

GROWTH PARAMETERIZATION FOR BLUE CRABS, *CALLINECTES SAPIDUS*,
OF GALVESTON BAY, TEXAS

by

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ABSTRACT

GROWTH PARAMETERIZATION FOR BLUE CRABS, *CALLINECTES SAPIDUS*,
OF GALVESTON BAY, TEXAS

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The blue crab (*Callinectes sapidus*) is both ecologically and economically important to the coastal states of the Atlantic and Gulf of Mexico. Although most of blue crab life history has been described, there is still a lack of data concerning crabs' growth parameters and patterns in the wild, making it harder to obtain an overall understanding of their population dynamics. Because blue crabs lack hard body parts commonly used to estimate age, such as otoliths and scales, they are difficult to age. Consequently, an age-based growth model cannot be calculated. Instead, incorporating growth increments into the growth model provides a better estimation of population growth parameters. Using micro Coded Wire Tags (CWT), I internally tagged juvenile blue crabs larger than 15 mm for 20 months starting January 2012. I also documented the growth of blue crabs that were kept in enclosures. Using dates and size at mark and recapture events and weekly field enclosure visits, growth parameters were compared using variations of the Von Bertalanffy model, including Fabens and Appeldoorn models. The comparison of three

different Fabens models and two different Appeldoorn models indicated that the seasonal Appeldoorn model better characterizes the growth of blue crabs in enclosures. The growth parameters L_{∞} and k for the Appeldoorn model, using Excel and Solver to minimize the sum of square errors, yielded the best fit of all models and were estimated to 204.9 and 1.30 respectively. Growth per molt (GPM), the physiological zero temperature (T_{\min}), and intermolt period (IP), which are used in discontinuous crustacean growth models, were also parameterized for enclosure blue crabs and estimated to $122 \% \pm 6.8$, 6.1 ± 0.05 °C, and 568 ± 31 degree-days respectively. Growth parameters for blue crabs that were marked and recaptured could not be estimated due to lack of growth data for crabs larger than 50 mm carapace width. However, the use of CWT showed to be an effective and promising way to study growth of blue crabs in the wild in future studies.

TABLE OF CONTENTS

Chapter	Page
I. Introduction	1
Blue Crab’s Life History and the Gulf of Mexico	1
Blue Crab Growth and Ageing	3
Fisheries Status and Management Needs.....	6
Growth Models	7
Project Significance	13
Project Objectives	13
II. Methods.....	14
Area of Study	14
Environmental Data	16
Tagging	17
Cage Study	19
Mark-Recapture Study	20
Data Analysis	22
Model Development.....	22
III. Results.....	24
Environmental Data	24
Field Enclosure Study	25
Statistical Analysis.....	26
Growth Models	37

Mark-Recapture Study	51
Statistical Analysis.....	51
Growth Models	56
IV. Discussion.....	60
V. Future Recommendations	68
VI. References.....	69

LIST OF TABLES

Table 1: Molting frequency of blue crabs in enclosures.....	25
Table 2: ANOVA (GLM, Minitab) results for growth per molt (GPM) of <i>Callinectes</i> <i>sapidus</i> used in cage study.....	27
Table 3: Regression output (Minitab) for growth per molt (GPM) of <i>Callinectes</i> <i>sapidus</i> used in cage study as function of initial size and temperature.....	29
Table 4: Analysis of variance (ANOVA) of intermolt period (IMP) as a function of sex, feeding, and missing limbs for <i>Callinectes</i> <i>sapidus</i> kept in field enclosures.	31
Table 5: Analysis of variance (ANOVA) results on intermolt period (IMP) in degree-days of four different size classes of <i>Callinectes</i> <i>sapidus</i> kept in enclosures that presented no limb losses.	34
Table 6: Tukey's 95% simultaneous confidence interval post-hoc test for analysis of variance (ANOVA) on intermolt period (IMP) in degree-days of four size classes of <i>Callinectes</i> <i>sapidus</i> kept in enclosures that presented no limb losses.....	34
Table 7: Analysis of variance (ANOVA, Minitab) results for log-transformed growth rate of <i>Callinectes</i> <i>sapidus</i> used in cage study.....	36
Table 8: Calculated model parameters, sum of square residuals (SS), R^2 and adjusted Aikike Information Criterion (AICc) for Fabens constant variance model, Fabens inverse linear variance model, Fabens power law variance model, Appeldoorn FISAT model, and Appeldoorn Solver model.	50

Table 9: General linear model (GLM, Minitab) results for log-transformed growth rate of <i>Callinectes sapidus</i> from mark-recapture study	52
Table 10: Regression output (Minitab) for mark-recapture growth rate of <i>Callinectes sapidus</i> as function of temperature and initial carapace width.	53
Table 11: Different estimates of the von Bertalanfy growth function (VBGF) parameters for <i>Callinectes sapidus</i>	65

LIST OF FIGURES

Figure 1: Moses Lake in relation to Galveston Bay, Texas.	15
Figure 2: Moses Lake.	15
Figure 3: Areas 1 and 2 within Moses Lake.	16
Figure 4: Sequential pre-cut coded wire tags (CWT).	17
Figure 5: Tagging a blue crab with a CWT using single-shot injector.	18
Figure 6: Minnow trap used to encage <i>Callinectes sapidus</i> in field enclosure study.	19
Figure 7: Sites 1-5 where collapsible crab pots were kept for mark-recapture study.	21
Figure 8: Daily average water temperature of study sites between January 1st, 2012 and July 1st, 2013.	24
Figure 9: Normal probability plot of GPM of crabs kept in enclosures	27
Figure 10: Growth per molt (GPM) as a function of limb losses for <i>Callinectes sapidus</i> kept in enclosures.	28
Figure 11: Growth per molt (GPM) as a function of pre-molt carapace width for <i>Callinectes sapidus</i> kept in enclosures.	29
Figure 12: Growth per molt (GPM) as a function of temperature for <i>Callinectes sapidus</i> kept in enclosures.	30
Figure 13: (a) intermolt period (IMP) as function of temperature ($R^2=17.5\%$, $P=0.00$) and (b) inverse intermolt period ($1/IMP$) of <i>Callinectes sapidus</i> kept in enclosures that presented no limb losses.	32

Figure 14: Scatter plot of intermolt period in degree-days as function of initial carapace size for <i>Callinectes sapidus</i> kept in enclosures that presented no limb losses.	33
Figure 15: Normal probability plot of growth rates for <i>Callinectes sapidus</i> kept in enclosures.....	35
Figure 16: Normal probability plot of log-transformed growth rates for <i>Callinectes sapidus</i> kept in enclosures.	35
Figure 17: Scatter plot of growth rate of <i>Callinectes sapidus</i> as a function of limb losses.	37
Figure 18: Gulland-Holt plot (Minitab) for <i>Callinectes sapidus</i> kept in enclosures that exhibited no limb losses.....	38
Figure 19: Forced Gulland and Holt plot (FISAT II) for <i>Callinectes sapidus</i> kept in enclosures that exhibited no limb losses using fixed L_{∞} value of 175.9mm.	39
Figure 20: Gulland-Holt plot of residuals for <i>Callinectes sapidus</i> kept in enclosures that exhibited no limb losses.....	40
Figure 21: Fabens constant variance model results for <i>Callinectes sapidus</i> kept in enclosures that exhibited no limb losses.....	41
Figure 22: Residual plot of Fabens constant variance model results for <i>Callinectes sapidus</i> kept in enclosures that exhibited no limb losses.....	42
Figure 23: Fabens inverse linear model results for <i>Callinectes sapidus</i> kept in enclosures that presented no limb losses.	43
Figure 24: Residual plot of Fabens inverse linear model results for <i>Callinectes sapidus</i> kept in enclosures that presented no limb losses.	44

Figure 25: Fabens power model results for <i>Callinectes sapidus</i> kept in enclosures that exhibited no limb losses.....	45
Figure 26: Residual plot of Fabens power model results for <i>Callinectes sapidus</i> kept in enclosures that presented no limb losses.	46
Figure 27: Appeldoorn's growth curve (FISAT II) for <i>Callinectes sapidus</i> kept in enclosures that were not missing any limbs.....	47
Figure 28: Residual plot of Appeldoorn's model using FISAT II for <i>Callinectes sapidus</i> kept in enclosures that presented no limb losses.	48
Figure 29: Appeldoorn's growth curve calculated using Excel and Solver for <i>Callinectes sapidus</i> kept in enclosures that were not missing any limbs.	49
Figure 30: Residual plot of Appeldoorn's model using Excel and Solver for <i>Callinectes sapidus</i> kept in enclosures that presented no limb losses.	50
Figure 31: Normal probability plot of growth rate for <i>Callinectes sapidus</i> from mark-recapture study.....	51
Figure 32: Normal probability plot of log-transformed growth rate for <i>Callinectes sapidus</i> from mark-recapture study.....	52
Figure 33: Linear regression of growth rate as a function of initial size.	54
Figure 34: Linear regression of growth rate as a function of average temperature.	55
Figure 35: Gulland-Holt plot for <i>Callinectes sapidus</i> from mark-recapture study data that had no limb loss.	56
Figure 36: Forced Gulland-Holt plot of <i>Callinectes sapidus</i> from mark recapture study using a fixed L_{∞} value of 175.9 mm..	57

Figure 37: Forced Gulland-Holt plot of residuals for *Callinectes sapidus* from mark-recapture study..... 58

INTRODUCTION

Blue Crab's Life History and the Gulf of Mexico

The blue crab, *Callinectes sapidus*, is an epibenthic decapod crustacean belonging to the family Portunidae, the swimming crabs. Blue crabs are found in estuarine, freshwater and coastal environments from Nova Scotia and northern Massachusetts to northern Argentina (Williams 1974). Blue crabs have occasionally been captured in European and Mediterranean waters (Lewinsohn and Holthuis 1964). In the United States, blue crabs are mostly found in estuaries on the East Coast and the Gulf of Mexico. Most of the known life history of blue crabs is based on studies performed in the Chesapeake Bay. In contrast, very little is known about the blue crab's life history in the Gulf of Mexico (Guillory et al. 2001). Even less is known about blue crabs in Texas (Sutton et al. 2007). However, the many studies performed in the Chesapeake Bay can be used, when combined with data from the Gulf of Mexico, to predict the blue crab's life history and behavior in the Gulf of Mexico.

Blue crab spawning occurs during spring, summer, and fall seasons in the Gulf of Mexico (Daugherty Jr 1950; Perry 1975). Occasional spawning during mild winters has been observed in Louisiana and Texas waters by Adkins (1972) and Daugherty (1950). Spawning occurs within approximately two months after mating. Females mate right after undergoing terminal molt while they are still in the soft shell stage. The male protects the inseminated female until shell hardens, a process that takes two to four days (Churchill 1919). Mating usually occurs in shallow creeks of low salinity (Van Engel 1958).

Females carry eggs externally attached to the pleopod (abdomen) region by fine setae, forming an orange structure known as the sponge or berry, which contains up to two million eggs (Churchill 1919). As yolk is absorbed, the eggs change coloration, becoming darker, almost black (Sandoz and Rogers 1944). Sponge bearing females move to the lower estuary for spawning because blue crab hatchings are known to be sensitivity to low salinities (Millikin and Williams 1984; Sandoz and Rogers 1944).

