from the surface to 5500 m depth. Data from 0, 10, 20, 30, 50, 75, 100, and 150 m were used for this study, since none of the tagging sites were located at greater depths.

ArcGIS® was used for all spatial analyses. All layers were projected with North America Albers Equal Area projection, since it is the area around the tagging sites that was the subject of the analysis. Kriging was used to interpolate the temperature and salinity data to raster layers for sampling.

Tagging sites were assigned a single latitude/longitude coordinate usually corresponding to the harbour out of which the study was based. A 15 km buffer zone was delineated around each tagging site to account for the area covered by a typical tagging study as well as localized lobster movement. This was verified as an appropriate size by examining studies that reported latitude/longitude coordinates for each tagged lobster. This allowed the spatial extent of the tagging study to be determined. Tagging sites with 15 km buffers are shown in Figure 11. Each tagging location was assigned an identification field with a unique identification number. A new raster layer was created with the identification fields of each buffer zone. These identifying values could later be added to environmental data using the Raster Calculator in ArcGIS®.

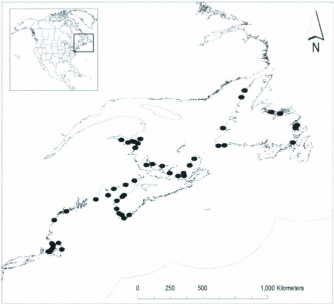

Figure 11: Tag site locations with 15 km buffer zones.

A polygon vector layer of world exclusive economic zones (the area of ocean extending from a country's coastline to 200 nautical miles offshore) was obtained from the Flanders Marine Institute (VLIZ, 2011). Polygons of exclusive economic zones for Canada, United States, and St-Pierre et Miquelon were merged to create a new vector. The combined polygon layer was then applied as a mask over the buffer zones when selecting raster data so that land values would not be sampled. This is demonstrated by the close-up of the Bay of Fundy shown in Figure 12. It shows the tag site buffer zones with the land values removed, so that only ocean values would be sampled. The masked buffer zones were then used to clip data from the bathymetry raster layer. Average depth values for each site were calculated in a spreadsheet.

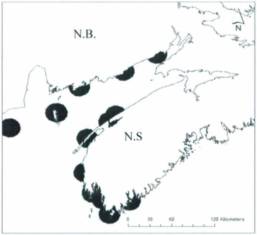

Figure 12: The Bay of Fundy showing sites that have been masked with the exclusive economic zones to eliminate land values.

Once average depth was determined, sites were assigned to the depth layer of salinity and temperature data that most closely represented the average bottom depth at each site. The number of sites in each depth layer is summarized in Table 10. Raster calculator was used to join tag sites with the temperature and salinity data for each depth layer. Data were then exported to a spreadsheet to calculate average values of bottom temperature and salinity at each site.

Table 10: Number of tag sites associated with each depth layer of salinity and temperature data.

Depth Layer	Number of Sites
0m	1
10m	10
20m	10
30m	12
50m	4
75m	5
100m	6
150m	4

4.2.3 Statistical Analysis

A GLM was performed with the von Bertalanffy growth rate, *k*, as the response variable. Explanatory variables were latitude (Lat), depth (D), temperature (Temp), and salinity (Sal). Adjusted (type III) sum of squares was used for tests. Separate analyses were carried out for males and females.

Model #1: $$k = \beta_o + \beta_{Lat} * Lat + \beta_D * D + \beta_{Temp} * Temp + \beta_{Sal} * Sal + res$$

In the model, β_o refers to the overall mean and the remaining coefficients refer to partial regression coefficients.

Explanatory variables were examined for correlation, and a second multiple regression was carried out eliminating latitude as an independent factor:

Model #2: $$k = \beta_o + \beta_D * D + \beta_{Temp} * Temp + \beta_{Sal} * Sal + res$$

4.3 Results

The relationships between growth rates of males and females and environmental variables are expressed graphically in Figures 13 and 14 respectively.

