A plain language summary by Kate Wilke

Adapted from:

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

by
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Summary of MSc Thesis

This thesis presents an examination of methods for estimating growth rates in American lobster and an analysis of von Bertalanffy growth parameters (growth rate and maximum size) 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. 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 estimates of death rates and for a 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), meaning growth rates decrease as you go north. The decrease in growth rate per degree of latitude is approximately 0.3% for both male and female. Growth rate for American lobster can now be estimated on a site-specific basis using latitude, reducing the need for resource-intensive tag-recapture field studies. The results also show that latitudinal variation in growth rates is largely due to latitudinal gradients in temperature (Chapter 4).

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Chapter 1: Introduction and Goals

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 (number of eggs and frequency of spawning) and mortality. Throughout a lobster's life, 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 mass and so increases steadily throughout its lifespan. The American lobster is a good candidate for the comparison between reproductive and economic value. It is long-lived and produces more eggs as it gets larger. Reproductive value of this species, as with economic value, will not necessarily decline with age. Accurate biological information is required to estimate reproductive value, specifically we need to know how much an individual grows during each year of its life, so that we can use that information to produce mortality estimates (death rates) throughout the lifespan, 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 forecasting models that predict future yields (Fogarty, 1995).

Lobster Growth

Like all crustaceans, lobsters exhibit discontinuous growth, meaning that they increase in size only during discrete molting periods 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 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 so they can carry eggs. In large lobsters, as molting incidents become rarer, individuals may go three or more years without molting (Waddy et al., 1995).

One challenge to the study of lobster growth throughout its lifetime is the absence of a reliable method to determine age in the wild. All hard tissues are shed and replaced through regular molting, leaving no record of age in the body like the otolith (or ear bone) 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 will be similar to 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 measured 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).

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, meaning that scientists must choose to use data from another location when estimates are not available, and the data from another location may or may not be representative. Calculating the differences in growth throughout the species' geographic range would resolve this problem. Scientist would then have a mathematical equation that could produce an estimate of growth at any location within the range of the species. Having one, all-encompassing equation 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) showing that lobsters grew faster as you go south. His work also hinted that lobsters in northern locations can reach a larger maximum size than those in southern locations (Fig.2). These results support the idea that a general growth model based on latitude could potentially be applied to all lobster stocks.

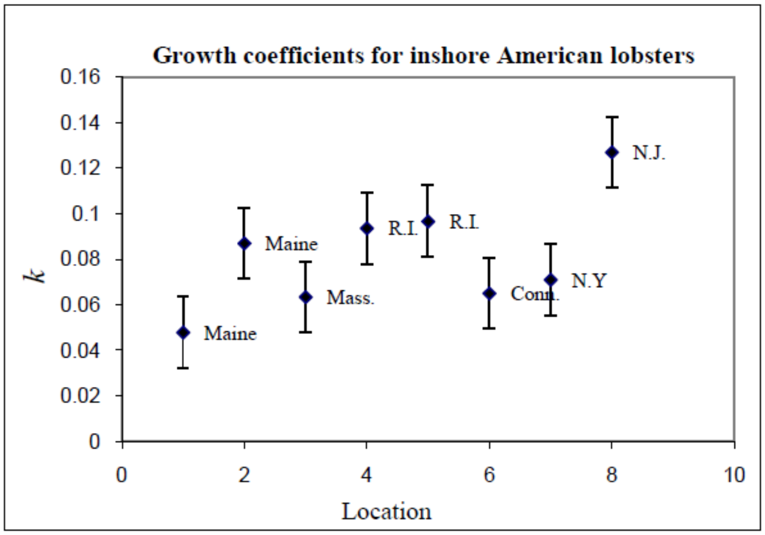

Figure 1. Growth parameter, k, reproduced from Russell (1980), with 95% confidence limits calculated from Location 1 (Maine) and applied to all points.

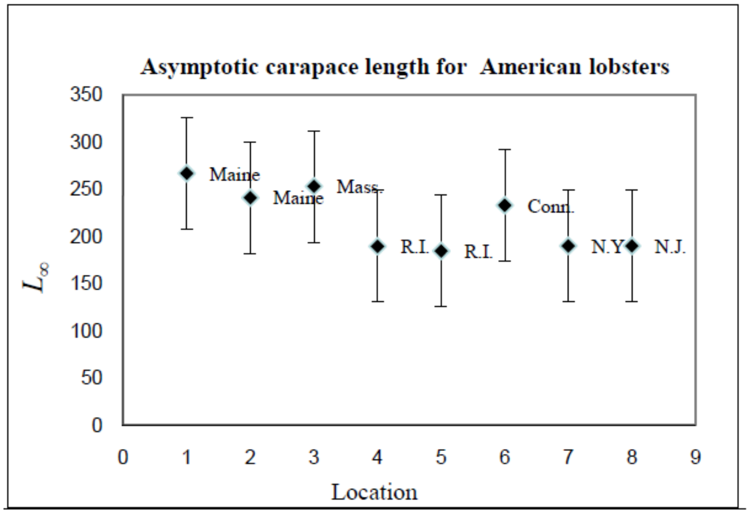

Figure 2. Maximum size, *L∞*, reproduced from Russell (1980), with 95% confidence limits calculated from Location 1 (Maine) and applied to all points.

Goals

The goal of this project is to construct a general growth model (which is a mathematical equation) for American lobster that can be used at any location in the commercial range of the species. This model will also include estimates of death rates for each stage of a lobster's life. Preliminary findings led to an additional goal which will be discussed in the next section.