The ideal salinity for successful hatching is between 18 to 29 parts per thousand (p.p.t.) (Sandoz and Rogers 1944). Eggs hatch within 2 weeks and blue crabs enter the first larval stage, zoëa, which morphologically resembles a shrimp. In the Chesapeake Bay, the zoëa stage lasts approximately a month and within this time the zoëa will molt and slowly transform through seven zoeal stages before transforming into megalopa larva (Costlow and Bookhout 1959). When reaching the megalopa stage, crabs morphologically resemble a miniature scorpion. Blue crabs enter estuarine systems as megalopae larvae upon reaching optimal sheltered areas for development. Once in the estuary, the megalopa molts and acquires the form of a juvenile crab (Van Engel 1958). The megalopa stage is short, lasting less than a month. Very little is known about the timing and development of larval stages of blue crabs in the Gulf of Mexico (Perry and McIlwain 1986). Megalopae of the genus *Callinectes* have been found throughout the year in parts of the Mississippi Sound and coastal Texas (Daugherty Jr 1950; Perry 1975).

Juveniles can be found throughout the year in the Gulf of Mexico, while in the Chesapeake Bay they are commonly found between late spring and early fall (Perry 1975; Stuck and Perry 1982; Van Engel 1958). Salinity appears to be a factor when it

comes to juvenile distribution, with higher numbers of juveniles being found in brackish areas of low and intermediate salinity (Stuck and Perry 1982). Juveniles tend to gradually migrate to low salinity and shallow waters until they reach maturity and are ready to mate (Fischler and Walburg 1962). Once water temperature starts increasing, development and molt rates of juveniles also increase until they reach maturity (Brylawski and Miller 2006). Very little research has been done on the combined effects of temperature and salinity on juvenile crabs in the Gulf of Mexico.

Female and male blue crabs reach maturity after about 18 to 20 molts. Females stop growing after undergoing a terminal molt, which is followed by mating. Females will only mate once in their lifetime. Males, on the other hand, will molt up to 5 times after reaching maturity and can mate multiple times (Van Engel 1958). In the Gulf of Mexico, females with mature ovaries can be found year around and egg bearing females are more common during summer months (Perry and McIlwain 1986).

Blue Crab Growth and Ageing

Blue crab growth can only be achieved through molting. Before molting, the blue crab will develop a new dark, soft shell underneath the existing hard shell. The molting process of blue crabs, as well as many other crustaceans and arthropods, is characterized by four phases: metecdysis, anecdysis, proecdysis, and ecdysis (Chan et al. 1988; Drach 1939). Metecdysis includes the soft shell period (stage A) and the paper thin period (stage B), both occurring right after molting. During metecdysis, the crab absorbs large amounts of water from the environment, helping it expand its size (Van Engel 1958). The

anecdysis or inter-molt stage (stage C) is characterized by extreme food consumption, which promotes tissue growth. The proecdysis phase is the last phase before molting, leading to many physiological and morphological changes. The proecdysis phase is divided into five stages: D0, D1, D2, D3 and D4. These stages can be identified by carefully observing different colorations on the fifth pereopod of the blue crab. Finally, the last phase, ecdysis, is characterized by the complete shedding of the old carapace, allowing crab's expansion (Chan et al. 1988; Drach 1939). In preparation for and during ecdysis, the blue crab ceases all its activities, including feeding, for about three to four days (Van Engel 1958).

Juveniles tend to molt more frequently than adults. Churchill (1919) and Robertson (1938) observed that, under laboratory conditions, crabs under 5 mm molt every 3 to 5 days, while crabs between 12 mm to 25 mm and larger than 101 mm carapace width (CW) will molt every 10 to 15 days and 20 to 50 days respectively. Van Engel (1958) suggested that crabs stop molting after achieving a fixed number of molts (18 to 20 molts). Many lab experiments have been performed to estimate growth rates of blue crabs, but very little is known about their growth in the wild (Leffler 1972; Miller and Smith 2003; Sulkin 1975).

Blue crab growth is known to be temperature dependent. Leffler (1972) found that, under lab conditions, the number of molts increased when temperature increased from 13°C to 34°C. Growth rates were highest in temperature between 20°C and 27°C (Leffler 1972). Leffler (1972) also found that growth almost ceased when crabs were exposed to temperatures below 13°C. Winget et al. (1976), using a recirculating culture system, found that percent growth per molt increased at 20°C. The idea of a fixed number

of molts is also defended by Leffler (1972), who believed that because of this fixed number of molts, blue crabs from different regions and different seasonal temperatures reach maturity at different sizes. Blue crabs of 22 mm CW will molt an average of 5 times at 15°C to achieve 60 mm, while at 27°C and 34°C it would take an average of 6 and 7 molts respectively to achieve same size (Leffler 1972). Tagartz (1968), on the other hand, found that growth per molt did not change significantly between summer and winter months, suggesting that temperature does not influence growth per molt in the wild, within the range of conditions observed (13.8 to 32.1°C; 7.5 to 25.8 p.p.t.).

Salinity is another parameter that may influence blue crab growth. As already mentioned, during ecdysis, large amounts of water are consumed by the blue crab, contributing to its extension. Therefore, Van Engel theorized that lower salinity water would be more easily absorbed by crabs in contrast to higher salinities, resulting in larger crabs in the upper estuary (Van Engel 1958). However, Tagartz (1968) and Guering and Stickle (1997) found that growth per molt and molt rates were not directly influenced by salinity, within the range of test conditions.

Limb losses and food availability can also influence growth and molt rates. Under lab conditions, Smith (1990) determined that one limb loss did not significantly affect CW growth increment, but two or more losses decreased growth increment after molt. As with other organism, blue crabs tend to grow more when more food is available (Seitz et al. 2005). Therefore, food availability and their position on the food chain could impact growth rates.

Age determination of blue crabs is difficult to study due to the lack of hard or ossified body parts such as otoliths, scales, or teeth which possess daily or annual growth rings. The only hard part a blue crab has is its carapace, which is completely shed and discarded after molting. Lipofuscin, also known as age pigments, have been used for ageing many crustaceans, such as lobster, crayfish, and prawn (Belchier et al. 1998; Belchier et al. 1994; Sheehy et al. 1995). Ju et al (1999; 2001) used lipofuscin accumulation levels from nervous tissues of blue crabs for age determination and suggested that their methods is a reliable tool to age blue crabs in the wild. However, the reliability of this model has been questioned due to problems associated with the use of lipofuscin including errors in the performance of past experiments (Sheehy 2008).

Fisheries Status and Management Needs

Blue crabs support the largest crab fishery in the United States (Hill et al. 1989). In 2011, the annual commercial blue crab landings in the United States totaled a little over 196 million pounds, with 28% of those coming from Gulf States (National Marine Fisheries Services). In Texas, blue crab annual landings rank third behind shrimp and oyster landings. The average commercial landings in Texas, between the years of 2007 and 2010, were 3.1 million pounds crabs, worth a total of 2.7 million dollars. An observed decline in the blue crab harvest in the past 30 years suggests a decline in the blue crab population in Texas. In 2005, only 3.1 million pounds of blue crabs were landed, a low number when compared with the historic average of 6.3 million/year and the peak landing observed in 1987 (11.9 million) (Sutton and Wagner 2007). In 2006, the

lowest historical annual commercial landing of 2.0 million pounds was recorded (Sutton and Wagner 2007).

Stock assessments to better manage any given species must take into consideration every factor that might influence their life history, including habitat preference, diet, reproduction, recruiting, natural mortality, ageing, growth rates, and many other factors. Therefore, the estimation of blue crab's growth parameters is essential for development of population models to better understanding their population dynamics and better manage this species (Miller and Smith 2003). As already mentioned, an accurate growth model is unavailable for blue crabs, which can result in erroneous assumptions during stock assessments which can ultimately lead to flawed management recommendations.

Growth Models

One of the most commonly used growth models in fishery biology is the Von Bertalanffy Growth Function (VBGF, equation 1) developed by von Bertalanffy (1938). The VBGF is a continuous growth curve of length at age. The parameters obtained from the function (L_{∞} , k , and t_0) are important parameters used on stock assessment models. The L_{∞} term represents the asymptotic average maximum body length of a certain individual, K the growth rate coefficient, and t_0 is the age at length zero.

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

Although the VBGF has been used in the past to model growth of blue crabs (Pellegrin et al. 2001; Rothschild et al. 1992; Rugolo et al. 1998), there are many issues associated with the use of this function. First, the function does not take into consideration the sex specific growth characteristics of blue crabs, in which females stop growing after undergoing terminal molt, usually within their first year of life in the Gulf of Mexico, while males continue growing (Pellegrin et al. 2001). Second, length at age is unknown since there are no reliable ways to age blue crabs thus far. Finally, the VBGF models continuous growth, while blue crabs grow in a discontinuous manner.

The discontinuous growth model, also called the molt-process model, uses growth per molt (GPM) as the dependent variable in response to intermolt period (IMP) as the independent variable to describe growth in a step manner (Hiatt 1948). The molt-process model has been used to model growth of many crustaceans (McCaughran and Powell 1977; Wainwright and Armstrong 1993). GPM is easy to obtain by getting a measurement before and after molting. However, modeling IMP can become problematic, especially during field studies, where time elapsed and temperature are harder to monitor.

Smith (1997) described a discontinuous growth model for crustaceans that also uses GPM, but IMP has been modified to accommodate the fact that temperature will influence the time between molts. In this method, IMP is no longer a chronological measurement of time, but a physiological measurement of time in the form of degree-days (dd) and is relabeled as $IMP(dd)$. IMP in degree-days is calculated by using equation 2 below

$$IMP(dd) = \sum T_j^* - T_{min}$$

Where,

(2)

$$T_j^* = \begin{cases} \bar{T}_j & , \quad T_{min} \leq \bar{T}_j < T_{max} \\ T_{max} & , \quad \bar{T}_j \geq T_{max} \end{cases}$$

\bar{T}_j is the daily average temperature over j days, while T_{min} and T_{max} are the minimum and maximum temperature threshold that a species can withstand. T_{min} can be calculated by obtaining the x-intercept of the inverse IP in days (d) as a function of temperature, for that reason T_{min} is considered to be a species “physiological zero”. Brylawski and Miller (2006) used Smith’s method to parameterize the discontinuous growth of blue crabs under lab and field enclosed conditions in the Chesapeake Bay and obtained a value of 10.8°C for T_{min} . In contrast, Smith (1997), estimated T_{min} to be 9.8°C, for blue crabs in the Chesapeake Bay.

Eggleston et al. (2004) used a discontinuous growth model application for blue crabs in North Carolina without converting IP to degree-days. Their study compared the GPM and IP of blue crabs reared in laboratory and field tagged crabs and found that GPM was not significantly different for laboratory reared and field tagged crabs. However, IP was smaller for laboratory reared crabs, suggesting that under laboratory settings crabs grew at a faster pace than crabs in the wild. Eggleston et al (2004) also compared pattern of their discontinuous blue crab growth model with a VBGF curve and

concluded that the continuous model (VBGF) can be satisfactorily used to fit the discontinuous growth of blue crabs.

To calculate VBGF parameters, one must first enter initial estimates for these parameters to initiate the search algorithm. The best way to obtain preliminary estimates is to use the Gulland and Holt plot (Gulland and Holt 1959). The plot is a simple linear regression as described on equation 3

$$\frac{\Delta L}{\Delta T} = a + b\bar{L} \quad (3)$$

, where ΔL and ΔT are the change in length and time, respectively, and \bar{L} is the average of initial and final length. Since most individuals' growth rates decline with increase in length, the equation will have negative slope. The slope (-b) is used as an initial estimate for the parameter K in the VBGF. L_{∞} is the x-intercept of the equation.