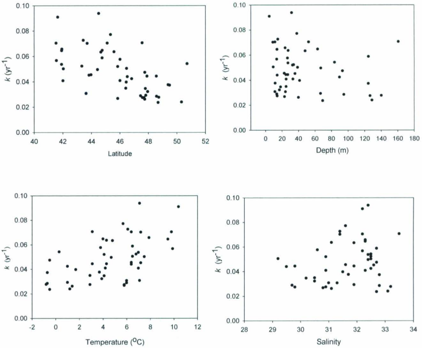

Figure 13: von Bertalanffy growth parameter *k*, in relation to latitude, depth, temperature, and salinity, for male American lobsters.

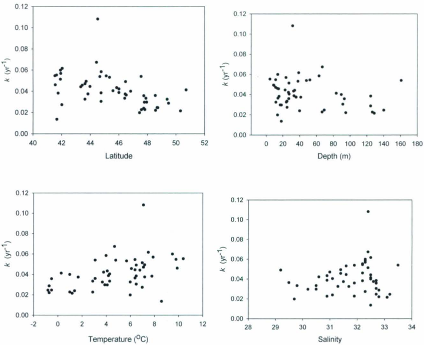

Figure 14: von Bertalanffy growth parameter *k*, in relation to latitude, depth, temperature, and salinity, for female American lobsters.

Model #1 produced no significant relationships between growth rates, latitude, depth, temperature, or salinity.

Correlation coefficients (r) associated with the explanatory variables are displayed in Table 11. Significant correlations were found between latitude and depth ($r = 0.51$), latitude and temperature ($r = -0.87$), depth and temperature ($r = -0.63$), and depth and salinity ($r = .56$).

Table 11: Correlation coefficients (r) with associated p-values between latitude, depth, temperature, and salinity variables.

	Lat	**D**	**Temp**	**Sal**
Lat	1.0			
D	0.51 ($p = 0.002$)*	1.0		
Temp	-0.87 ($p < 0.0001$)*	-0.63 ($p < 0.0001$)*	1.0	
Sal	0.13 ($p = 0.38$)	0.56 ($p = 0.002$)*	0.12 ($p = 0.42$)	1.00

Model # 2, without the independent variable *Lat*, shows that the von Bertalanffy growth rate significantly depends on temperature. The regression coefficients are 0.0036 (df = 1, F = 6.05, $p = 0.018$) for males and 0.0023 (df = 1, F = 14.71, $p < 0.001$) for females. No other significant relationships were found.

4.4 Discussion

Neither latitude, depth, temperature, nor salinity had a significant effect on lobster growth rates when accounting for the other variables (Model #1). This did not correspond with results from Chapter 3 that demonstrated a negative relationship between latitude and growth. However, when latitude was removed from the model as an explanatory variable (Model #2), growth rate was significantly dependent on temperature. This can be explained by examining the correlation results of the environmental factors. Latitude and temperature were highly correlated ($r = -0.87$), even more so than temperature and depth ($r = -0.63$). Therefore, in Model #1 the variance explained by latitude overlapped with the variance explained by temperature. This prevents either variable from emerging as a significant predictor over the other. When latitude was removed from the model, the positive relationship between growth rate and temperature emerged.

The fact that there was no relationship between salinity and growth rates is consistent with other studies (Aiken & Waddy, 1986), which found that salinity doesn't affect physiology above a threshold rarely reached in the benthic environment. There are other factors, however, that may play a part in growth rates, such as primary production and substrate composition (*e.g.* grain size). Future examination could include these other criteria for a more comprehensive examination of environmental factors affecting lobster growth rates across latitudes.

There is a spatial limitation associated with this study due to the scale of oceanographic data that is readily available for public use. The temperature and salinity data used here were obtained in point format, with points spaced evenly ¼ of a degree apart. One-quarter degree is approximately equal to 28 km. This corresponds to the 30 km diameter buffer zones that were applied to the tagging sites. Since it was these points that were smoothed to create the raster to be sampled, the spatial scale of these data was not ideal for the size of the sites.