This research addresses the following objectives:

1. Use tag-recapture data to create a mathematical growth model for American lobster applicable to any location.
2. Develop mathematical equations that can predict lobster growth based on latitude and/or environmental factors (such as temperature) to make the model geographically flexible.

Von Bertalanffy Growth Model and an Additional Goal

The von Bertalanffy growth function is the most commonly used mathematical model to describe growth in lobsters. American lobster 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:

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

where L_t is the length of the animal at time t, $L\infty$ 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).

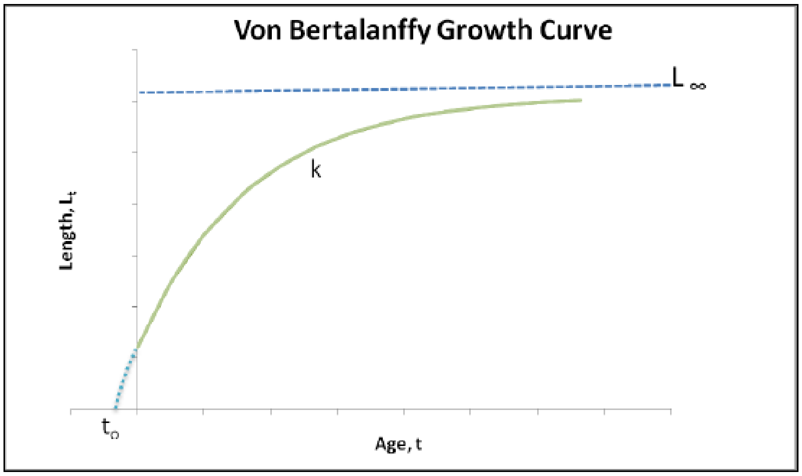

Figure 3. Illustration of the von Bertalanffy growth function. t_0 represents age 0. An organism grows quickly at the beginning of its life and as it gets older, growths slows and eventually levels off.

This model can also be used with mark-recapture data (Fabens, 1965) by using the change in length between captures and the time between captures.

The von Bertalanffy model was chosen for this analysis over other possible models (e.g. Logistic, Gompertz, Richards) because the different parts of the model each have biological meaning. Despite a few problems with the model, the von Bertalanffy function still produces graphs that closely resemble: 1) graphs of organisms that show never-ending growth, who tend to put more energy toward reproduction rather than growth as they age (Kozlowski, 1996) which is the reason growth slows down with age, and 2) stepwise growth increments based on crustacean molt intervals (Caddy, 2003), rather than continuous, little-by-little growth as in humans. Parts of the von Bertalanffy model can also be used to produce estimates of death rates required for determining reproductive value. Another benefit of the model is the fact that it is so often used in scientific studies makes it useful for management and conservation, since it allows for comparison of biological and population information in different regions.

The data analysis for this project uncovered several statistical problems when trying to use the von Bertalanffy model. These difficulties led to the development of an additional objective for this project: to search for a more reliable method of fitting lobster tag-recapture data into the model.

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Chapter 2: Comparison of lobster growth using the von Bertalanffy model throughout the species' range.

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). In these studies, a lobster is tagged, measured, and released. After a period of time, the lobster is caught again and re-measured to see how much it has grown. The majority of these studies report on growth using the von Bertalanffy model, but depending on the methods used in each study, the results from different areas may or may not be comparable. If growth estimates not comparable, we cannot use them to develop a model that is applicable to the entire geographic range. In this case, we would have to recalculate the growth estimates from each study using consistent methods.

The von Bertalanffy model is made up of numbers called parameters. These parameters represent growth rate (k), maximum length ($L\infty$), and time at hatch (t_o). Several parameter estimates from other studies were summarized and compared, and 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, $L\infty$ values (maximum size) 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 this much, even if they are found in different geographic regions. For time at hatch, t_o, to be biologically meaningful, it must be a negative number. Several of these studies report a positive t_o value. This implies that a newly hatched lobster has a negative size.

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 methods used in the first two 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 one type of methodology.

Methods

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 Eastport (Duck Islands and Round Island) and Leading Tickles, Newfoundland. Tagging was conducted from July to October in 1997 and 2004 - 2008 in Duck Islands and Round Islands, and June to October from 2004 - 2006 in Leading Tickles. 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 (egg-bearing 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.

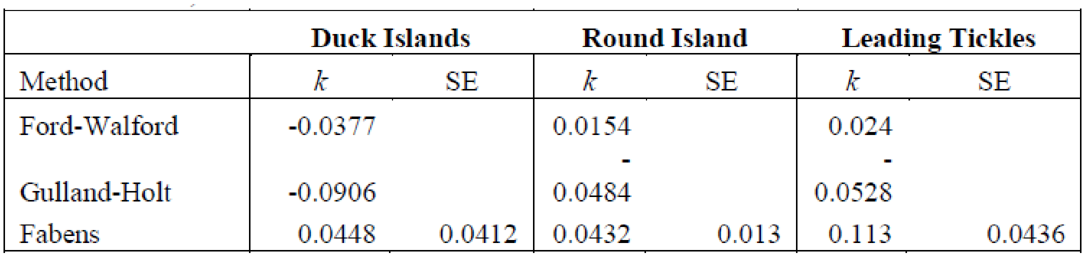
Data Analysis

All lobsters that did not grow 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. Von Bertalanffy growth parameters (growth rate (k), maximum length ($L\infty$), and time at hatch (t_o)) were calculated for each location using the three common methods, Ford-Walford, Gulland-Holt , and Fabens (for more mathematical detail, see Raper original MSc thesis).