The VBGF has been modified by multiple authors to better accommodate mark-recapture data and seasonality. Fabens (1956) modified the VBGF so that mark-recapture data can be used without depending on ageing individuals. This model is preferred over the Munro (1982) method since it is known to yield more accurate parameter estimates (Sundberg 1984). The Fabens model is illustrated in equation 4

$$\Delta L = (L_{\infty} - L_t)(1 - e^{-k\Delta t}) \quad (4)$$

, where L_{∞} and k are the same VBGF parameters described in equation 1, ΔL is the change in length for an individual of initial length L_t over a Δt period. It should be noted

that in this model, the parameter t_0 cannot be estimated. Fabens method is a great tool to model growth, but fails to consider that there will be variation in the growth of individuals (Sainsbury 1980). Variance of residuals in respect to the expected ΔL appears to increase at larger ΔL values (Haddon 2010). Francis (1988) developed a maximum likelihood approach for the Fabens model to account for this variance. Francis (1988) suggested that growth's variance could follow normal (constant), inverse linear, log-normal or power trends.

Seasonality influences the growth of fish and aquatic invertebrates even when inhabiting the tropics (Longhurst and Pauly 1987). For that reason, many authors have modified the VBGF to account for seasonal growth (Appeldoorn 1987; Pauly and Gaschutz 1979; Pitcher and MacDonald 1973; Soriano and Pauly 1989). Appeldoorn (1987), in particular, modified Pauly and Gaschutz (1979) seasonal growth equation to be used with mark-recapture data. The equation was modified to the following

$$l_d = L_\infty \left(1 - \frac{l_t}{L_\infty}\right) \left\{1 - \exp \left[- \left[Kd - \frac{CK}{\pi} \sin(-\pi d) \cos \pi(2t^* + d - 2t_s^*) \right] \right] \right\} \quad (5)$$

The input variables for this model are l_t , l_d , d , and t^* . l_t is length at time t , l_d is length at time $t+d$, d is change in time, and t^* is time t as a fraction of the year from January 1st.

The VBGF parameters, L_∞ and K , and the additional parameters C and t_s^* are estimated by minimizing the sum of squares between predicted and observed values of l_d . The additional parameters C and t_s^* represent the magnitude of growth oscillation and fraction of time in relation to January 1st when maximum growth rates occur, respectively.

The VBGF is just one of the many growth curves used to explain growth pattern of individuals. As stated earlier the VBGF model is preferred because it provides estimates of the parameters K , L_{∞} and sometimes t_0 , which are needed for multiple population models.

Project Significance

The stock assessment process is essential for better understanding and managing fisheries. Estimation of growth patterns through model fitting and the computation of associated parameters (k and L_{∞}) are important when creating computer models to estimate a species' population dynamics, and can create limitations to stock assessment when missing.

Growth parameters for blue crabs in Texas are yet to be estimated. This project has the intent to provide estimates of growth parameter for blue crabs in Texas, which can then be used in future stock assessment models.

Project Objectives

1. Establish methodology of using coded-wire tags in the study blue crab growth in the wild.
2. Estimate growth parameters for blue crabs in Galveston Bay, Texas both in the wild and in field enclosures.
3. Identify the importance of temperature and seasonality on growth of blue crabs in Galveston Bay, Texas.
4. Compare growth curves and parameters between crabs in the wild and retained inside field enclosures.

METHODS

Area of Study

Galveston Bay (Figure 1) is an estuary measuring approximately 1,600 Km², located on the south-east coast of Texas. Galveston Bay is connected to the Gulf of Mexico and receives the majority of freshwater inflows from the San Jacinto and Trinity Rivers. Within Galveston Bay, Moses Lake was the site selected for this study due to its somewhat enclosed geography which facilitated mark recapture studies.

In 1954, a seawall was constructed in Moses Lake as a protection measurement against hurricanes (Figure 2) and in 1966, a tidal control gate was built at Miller's Pointe to control the flow in and out of Moses Lake ("Moses Lake", Handbook of Texas Online, accessed on September 10, 2014). Therefore, the only way blue crabs can enter this water body from Galveston Bay is through the tidal control gate pass into Galveston Bay. Moses Lake receives freshwater inflow upstream from Moses Bayou.

I selected two smaller areas in Moses Lake to conduct the study. The first area (area 1) is a canal and located adjacent to a manmade seawall and it is shown on Figure 3. The second area (area 2) is a more natural saltmarsh that connects to area 1 through a narrow channel (Figure 3).



Figure 1: Moses Lake in relation to Galveston Bay, Texas. Figure courtesy of Google Earth.



Figure 2: Moses Lake. Figure courtesy of Google Earth.



Figure 3: Areas 1 and 2 within Moses Lake. Figure courtesy of Google Earth.

Environmental Data

Water temperature, salinity, and dissolved oxygen (D.O.) were collected with a Stevens Greenspan Multi-Parameter Data Logger (Model CS304) with battery pack during the years of 2011 and 2012. In 2013, we switched to using Onset HOBO Conductivity Data Logger (U24-001) and Onset HOBO Dissolved Oxygen Logger (U26-001), both which also collect water temperature readings. Values collected from data loggers were checked and corrected if necessary against point measurements collected in the field with a multi-parameter YSI meter. Any missing temperature values were estimated using scaled values of nearby independently collected Hydrolab DataSonde operated by the Texas Water Development (unpublished data).

Tagging

Due to molting, externally tagging a crab for growth analysis is not an option. Internal tags, such as microwire or coded wire tags (CWTs) and visual implant fluorescent elastomer (VIFE) tags, are preferred for marking crustaceans. Although VIFE tags are cheaper and yield lower immediate mortality than CWTs, the latter are preferred due to tag efficiency and longer retention rates (Davis et al. 2004). For those reasons, I used Coded Wire Tags (CWT) from Northwest Marine Technology (Northwest Marine Technology, Shaw Island, Washington 98286). Since I needed to be able to individually identify each tagged crab, I used the sequential pre-cut CWTs, measuring 1.1 mm long and 0.25 mm diameter (Figure 4).

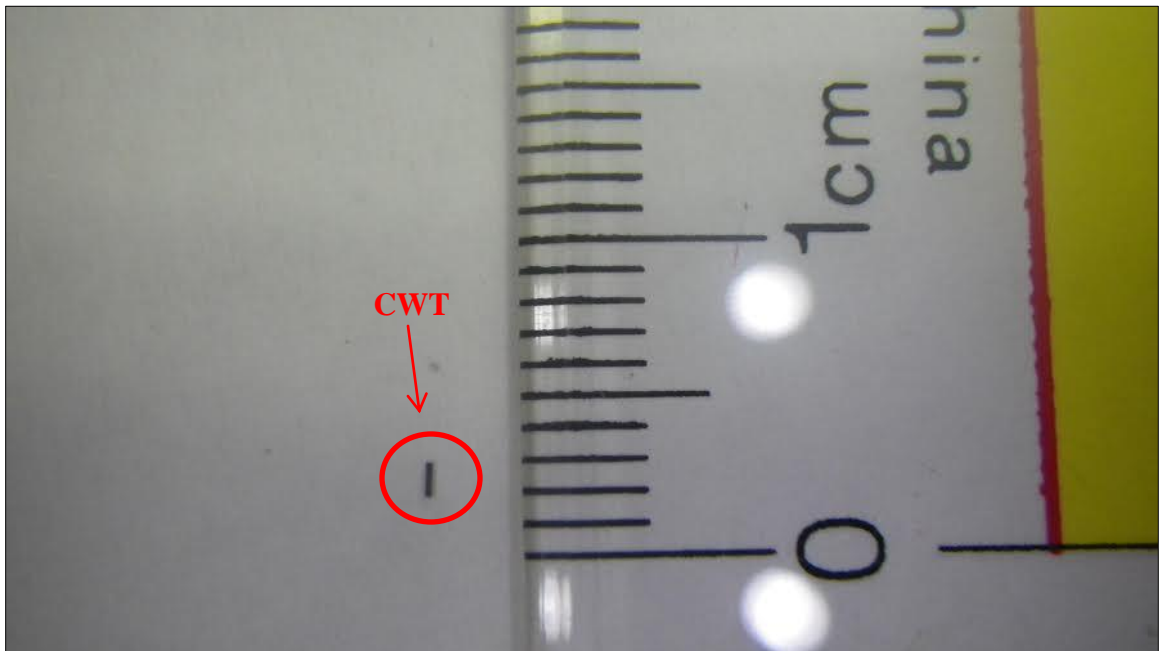


Figure 4: Sequential pre-cut coded wire tags (CWT) by Northwest Marine Technology.

Tags were inserted into the basal muscle of blue crabs' fifth pereiopod using single shot injector, also from Northwest Marine Technology (Figure 5). When correctly inserted, tag retention rates ranged between 88% through the first molt and 100% after the second molt in juvenile blue crabs between 18 and 28 mm carapace width (van Montfrans et al. 1986). Tag retention rates are even higher through first molt (98.2%) when tagging individuals over 29 mm carapace width. The CWTs are magnetized. To assure tags were successfully inserted, I scanned each crab with Handheld Wand detector that detects the magnetic field (Northwest Marine Technology, Shaw Island, Washington 98286).



Figure 5: Tagging a blue crab with a CWT using single-shot injector. Photo from Laila Pronker.

Cage Study

A total of 24 rectangular minnow traps (18”L x 8”W x 8”H with 1” mesh) were modified by closing the funnel entrance so crabs could not escape once encaged (Figure 6). I then placed the modified traps in area 1, side by side, about one meter apart.



Figure 6: Minnow trap used to encage *Callinectes sapidus* in field enclosure study.

Juvenile blue crabs used in the cage study were collected with the aid of seines, traps, or dip net. Each crab was measured by its carapace width (CW), sexed, and tagged with CWT as described above in the “tagging” section, and placed into its own individual cage to avoid cannibalism. Molt stage and limb losses were also noted. Every week, I

went to the site and re-measured the same variables (carapace width, sex, limb losses and molt stage).

I also on a weekly basis fed medium size (~4 cm) bait shrimp to blue crabs kept in even numbered traps. Many blue crabs growth studies in the past used frequent or ad libitum feeding (Brylawski and Miller 2006; Leffler 1972; Tagatz 1968), which might influence their growth rates. My goal was to feed only half of the encaged individuals and see if their growth rates were significantly higher than individuals not being fed weekly but instead feeding on ambient prey that might venture into the traps. Even though half of the blue crabs in cages were not being fed by me weekly, plenty of potential prey items appeared to be available. Every week when I went to take measurements I would find small fishes (gobies, pinfish), small blue crabs, mud crabs, amphipods, mussels, and other individuals that were small enough to pass through the 1" mesh.

Mark-Recapture Study

Collapsible crab pots were placed at sites 1, 2, 3, 4, and 5 to collect and recapture free roaming tagged crabs (Figure 7). Each site received 5 collapsible traps. Aside from collapsible crab pots, I also used seines, dip nets and regular crab pots to aid in crab collection. Crabs collected at a specific site were also released at the same site. Mark-recapture events were performed once or twice a week between February 2012 and May 2013.