There is also a temporal limitation. The lobster tagging data collected for this study come from projects carried out from 1960-2010. This represents 50 years of fluctuating environmental variables. However, the available data provide only annual means. This would not affect a stable variable like bathymetry, but it could influence results of dynamic variables such as temperature and salinity. Average annual ocean temperatures have increased over the last 50 years (Levitus et al., 2005). In addition, temperatures can fluctuate from year to year and growth would be affected by the temperature conditions during the specific time period the tagging studies were carried out. Temperature information from the specific locations and years of the historical studies would be preferable to the annual means employed in this analysis.

This study shows that temperature does have a significant relation to lobster growth when controlling for depth and salinity. The relationship was approximately 0.36% increase in growth rate per degree C increase in temperature for males and 0.23% increase in growth rate per degree C increase in temperature for females. These results support the idea that latitudinal gradients in von Bertalanffy growth rates for American lobster are largely caused by the corresponding latitudinal gradient in temperature throughout the range of the species.

4.5 References

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Chapter 5: Conclusion

This thesis presents an examination of methods for estimating growth rates in the American lobster and an analysis of von Bertalanffy growth parameters throughout the species' range. The goals of this project were to compare lobster growth rates in different locations and determine if latitude could be used as a predictor of growth parameters. Growth rates are desired in order to estimate reproductive value, a tool which can then be used to evaluate fisheries management measures. They are also required for mortality estimates and for the Beverton and Holt yield-per-recruit model. The results presented here show that existing estimates of von Bertalanffy growth parameters are not comparable between studies (Chapter 2), and that new estimates of growth rates have a negative relationship with latitude (Chapter 3). They also show that latitudinal variation in growth rates is partially due to latitudinal gradients in temperature (Chapter 4).

Upon examination of published growth parameters in Chapter 2, it was determined that parameter values are not comparable across locations. Different methods of von Bertalanffy parameter estimation carried out on the same datasets produced growth rates that varied substantially. Since existing parameter estimates were calculated from a variety of estimation methods, new parameter estimates must be calculated from a consistent method across locations in order to establish a general growth model.

In Chapter 3, employing Fabens' method of nonlinear least squares to estimate the growth rate and maximum attainable size of the lobster produced inconsistencies in both parameters. Fixing one parameter (maximum size) to a biologically reasonable value for the species resulted in more realistic estimates of growth across the range. In addition, the bias associated with this method of parameter estimation was examined and found to be minor. A negative relationship between latitude and von Bertalanffy growth rate was significant for both male and female lobsters. This regression can now be used to estimate lobster growth rates for specific locations based on latitude.

Using GIS to examine oceanographic factors throughout the lobster's range resulted in a significant positive relationship between von Bertalanffy growth rates and water temperature, while controlling for salinity and depth, in Chapter 4. This relationship was present for both male and female lobsters. It indicates that the latitudinal variation in growth rates found in Chapter 3 can be explained by a latitudinal gradient in water temperature. Further research could examine the effects of other environmental variables, such as primary production and substrate composition.

This project provides a general model to estimate von Bertalanffy growth rates on a site-specific basis. Tagging studies are resource intensive and must be carried out over multiple years, while this model provides estimates of growth rates that can be used immediately or when a local tag-recapture study is not feasible. It will also allow growth parameters to be averaged over a latitudinal range, providing estimates at whatever spatial scale is deemed appropriate. These estimates will allow the construction of life history tables for American lobster that are necessary for calculating reproductive value and other fisheries management models. This fishery is associated with high exploitation rates and various management and conservation techniques. A comparison between reproductive value and economic value of the lobster will be useful for determining the effectiveness of the management measures currently in place throughout the commercial range.