Results

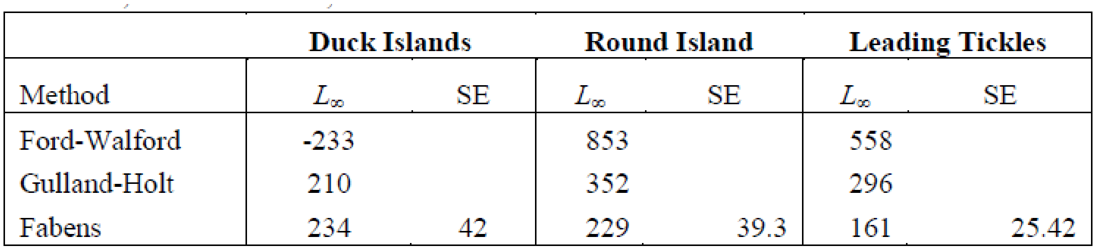
The results from each method are summarized in Tables 1, 2, & 3.

Table 1. Estimates of growth rate, *k*, for three sites in Newfoundland using Ford-Walford, Gulland-Holt, and Fabens methods.



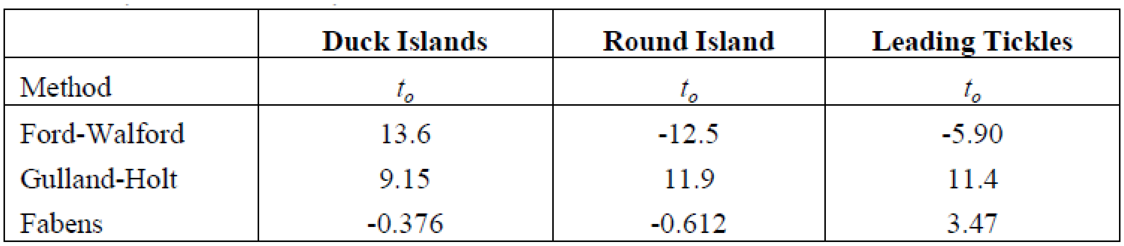
	Duck Islands		Round Island		Leading Tickles	
Method	*k*	SE	*k*	SE	*k*	SE
Ford-Walford	-0.0377		0.0154		0.024	
Gulland-Holt	-0.0906		-0.0484		-0.0528	
Fabens	0.0448	0.0412	0.0432	0.013	0.113	0.0436

Table 2. Estimates of maximum size, $L\infty$, 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 3. 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* range from 0.0488 yr-1 to -0.377yr-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 -233mm to 234mm, 229mm to 853mm, and 161mm to 558mm 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.

Discussion

Parameter values not only vary within sites, but are physiologically unrealistic in some cases. For instance, attempts at applying the Ford-Walford method gave negative values for $L\infty$ and *k*. After further examination, this result 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 $L\infty$ (-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. 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 $L\infty$ at all locations, but were still inconsistent with the other two methods. When parameters were estimated from the same data set, using different methodologies, results were not consistent. This means that results from studies using different methodologies cannot be reliably compared. As a result, parameter estimates from past tagging studies cannot be used to create a growth model for use throughout the lobster's entire geographic range, which is the primary objective of this study. Parameter estimates will have to be recalculated from original tagging data using one consistent method.

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Chapter 3: A Latitudinal Growth Model for American Lobster

Introduction

There are numerous growth models available in fisheries research to describe size-at-age. Growth models are mathematical equations that describe the way an organism grows as it ages. Different types of organisms grow in different ways as they age. The simplest model describes growth of species that do not approach a maximum size as they age, such as Pacific halibut (Quinn & Deriso, 1999). Other models (Ratkowsky, 1990) have been used to describe the growth of different types of organisms from mussels (Akiyama & Iwakuma, 2009) to cetaceans (Stolen et al, 2002). The von Bertalanffy growth is the most widely used growth model in fisheries research (Quinn & Deriso, 1999).

Growth model parameters, such as growth rate, or maximum size, have been shown to vary geographically in depending on the organism. 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 5^{o}C (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 rate and maximum size 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.

The von Bertalanffy growth model is the most widely used growth model to describe size-at-age in crustaceans, and its parameters (growth rate (k), maximum length ($L\infty$), and size at hatch (t_o)) 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 certain statistical analysis manageable and do not provide estimates of error associated with the growth parameters. Fabens' straightforward method involves determining the k and $L\infty$ parameters (from Eq.2.3b, Chapter 2) via non-linear least squares analysis. After extensive literature review, I have determined that, 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.

Methods

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.