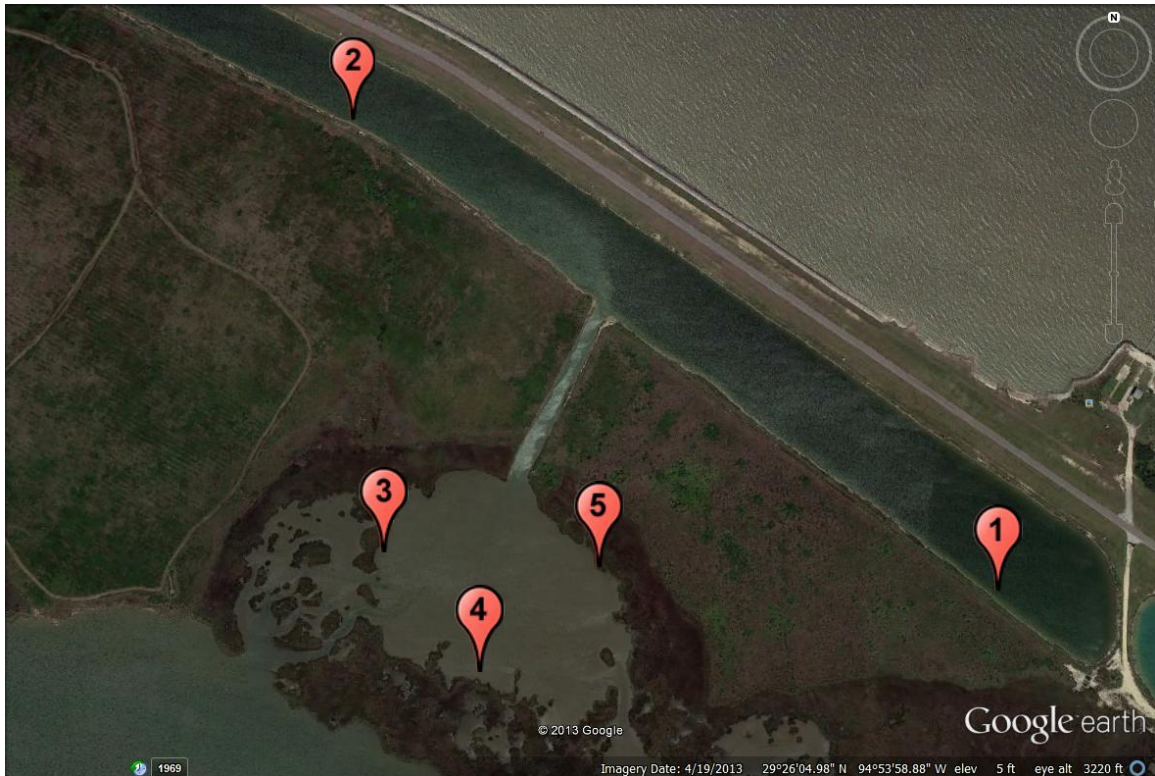


Figure 7: Sites 1-5 where collapsible crab pots were kept for mark-recapture study.

Blue crabs were tagged in the field using the same CWT protocol described above. In addition to internal tagging, each crab was externally marked with light blue nail polish or paint to identify whether molting had occurred. Recaptured tagged crabs were recognized using a Handheld Wand CWT Magnetic Detector. If a tagged crab still had the external nail polish or paint pen mark, it meant that the crab had not yet molted and was then returned to the water. If the external mark was absent, we then brought crabs back to the lab for tag extraction. We carefully dissected recaptured crabs to extract tags, which were read with MagniViewer from NMT. Each tag has 4 sets of numbers: a 2-digit agency code, a 2-digit Data 1 code, a 2-digit Data 2 code (batch number), and a 5 digit sequence number, which is unique to each tag. The sequence number can then be

easily matched to its corresponding reference tag sheet which was used to cross-reference information on the tagged individual.

Data Analysis

To identify whether certain factors, such as sex, feeding, missing limbs, initial CW and temperature had an effect on GPM and growth rates, I performed analysis of variance (ANOVA) and regression analysis with these variables using Minitab 16 software package.

Model Development

All the growth increment VBGF derived models previously discussed that I used during my research (Gulland-Holt, Faben, and Appeldoorn) are available in the Fish Stock Assessment Tool (FISAT II) software package offered by the Food and Agriculture Organization of the United Nations (FAO) which I used in my study. However, for some reason I could not determine, the Fabens method implemented by FISAT II provided unreasonable results or error messages during computation. I contacted the software developers, and they informed me that I wasn't the only one having the same issues. Therefore, I followed methodology by Haddon (2010) to estimate the parameters of the Fabens model, using Microsoft excel and the Solver add-in to determine the best fitting (minimize negative log likelihoods) model. Three out of four variation patterns were successfully simulated for the Fabens model using the maximum likelihood approach including the constant variance, inverse linear variance, and power law variance methods.

Lognormal variance was simulated but with unsuccessful results (yielded computational errors when minimizing negative log likelihood). For the constant variance approach, we minimized the negative log likelihood ($-veLL$) in equation 6 by changing the standard deviation (σ) in addition to the parameters L_{∞} and K . This method will be referred as Fabens constant variance method in this paper.

$$-veLL = - \sum \ln \left(\frac{1}{\sqrt{2\pi}\sigma} e^{-\frac{(\Delta L - \Delta \hat{L}^2)}{2\sigma^2}} \right) \quad (6)$$

Francis (1988) suggestion of power law and inverse linear residual standard deviation were simulated using equations 7 and 8 respectively, where v and τ are constants to be estimated separately. Once additional constants are estimated, equations 5 and 6 are substituted in equation 4 in place of standard deviation (σ).

$$\sigma = v\Delta\hat{L}^{\tau} \quad (7)$$

$$\sigma = v(\Delta\hat{L}) \quad (8)$$

Models were compared using adjusted Akaike's Information Criterion (AICc) shown on equation 9

$$AICc = n * \ln \left(\frac{RSS}{n} \right) + 2k + \left(\frac{2k(k+1)}{n-k-1} \right) \quad (9)$$

Where n is the number of data points, RSS is the residual sum of squares, and k is the number of parameters in the model.

RESULTS

Environmental Data

Average daily water temperatures from January 1st, 2012 to July 1st, 2013 ranged from a low of 8.9°C in mid-January 2013 to a high of 32.7°C at the end of June 2013 (Figure 8). Mean daily temperature was $21.3^{\circ}\text{C} \pm 0.26$ (95% CI) during the study period.

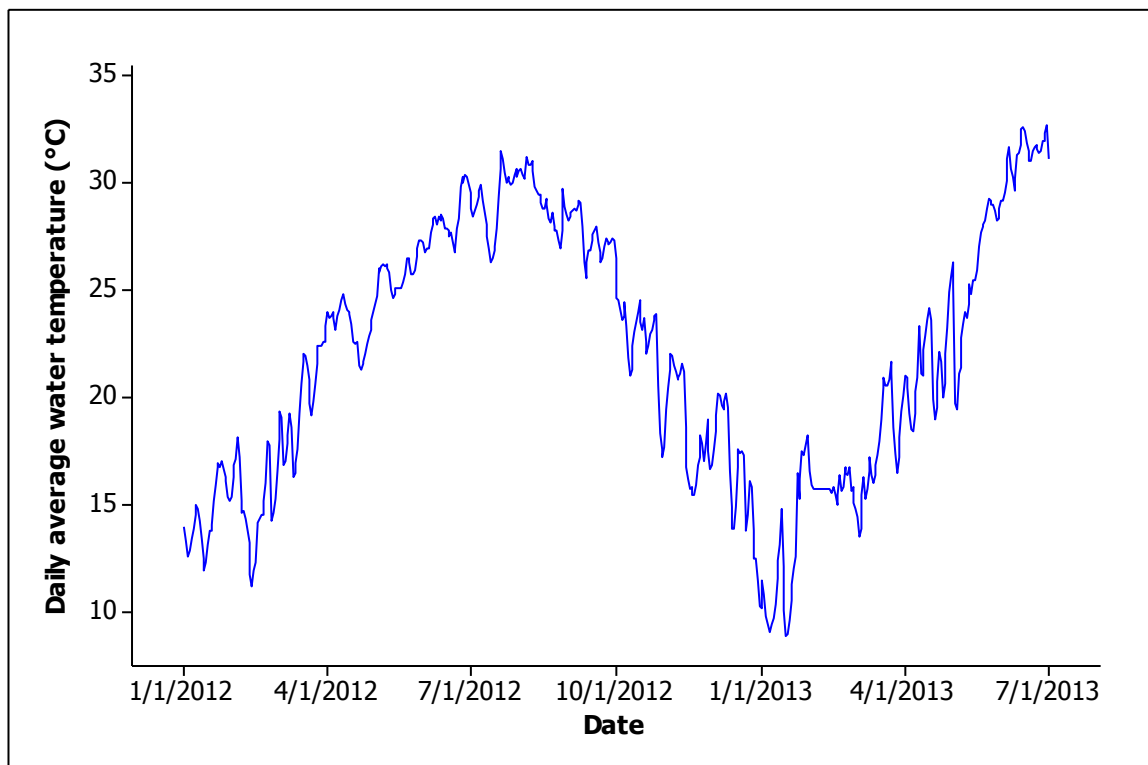


Figure 8: Daily average water temperature of study sites between January 1st, 2012 and July 1st, 2013.

Due to technical problems, many salinity and D.O. readings from data loggers were inconsistent with field collected quality assurance data and were therefore discarded from further data analysis.

Field Enclosure Study

A total of 92 crabs were used in enclosures, but only 63 crabs made through at least one molt. Most of the crabs placed in enclosures were between 19 and 28 mm CW (49 crabs) and most molted more than five times (Table 1). The highest number of molts was achieved by a crab initially 24.2 mm CW which molted 11 times in a period of 307 days to achieve a final measured CW of 145.9 mm.

Table 1: Molting frequency of blue crabs in enclosures.

Width Group (mm)	N	1 molt	2 Molts	3 molts	4 molts	5 + molts
19-28	49	8	7	5	2	27
29-38	11	3	4	1	0	3
39-48	1	0	0	0	1	0
49-58	1	0	0	0	1	0
129-138	1	1	0	0	0	0
Total	63					

Statistical Analysis

Growth per molt (GPM) data was highly variable but followed a normal distribution (Anderson-Darling test, $p=0.133$, Figure 9). A total of 284 GPM data points with mean of 22.0 ± 0.4 % (mean \pm SE) were used for my analysis. The lowest GPM (5.4%) was observed in a female crab that grew from 34.8 mm to 36.7 mm carapace width. This particular crab, however, was missing 9 limbs, having only its right claw when measured the week before it molted. The lowest GPM (8.6%) for a male crab was measured in an individual crab without missing limbs that molted from 121.3 mm to 131.7 mm carapace width. This was its last molt before it died inside the enclosure. This crab was initially placed in the enclosure when it was 25.6 mm carapace width, and molted 8 times between July 2012 and June 2013. The largest GPM (57.7%) was achieved by a male crab that was missing three limbs before it molted from 24.3 mm to 38.3 mm carapace width. This crab was placed in the enclosure on August 9, 2012 at a CW of 19.4 mm and it molted 6 times until it reached a CW of 90.4 mm on November 7, 2012.