Appendix 1

Derivation of Bias-Corrected Equations for Growth Parameter k

The mean length-at-age for a population (*pop.L$_t$*), given variability in growth among individuals of the population, is calculated as follows:

$$pop.L_t = L_\infty[1-(1+\frac{var(k)t}{mean(k)})^{-\frac{mean(k)^2}{var(k)}}]$$

This is the equivalent of Sainsbury's Eq. (7), where L_∞ is the von Bertalanffy maximum size parameter (mm), *t* is the age in years, and *var(k)* and *mean(k)* are defined by a gamma distribution of *k* (Sainsbury, 1980).

The bias in length at age (*Bias*) is described as the ratio between the length calculated for an individual (Eq. 1.1a) and the average length-at-age for a population (*pop.L$_t$*).

$$Bias = \frac{L_t}{pop.L_t} = \frac{L_\infty(1-e^{-kt})}{L_\infty[1-(1+\frac{var(k)t}{mean(k)})^{-\frac{mean(k)^2}{var(k)}}]}$$

Bias was calculated for all locations for ages 1-30 and found to have a linear relationship with *Lat* (Fig. 10). Bias could then be estimated $(\widehat{Bias})$ as a function of latitude. A bias-corrected *k* value, *pop.k,* was defined as the product of *k* estimated using Fabens' method, and the estimated bias in length-at-age $(\widehat{Bias})$:

$$pop.k = k * \widehat{Bias}$$

Here, both *k* and $\widehat{Bias}$ are functions of *Lat*, so $k = \alpha_k + \beta_{Lat,k} * Lat$ and $\widehat{Bias} = \alpha_{Bias} + \beta_{Lat,Bias} * Lat$. The bias-corrected *k* was then estimated by:

$$pop.k = (\alpha_k + \beta_{Lat,k} * Lat)(\alpha_{Bias} + \beta_{Lat,Bias} * Lat)$$

Estimates of regression coefficients α_k and $\beta_{Lat,k}$ are taken from Eq. 3.2 (males) or Eq. 3.3 (females). The coefficients from regression of bias on latitude (α_{Bias} and $\beta_{Lat,Bias}$) were found to depend on age (*A*) as shown in Figures 15 and 16.

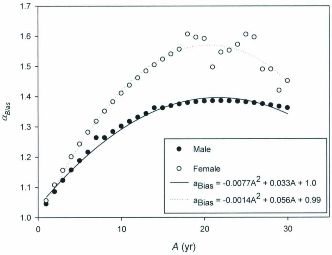

Figure 15: Relation of the intercept coefficient α_{Bias} to age.

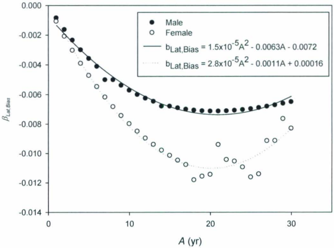

Figure 16: Relation of slope coefficient $\beta_{Lat,Bias}$ to age.

The calculation for bias-corrected *k* can be expanded to the following:

$$pop.k = (\alpha + \beta_{Lat} * Lat)[(\alpha' + \beta'_{A} * A + \beta'_{A^2} * A^2) + (\alpha'' + \beta''_{A} * A + \beta''_{A^2})Lat]$$

Coefficients α', β'_{A}, β'_{A^2}, α'', β''_{A}, and β''_{A^2} were substituted from the quadratic equations in Figures 15 and 16 to produce the following correction equations:

Males

$$pop.k = (-0.003Lat + 0.177)[(-0.0077A^2 + 0.033A + 1.0) - (1.5 \times 10^{-5}A^2 - 0.0063A - 0.0072)Lat] \tag{3.8}$$

Females

$$pop.k = (-0.0035Lat + 0.195)[(-0.0014A^2 + 0.056A + 0.99) - (2.8 \times 10^{-5}A^2 - 0.0011A + 0.00016)Lat] \tag{3.9}$$