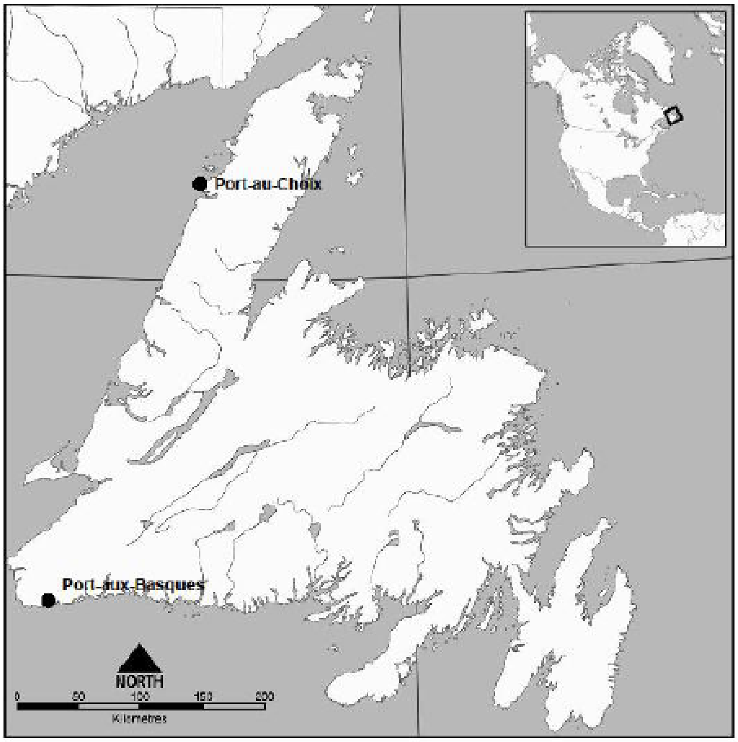


Figure 4. Location of field sites in Newfoundland.

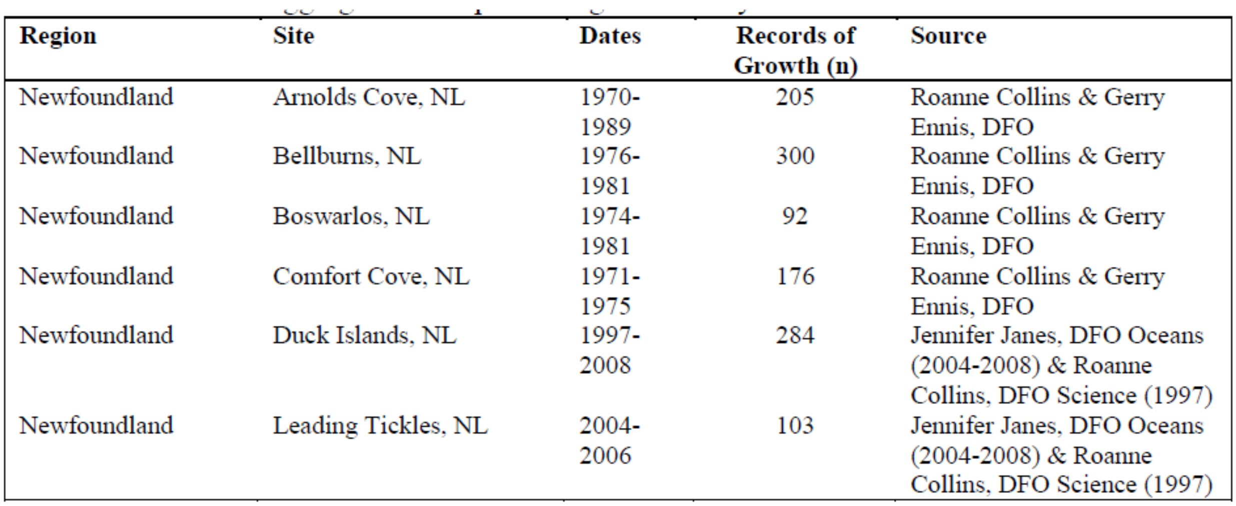
Lobsters were captured by professional fishermen using commercial lobster traps. Each lobster was tagged with a polyethylene streamer tag bearing a unique ID number. These tags are inserted through the dorsal musculature between the carapace and abdomen, and are usually retained through the molt. Detrimental 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 improve 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.

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 4. The locations of all tagging sites are shown in Figure 5.

Table 4. Historical tagging data compiled for growth analysis.



Region	Site	Dates	Records of Growth (n)	Source
Newfoundland	Arnolds Cove, NL	1970-1989	205	Roanne Collins & Gerry Ennis, DFO
Newfoundland	Bellburns, NL	1976-1981	300	Roanne Collins & Gerry Ennis, DFO
Newfoundland	Boswarlos, NL	1974-1981	92	Roanne Collins & Gerry Ennis, DFO
Newfoundland	Comfort Cove, NL	1971-1975	176	Roanne Collins & Gerry Ennis, DFO
Newfoundland	Duck Islands, NL	1997-2008	284	Jennifer Janes, DFO Oceans (2004-2008) & Roanne Collins, DFO Science (1997)
Newfoundland	Leading Tickles, NL	2004-2006	103	Jennifer Janes, DFO Oceans (2004-2008) & Roanne Collins, DFO Science (1997)

Table 5

continued.