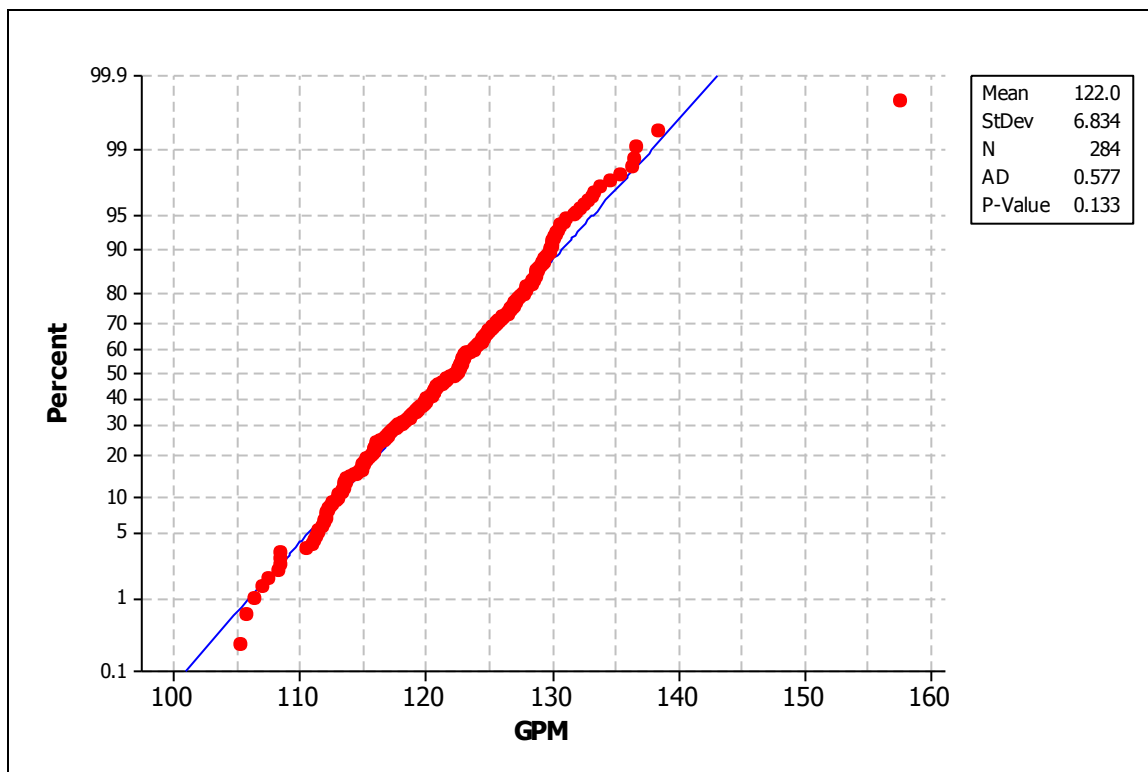


Figure 9: Normal probability plot of GPM of crabs kept in enclosures

Based on the results of the general linear model (GLM) analysis of sex, missing limbs and feeding on GPM, I concluded that sex and feeding had no effect on GPM, but missing limbs had an effect (Table 2).

Table 2: ANOVA (GLM, Minitab) results for growth per molt (GPM) of *Callinectes sapidus* used in cage study.

Source	DF	Adj SS	Adj MS	F	Probability
Feed	1	59.5	59.52	1.44	0.23
Sex	1	15.6	15.59	0.38	0.54
Missing Limbs	1	1585.4	1585.37	38.41	0.00
Error	280	11556.1	41.27		
Total	283				

Since missing limbs appeared to have a negative effect on GPM (Figure 10), I calculated the average GPM using only crabs that didn't have any limb losses. There were a total of 99 molt events in which crabs didn't show limb losses. Molt-process models assume that GPM is invariant (Brylawski and Miller 2006; Smith 1997). Therefore, I performed a regression of GPM as function of temperature and initial CW to verify whether this assumption is met using only GPM events where limb losses did not occur. The regression shows that the slope of GPM in relation to pre-molt CW (Table 3, Figure 11) and temperature (Table 3, Figure 12) is not significantly different from zero. The average GPM for blue crabs kept in enclosures that presented no limb losses was $122.0\% \pm 6.8$ (± 1 standard deviation, SD).

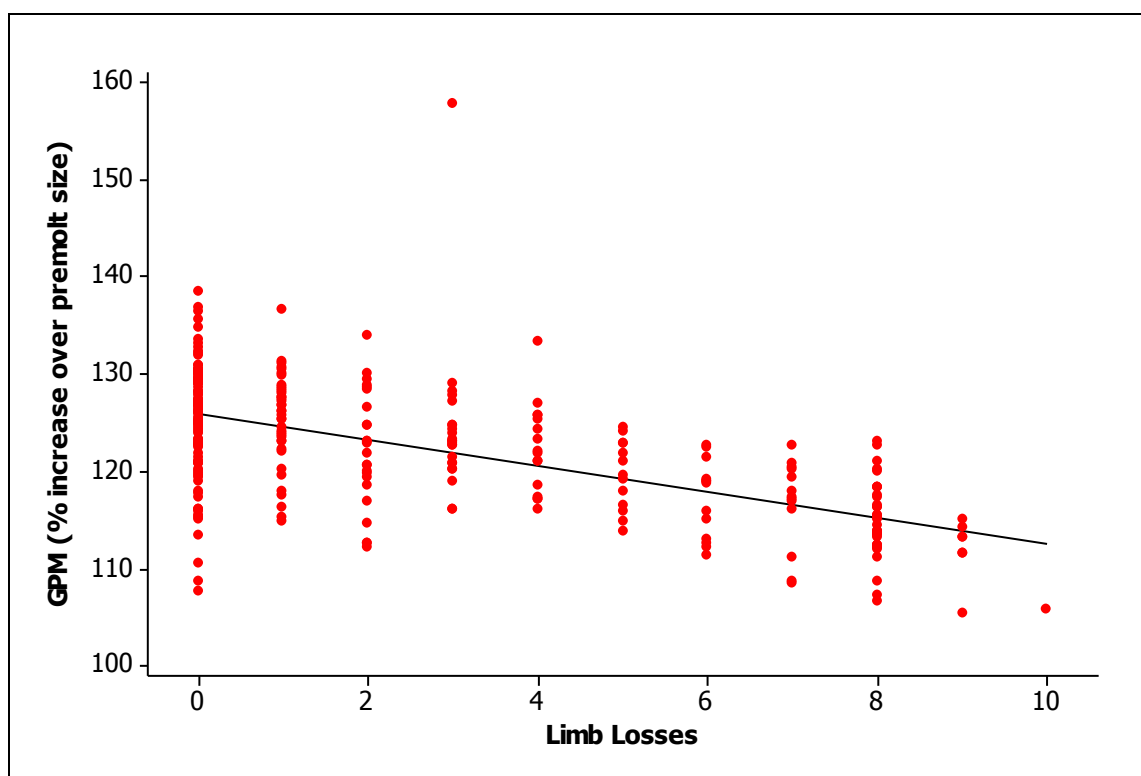


Figure 10: Growth per molt (GPM) as a function of limb losses for *Callinectes sapidus* kept in enclosures. $R^2=36.1\%$, $P=0.00$.

Table 3: Regression output (Minitab) for growth per molt (GPM) of *Callinectes sapidus* used in cage study as function of initial size and temperature. Probability parameter = 0.

Predictor	Coefficient	SE Coefficient	T	Probability
Constant	128.51	2.70	47.56	0.00
Temperature	-0.07	0.10	-0.76	0.45
Initial Size	-0.03	0.02	-1.61	0.11

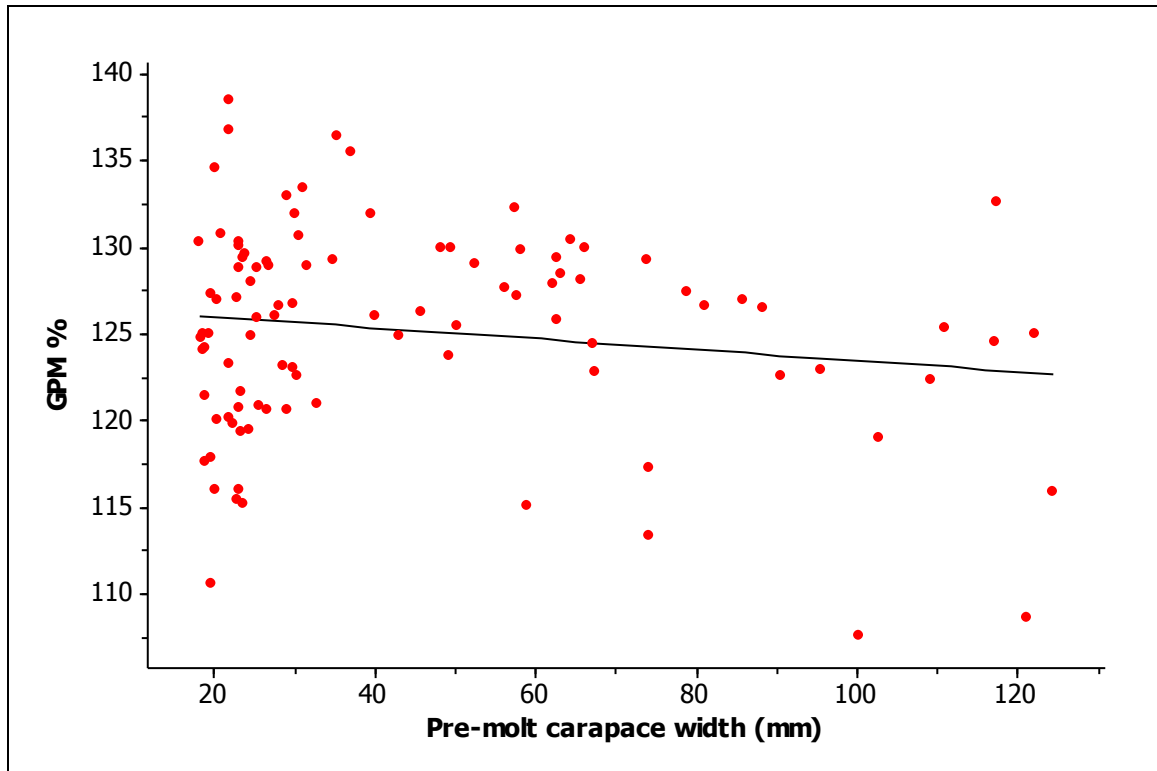


Figure 11: Growth per molt (GPM) as a function of pre-molt carapace width for *Callinectes sapidus* kept in enclosures. $R^2=2.5\%$. $P=0.11$.

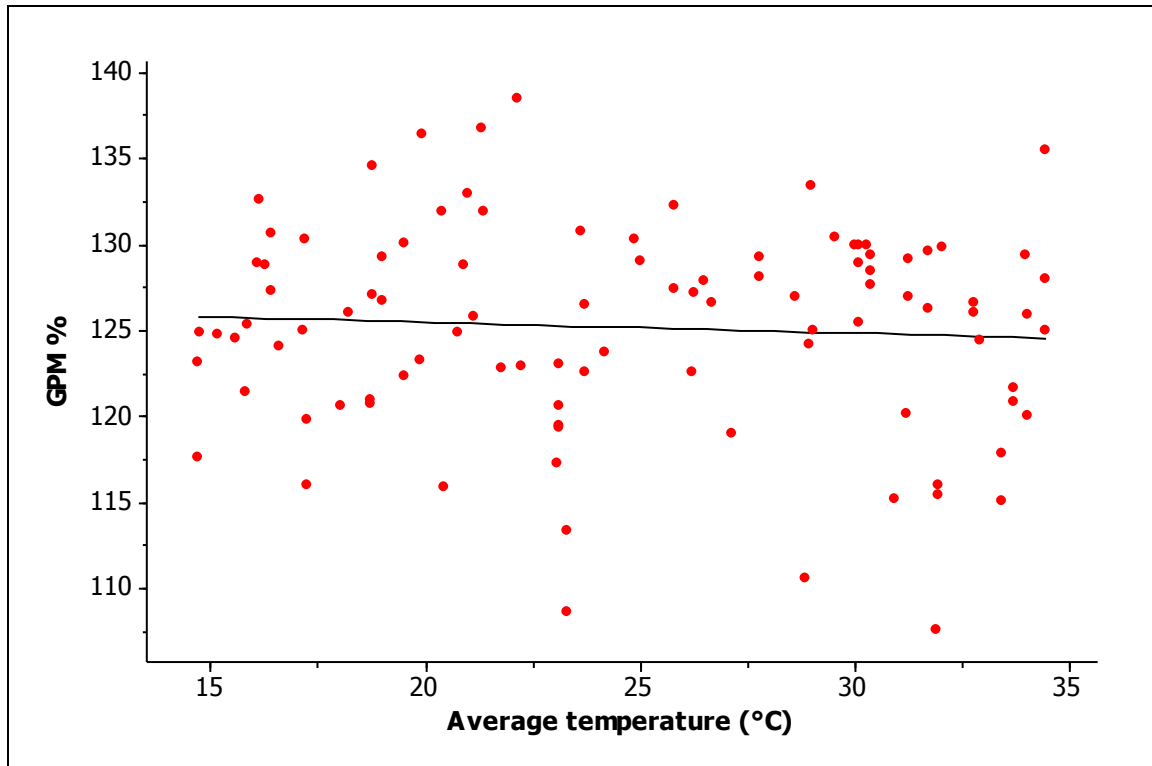


Figure 12: Growth per molt (GPM) as a function of temperature for *Callinectes sapidus* kept in enclosures. $R^2=0.4\%$. $P=0.45$.

Limb losses and gender did not appear to have an effect on IMP. Feeding, on the other hand, appeared to influence IMP (Table 4). Considering that feeding in the wild will vary depending on prey availability and that I only fed 1 medium size shrimp a week to some of the crabs, I used all molt events to calculate T_{\min} and physiological IMP.

Table 4: Analysis of variance (ANOVA) of intermolt period (IMP) as a function of sex, feeding, and missing limbs for *Callinectes sapidus* kept in field enclosures.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Sex	1	4.1	22.4	22.4	0.04	0.85
Feed	1	6356.0	6389.5	6389.5	10.64	0.00
Missing limb	1	489.6	489.6	489.6	0.81	0.37
Error	279	176794.6	176794.6	600.7		
Total	282	174444.3				

IMP in days (d) exhibited a negative trend when plotted against daily average temperature (Figure 13a). The inverse of IMP (Figure 13b), as expected, was positively related and its x-axis intercept provided an estimate of T_{\min} of 6.1 ± 0.05 °C (mean \pm standard error, SE).

The T_{\min} value I obtained is lower than the values calculated by Smith (1997) and Brylawski and Miller (2006), 8.9°C and 10.8°C respectively. A T_{\min} lower than those calculated during Chesapeake Bay studies was unexpected, but it might be explained by the lack of collection of IMP data from lower temperatures during this and other studies. Another reason could also be that those studies calculated T_{\min} using laboratory reared crabs.

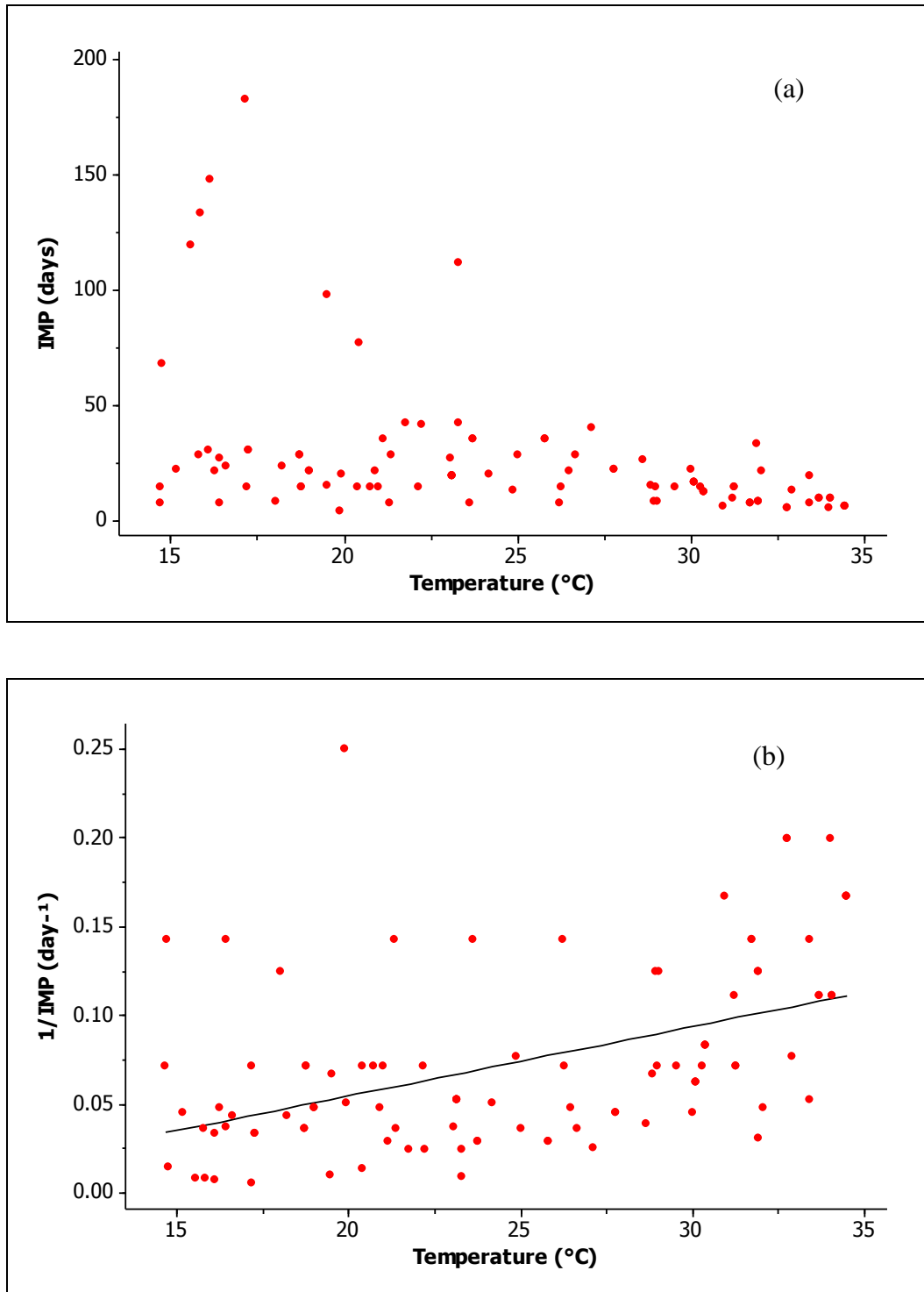


Figure 13: (a) intermolt period (IMP) as function of temperature ($R^2=17.5\%$, $P=0.00$) and (b) inverse intermolt period ($1/IMP$) of *Callinectes sapidus* kept in enclosures that presented no limb losses. Linear regression of inverse intermolt period is $IMP^{-1}=0.004 \times \text{temperature} - 0.0276$, where the x-axis intercept is the T_{\min} .

The average physiological IMP when using T_{\min} of 6.9 was estimated to 568 ± 31 degree-days. However, it appears that IMP increases when pre-molt carapace size between 70 mm and 100mm, and gets even higher in crabs larger than 100 mm (Figure 14). Therefore, I divided IMP into four size classes of 10-39mm, 40-69, 70-99mm, and 100-130 and performed an ANOVA to verify whether the mean IMP of these size classes are significantly different. The ANOVA indicate that there is a significant difference between means of these size classes (Table 5). Tukey's post-hoc analysis suggested that the IMP of size classes 40-69mm and 70-99mm are the only ones not significantly different from each other (Table 6).

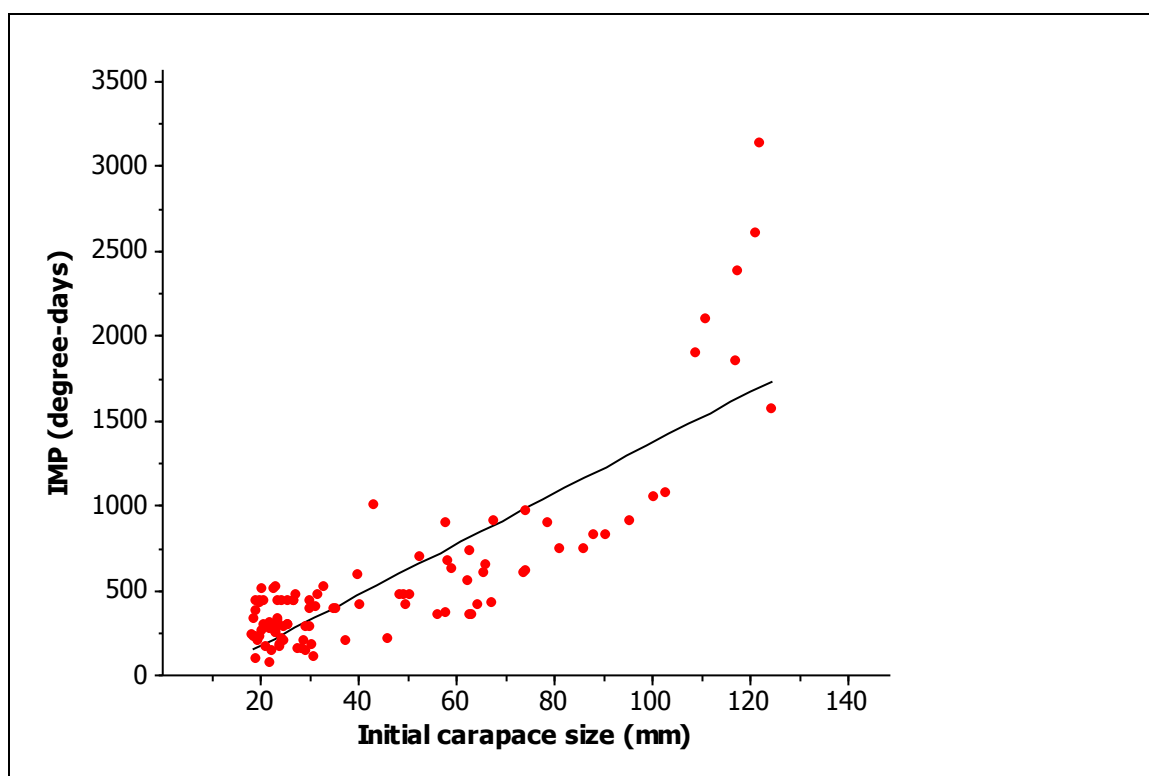


Figure 14: Scatter plot of intermolt period in degree-days as function of initial carapace size for *Callinectes sapidus* kept in enclosures that presented no limb losses. $R^2=69.8\%$.

Table 5: Analysis of variance (ANOVA) results on intermolt period (IMP) in degree-days of four different size classes of *Callinectes sapidus* kept in enclosures that presented no limb losses.