Region	Site	Dates	Records of Growth (n)	Source
Newfoundland	Round Island, NL	1997-2008	275	Jennifer Janes, DFO Oceans (2004-2008) & Roanne Collins, DFO Science (1997)
Newfoundland	Shag Rocks, NL	1976-1984	1034	Roanne Collins, DFO
Newfoundland	St Chads, NL	1968-1976	157	Roanne Collins, DFO
Gulf of St Lawrence	Anse-Bleu, NB	1994-1997	55	Michel Comeau, DFO
Gulf of St Lawrence	Ballantynes Cove, NS	1986-1987	124	Michel Comeau, DFO
Gulf of St Lawrence	Baxter's Cove, NS	2000-2001	2	Michel Comeau, DFO
Gulf of St Lawrence	Beach Point, PE	1982-1983	51	Michel Comeau, DFO
Gulf of St Lawrence	Belledune, NB	1980-1983	563	Michel Comeau, DFO
Gulf of St Lawrence	Caraquet, NB	1993-1999	343	Michel Comeau, DFO
Gulf of St Lawrence	Egmont Bay, PE	1982-1983	248	Michel Comeau, DFO
Gulf of St Lawrence	Le Goulet, NB	1996-1998	7	Michel Comeau, DFO
Gulf of St Lawrence	Malpeque, PE	1989-1990	401	Michel Comeau, DFO
Gulf of St Lawrence	Margaree, NS	1984-1993	375	Michel Comeau, DFO
Gulf of St Lawrence	Miscou, NB	1994-1998	73	Michel Comeau, DFO
Gulf of St Lawrence	Pleasant Bay, NS	1988-1993	262	Michel Comeau, DFO
Gulf of St Lawrence	Port Hood, NS	1988-1993	867	Michel Comeau, DFO
Gulf of St Lawrence	Stonehaven, NB	1994-2000	52	Michel Comeau, DFO
Gulf of St Lawrence	Tracadie Bay, PE	1984-1985	11	Michel Comeau, DFO
Gulf of St Lawrence	Val Comeau, NB	1984-1987	9	Michel Comeau, DFO
Bay of Fundy	Alma, NB	1979-1986	251	Peter Lawton, DFO
Bay of Fundy	Chance Harbour, NB	1979-1986	793	Peter Lawton, DFO
Bay of Fundy	Delaps Cove, NS	1979-1983	17	Peter Lawton, DFO
Bay of Fundy	Flagg Cove, NB	1990-1993	6	Peter Lawton, DFO
Bay of Fundy	Little River Harbour, NS	1986-1988	6	Peter Lawton, DFO

Table 6 continued

Region	Site	Dates	Records of Growth (n)	Source
Bay of Fundy	McNutts Island, NS	1982-1987	72	Peter Lawton, DFO
Bay of Fundy	North Head, NB	1977-1988	739	Peter Lawton, DFO
Bay of Fundy	St Martins, NB	1979-1994	133	Peter Lawton, DFO
Bay of Fundy	Victoria Beach, NS	1993-1995	9	Peter Lawton, DFO
Nova Scotia (SW)	Port Maitland, NS	1978-1987	84	Peter Lawton, DFO
Nova Scotia (SW)	Lower Wedgeport, NS	1983-1986	29	Peter Lawton, DFO
Nova Scotia (SW)	Lower West Pubnico, NS	1984-1987	5	Peter Lawton, DFO
Nova Scotia (SW)	Clarks Harbour, NS	1979-1982	16	Peter Lawton, DFO
Maine	Boothbay Harbour, ME	1975-1976	25	Krouse, 1977
Maine	Jonesport, ME	1975-1976	23	Krouse, 1977
Maine	Kennebunkport, ME	1975-1977	10	Krouse, 1977
Cape Cod	Cape Cod Canal, MA	1979-1981	9	Robert Glenn, Massachusetts Division of Marine Fisheries (MADMF)
Cape Cod	Chatham, MA	1984-1989	3	Robert Glenn, MADMF
Cape Cod	Cole`s Hole, MA	1971-1974	15	Robert Glenn, MADMF
Cape Cod	Manomet, MA	1970-1977	240	Robert Glenn, MADMF
Cape Cod	Provincetown, MA	1969-1972	14	Robert Glenn, MADMF
Cape Cod	Rocky Point, MA	1971-1977	154	Robert Glenn, MADMF
Cape Cod	White Horse, MA	1973-1977	111	Robert Glenn, MADMF
Buzzards Bay	Lower Buzzards Bay, MA	1971-1972	7	Robert Glenn, MADMF
Buzzards Bay	North Ledge, MA	1969-1972	103	Robert Glenn, MADMF
Buzzards Bay	Upper Buzzards Bay, MA	1982-1984	24	Robert Glenn, MADMF