Source	DF	SS	MS	F	P
Size	3	21900951	7300317	121.55	0.00
Error	95	5705787	60061		
Total	98	27606737			

Table 6: Tukey's 95% simultaneous confidence interval post-hoc test for analysis of variance (ANOVA) on intermolt period (IMP) in degree-days of four size classes of *Callinectes sapidus* kept in enclosures that presented no limb losses. Means that do not share a letter are significantly different.

Size	N	Mean	Grouping
100-130 mm	9	1963.5	A
70-99 mm	9	791.8	B
39-70 mm	22	549.1	B
10-40 mm	59	310	C

Growth rates (mm/day) of blue crabs used in enclosures did not fit normal distribution (Figure 15, $P < 0.005$). However, the log-transformed growth rates did follow normal distribution and were used for subsequent data analysis (Figure 16, $P = 0.253$).

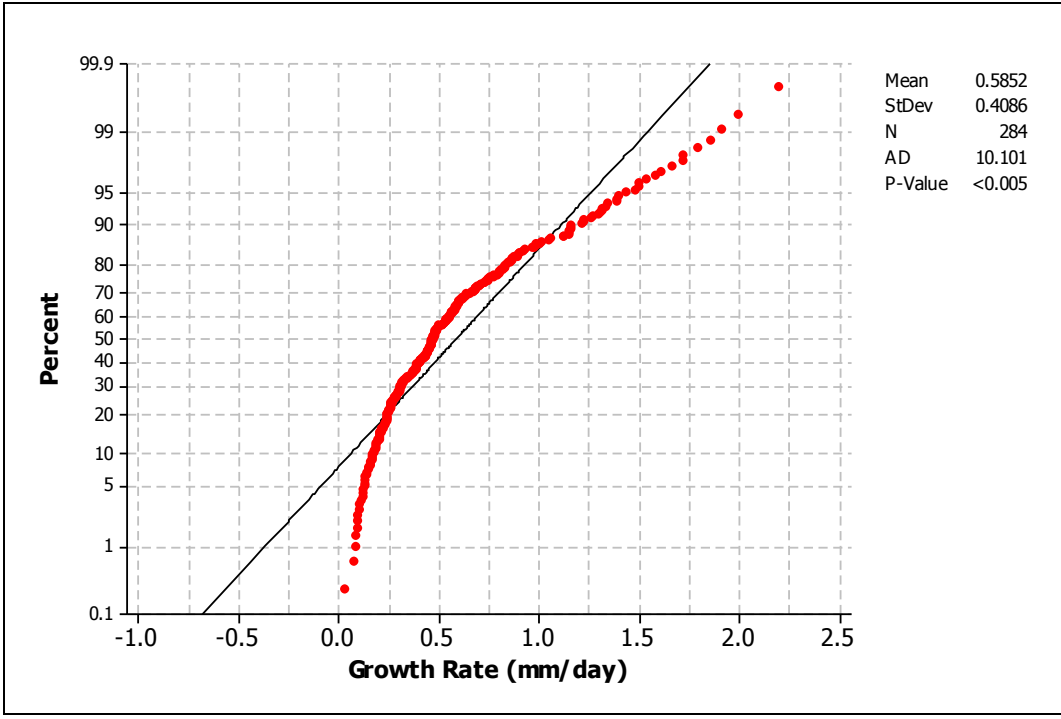


Figure 15: Normal probability plot of growth rates for *Callinectes sapidus* kept in enclosures.

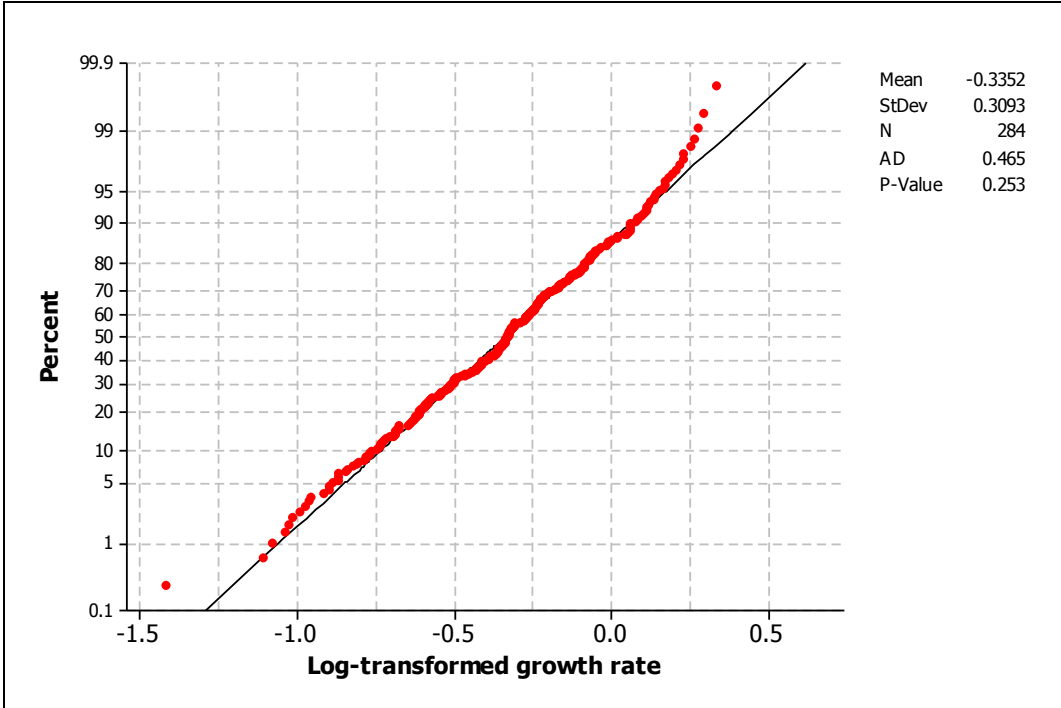


Figure 16: Normal probability plot of log-transformed growth rates for *Callinectes sapidus* kept in enclosures.

Based on the ANOVA results sex, feeding and initial size had no effects on log-transformed growth rate, but temperature and limb losses did have an effect (Table 7).

Table 7: Analysis of variance (ANOVA, Minitab) results for log-transformed growth rate of *Callinectes sapidus* used in cage study.

Source	DF	Seq SS	Adj SS	Adj MS	F	Probability
Temperature (covariate)	1	5.29	6.40	6.40	88.57	0.00
Initial Size (covariate)	1	0.06	0.05	0.05	0.69	0.41
Feed	1	0.00	0.00	0.00	0.01	0.91
Sex	1	0.12	0.12	0.12	1.73	0.19
Missing Limbs	1	1.54	1.55	1.55	21.46	0.00
Error	278	20.07	20.07	0.07		
Total	283	27.08				

Since limb losses appear to influence growth rates, and growth rates decrease as the number of lost limbs increases (Figure 17), models were developed and run using only molt events during which crabs did not exhibit loss of limbs.

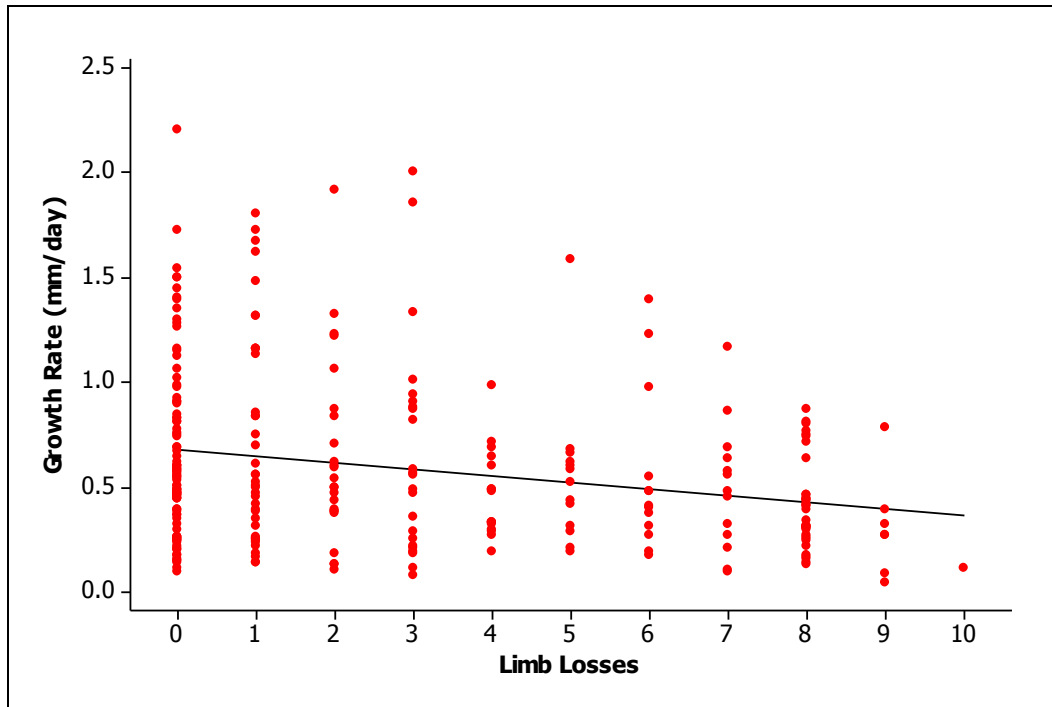


Figure 17: Scatter plot of growth rate of *Callinectes sapidus* as a function of limb losses.

Growth Models

The slope of Gulland-Holt plot for crabs missing no limbs was negative (Figure 18). However, the x-intercept, or L_{∞} , would have a value extremely high ($L_{\infty}=1130$ mm) and biologically unfeasible. Therefore, I estimated the parameter K by utilizing a “forced” Gulland-Holt plot, in which the value of L_{∞} is fixed beforehand based on previous literature values. To accomplish this I reviewed a variety of blue crab growth studies in the Chesapeake Bay that estimated growth parameters of blue crabs (Ju et al. 1999; Rugolo et al. 1998; Smith 1997). In the Gulf of Mexico, parameters have been estimated for Louisiana ($L_{\infty}=175.9$, $K=1.45$) (Smith 1997) and Florida ($L_{\infty}=276.0$, $K=0.66$) (Pellegrin et al. 2001). I decided to use L_{∞} estimate from Louisiana as a fixed value since this area has geographically closer and has the most similar weather and hydrological conditions in comparison to Galveston Bay.

L_{∞} was fixed to 175.90 mm, yielding a k value of 1.863 (Figure 19). The plot of residuals of this analysis showed significant and strong oscillation of data points, which suggests growth was seasonally influenced ($C < 0.50$) (Figure 20).