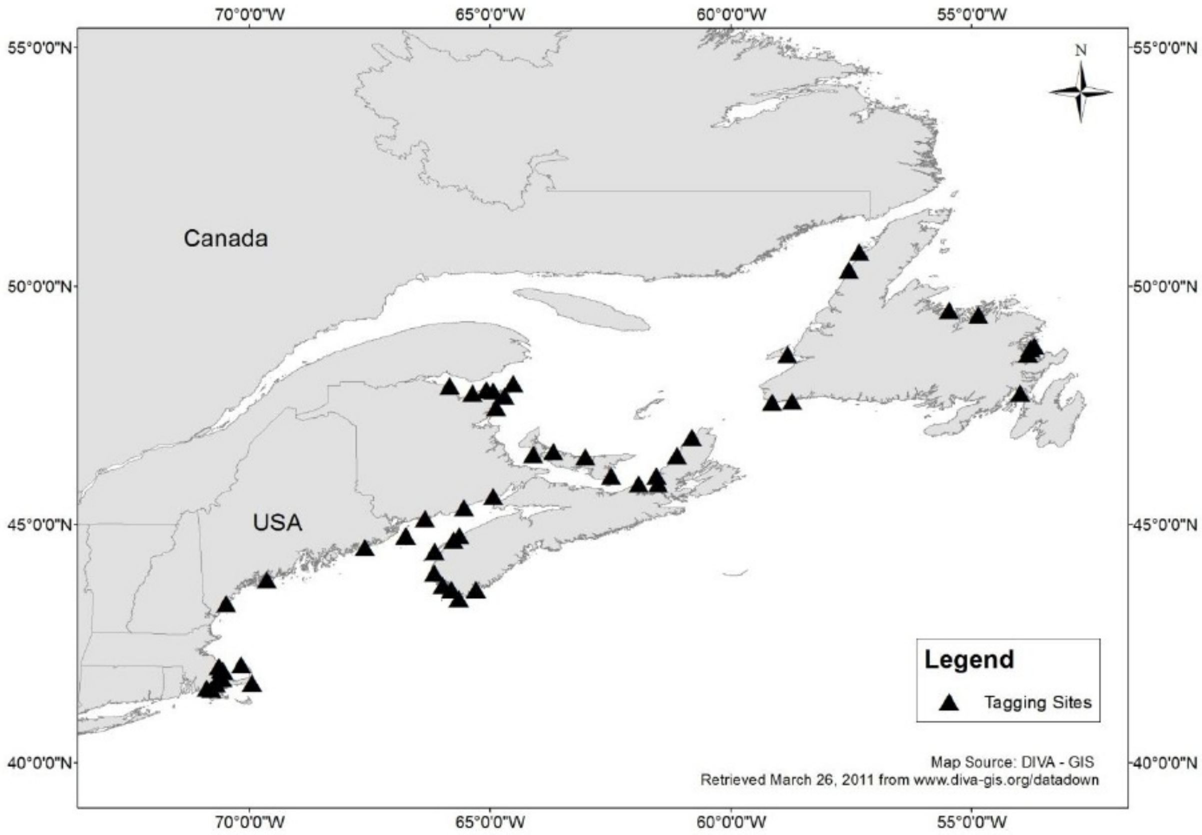


Figure 5. Tagging locations in the Northwest Atlantic.

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. This was to exclude lobsters that did not molt between captures, assuming a 3 mm measurement error based on lobsters that were captured and measured multiple times over the sampling period.

The von Bertalanffy parameters *k* (growth rate) and $L\infty$ (maximum size) were estimated for males and females at each site using statistical analysis on two versions of the Fabens tag-recapture equation and further analysis was done to determine which mathematical model was most appropriate for the data. Estimates of error and potential biases were considered as well. A general equation for estimating *k* (growth rate) from latitude was determined for males and females.

Results: 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.

Model Results and Discussion

After reviewing several models, the most reliable and biologically reasonable estimates of von Bertalanffy growth rates for lobster were established. These estimates of the growth parameter *k* demonstrated a negative relationship with latitude, or lower growth rates as you go north, 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.

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 (Fig. 6). 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 American lobster; according to Singer (2011), this region 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.

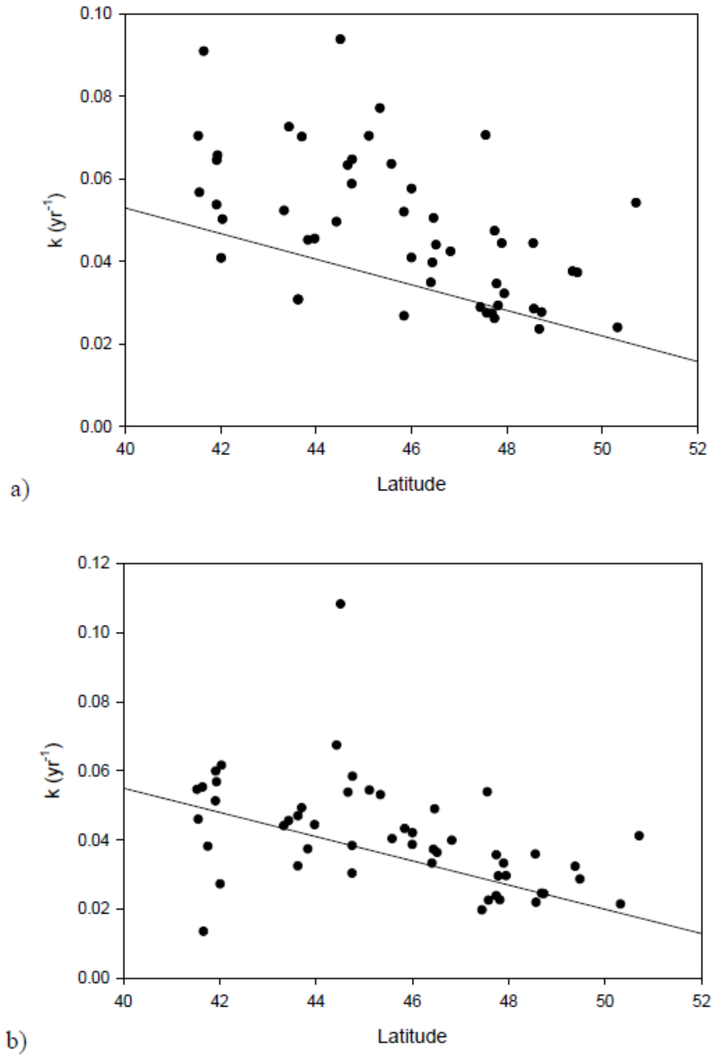


Figure 6. Relationship of von Bertalanffy growth parameter k to latitude for a) male and b) female American lobsters, with regression lines weighted by the inverse of the variance. r2= 0.21 and 0.41, respectively.

The latitudinal trend in growth rates can be obscured by the fact that size-at-maturity in lobsters decreases with increasing 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 large scatter around the regression lines in Figure 6, showing that all the data points don't fit the trend exactly, 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 they are close together. 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.

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: An Examination of Oceanographic Factors Affecting Growth Rates of American Lobster in the Northwest Atlantic.

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 parameters were estimated using the von Bertalanffy growth function modified for tag-recapture data (Fabens, 1965; Quinn & Deriso). For both male and female lobsters, growth rates were higher in more southerly latitudes and decreased as you move north.

In this chapter, I determine whether this south-north trend in growth rates can be explained by environmental variables. I will use 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.

Methods

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. 6).

GIS Analysis

Environmental data (depth, 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.

The computer mapping program ArcGIS® was used for all spatial analyses. 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 outlined 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 7. Each tagging location was assigned a unique identification number.

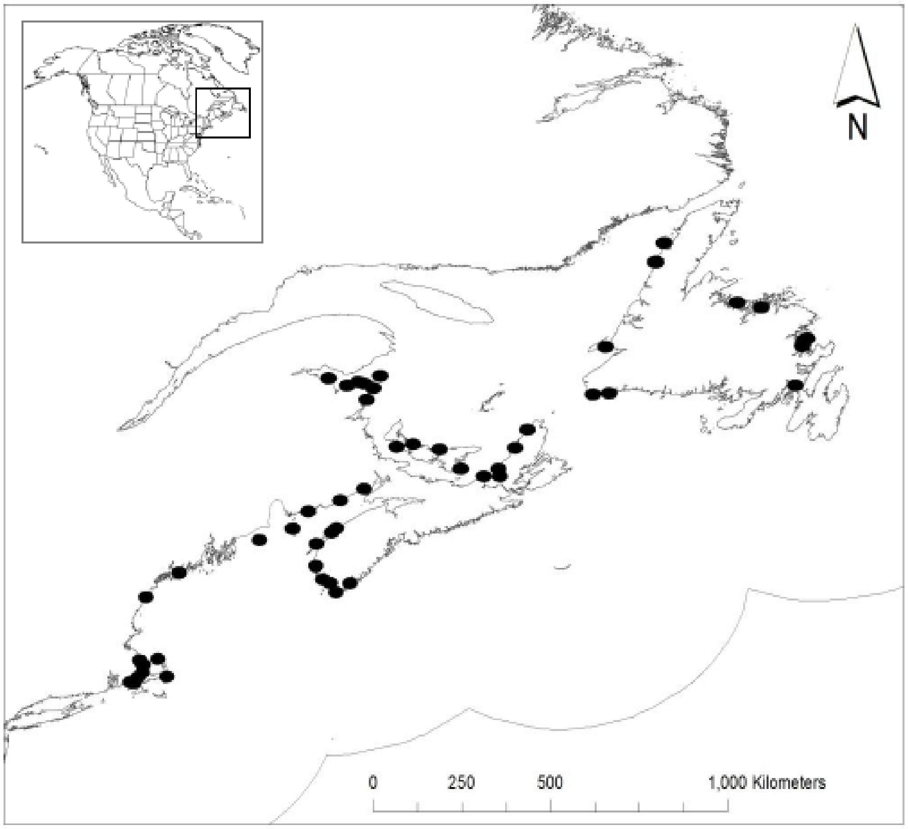

Figure 7. Tag site locations with 15 km buffer zones.

The map of tagging sites was cropped to include areas in the appropriate depth (cutting out any areas of the 15km buffer zone that would fall on land, Fig. 8). The maps of temperature and salinity were used to determine the average bottom temperature and salinity associated with each tagging site.

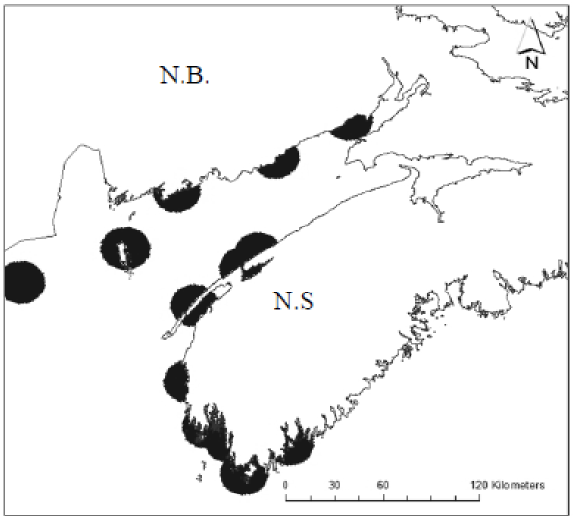

Figure 8. The Bay of Fundy showing how sites that have been clipped to eliminate locations that would fall on land.

Statistical Analysis

Two different statistical analyses were performed. The first was used to look for relationships between growth rates and explanatory variables including latitude, depth, temperature, and salinity. The second was used to look for correlation among explanatory variables latitude, depth, temperature, and salinity.

Results

The relationships between growth rates of males and females and environmental variables are shown graphically in Figures 9 and 10 respectively.

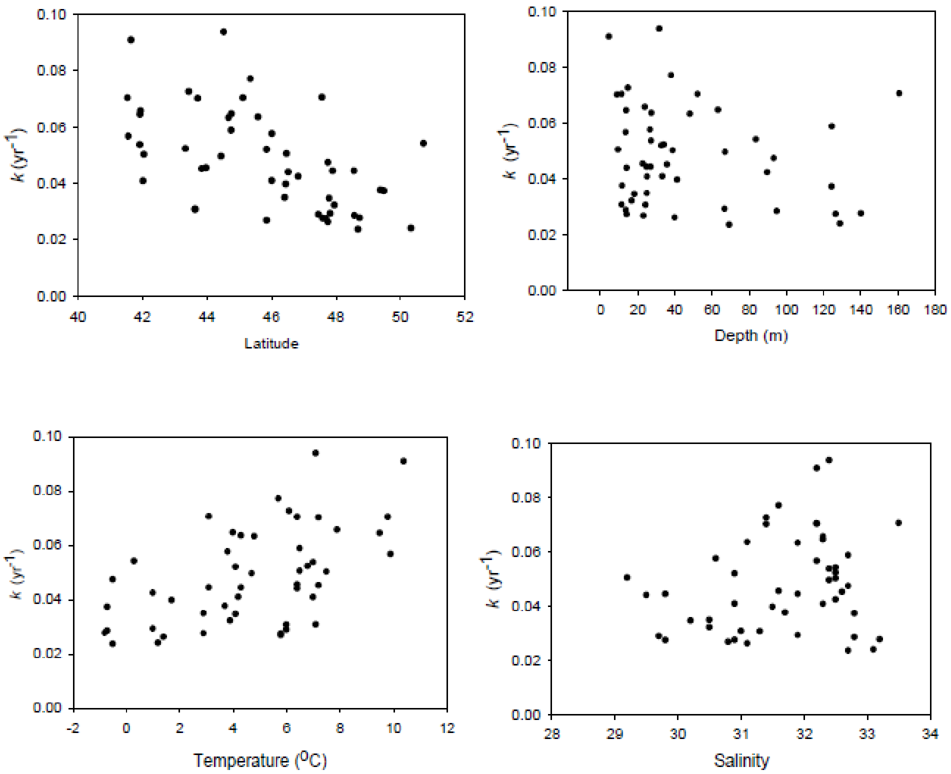

Figure 9. von Bertalanffy growth parameter k (growth rate), in relation to latitude, depth, temperature, and salinity, for male American lobsters.

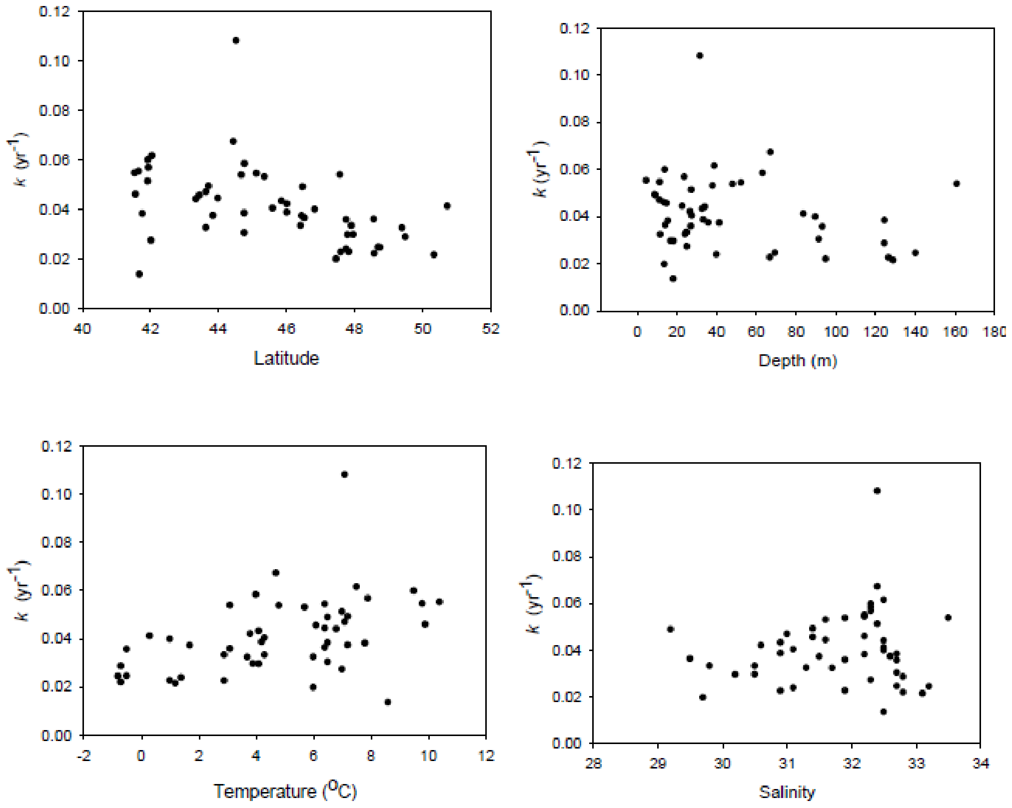

Figure 10. von Bertalanffy growth parameter k (growth rate), in relation to latitude, depth, temperature, and salinity, for female American lobsters.

The first statistical analysis produced no significant relationships between growth rates, latitude, depth, temperature, or salinity. Significant correlations 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) were found.

The second statistical analysis, done without incorporating *Latitude*, showed that the von Bertalanffy growth rate significantly depends on temperature. No other significant relationships were found.

Discussion

Neither latitude, depth, temperature, nor salinity had a significant effect on lobster growth rates when accounting for the other variables (first statistical analysis). 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 (second statistical analysis), 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 the first statistical analysis, 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 mathematical 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 of very high salinities which are rarely reached on the bottom where lobsters live. There are other factors, however, that may play a part in growth rates, such as substrate composition (*e.g*. grain size). Future examination could include 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 28 km apart. 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 environmental data provide only yearly averages. This would not affect a stable variable like depth, but it could influence results of fluctuating 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 depth and salinity are held constant. 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 the decrease in growth rates with as you go farther north are largely caused by the corresponding decrease in temperature with increasing latitude throughout the range of the species.

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Chapter 5: Conclusion

This thesis presents an examination of methods for estimating growth rates in 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. 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 largely 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, and indicates 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.