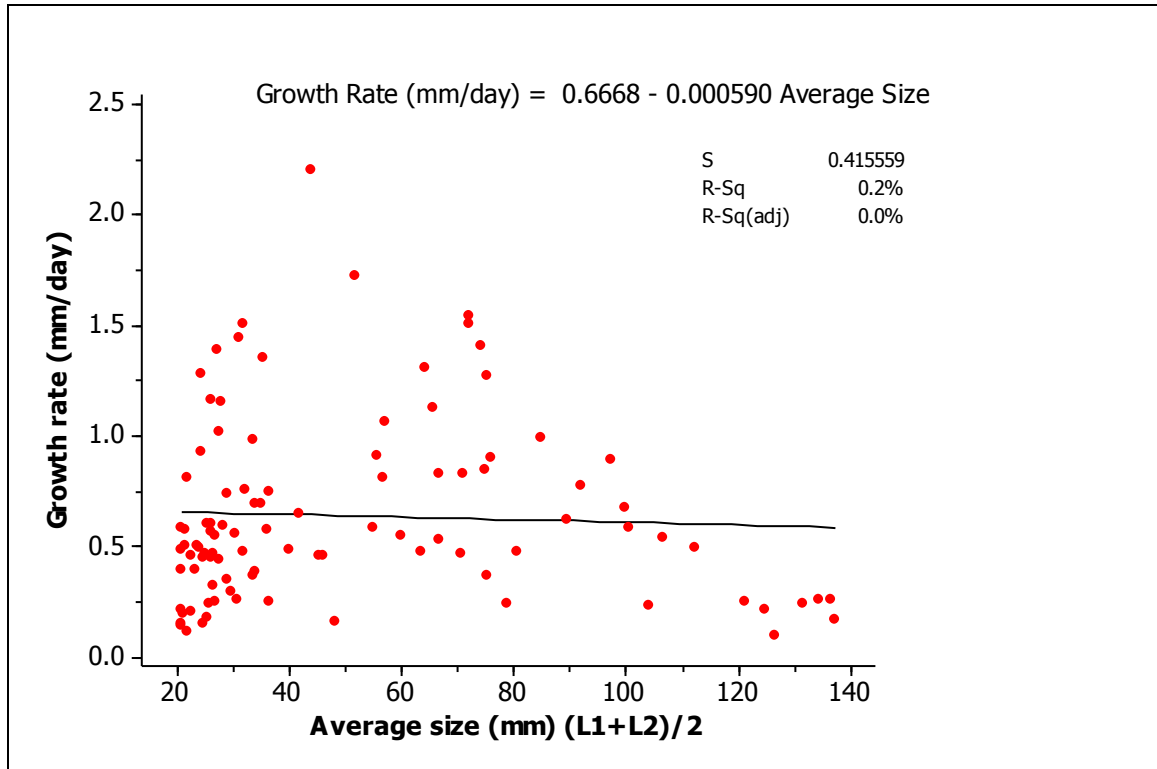
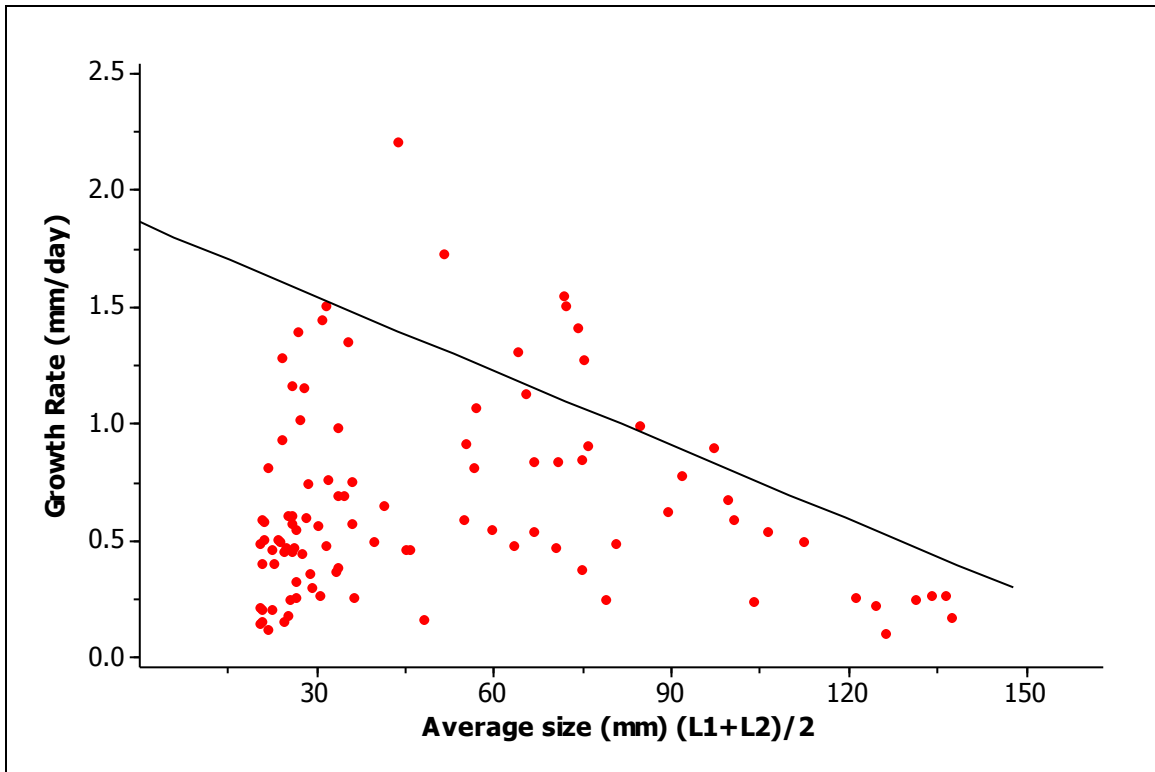


Figure 18: Gulland-Holt plot (Minitab) for *Callinectes sapidus* kept in enclosures that exhibited no limb losses.



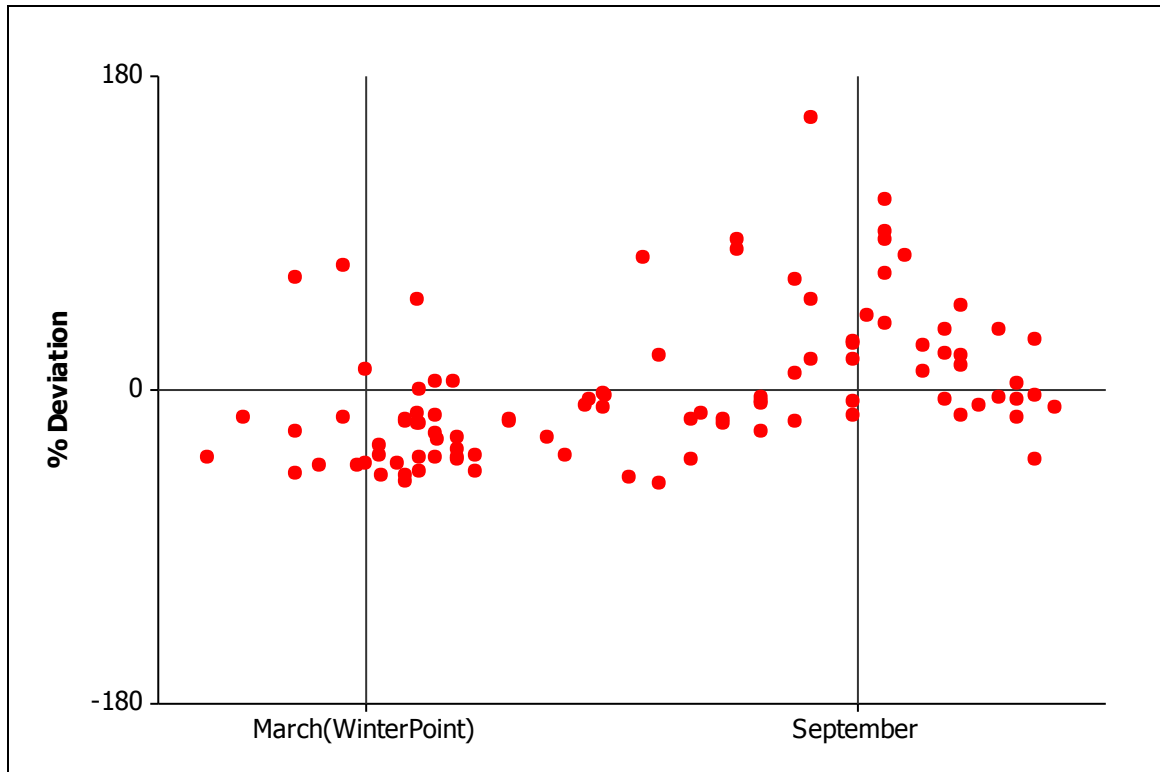


Figure 20: Gulland-Holt plot of residuals for *Callinectes sapidus* kept in enclosures that exhibited no limb losses. The analysis indicates a strong oscillation of data points indicating seasonality in the growth of specimens which is significant.

Fabens constant variance method was conducted using Excel and Solver to minimize the negative log likelihood estimate of L_{∞} and k which generated estimates of 223.8 mm and 0.92 respectively (Figure 21). The additional parameter σ was estimated to be 6.67. The residual plot for Fabens constant variance method is shown in Figure 22.

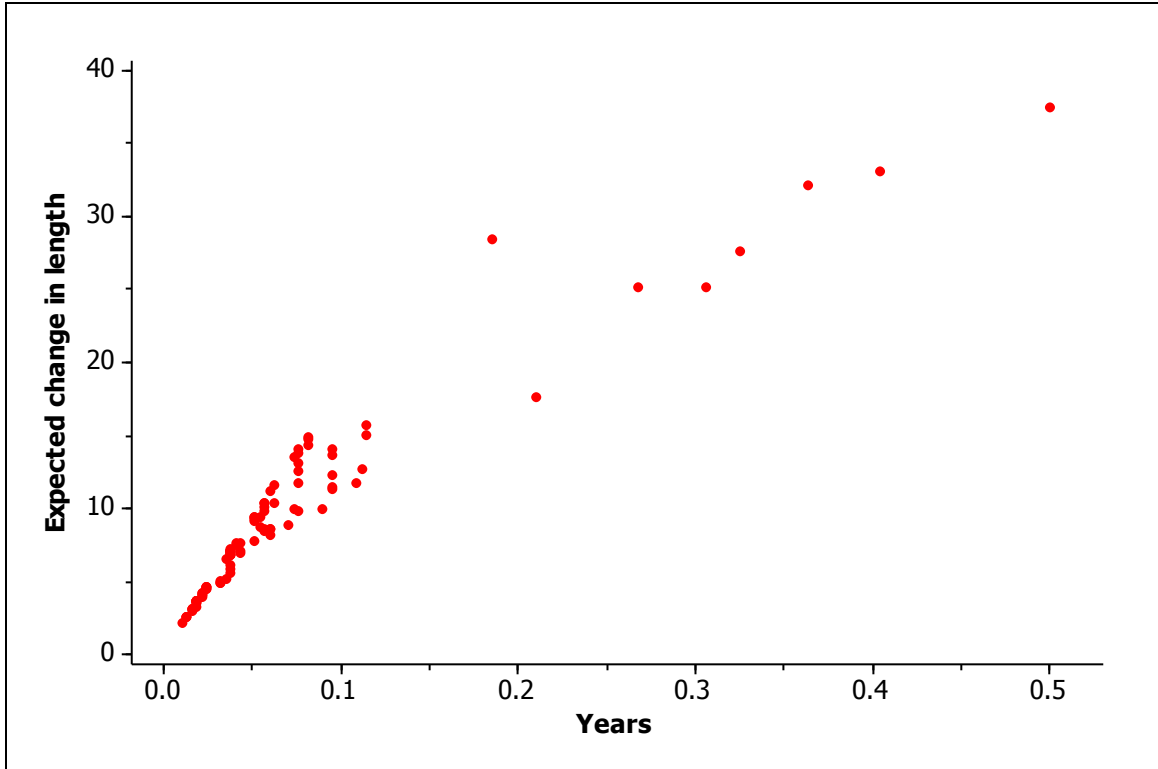


Figure 21: Fabens constant variance model results for *Callinectes sapidus* kept in enclosures that exhibited no limb losses. $L_{\infty}=223.8$, $k=0.92$, $\sigma=6.67$.

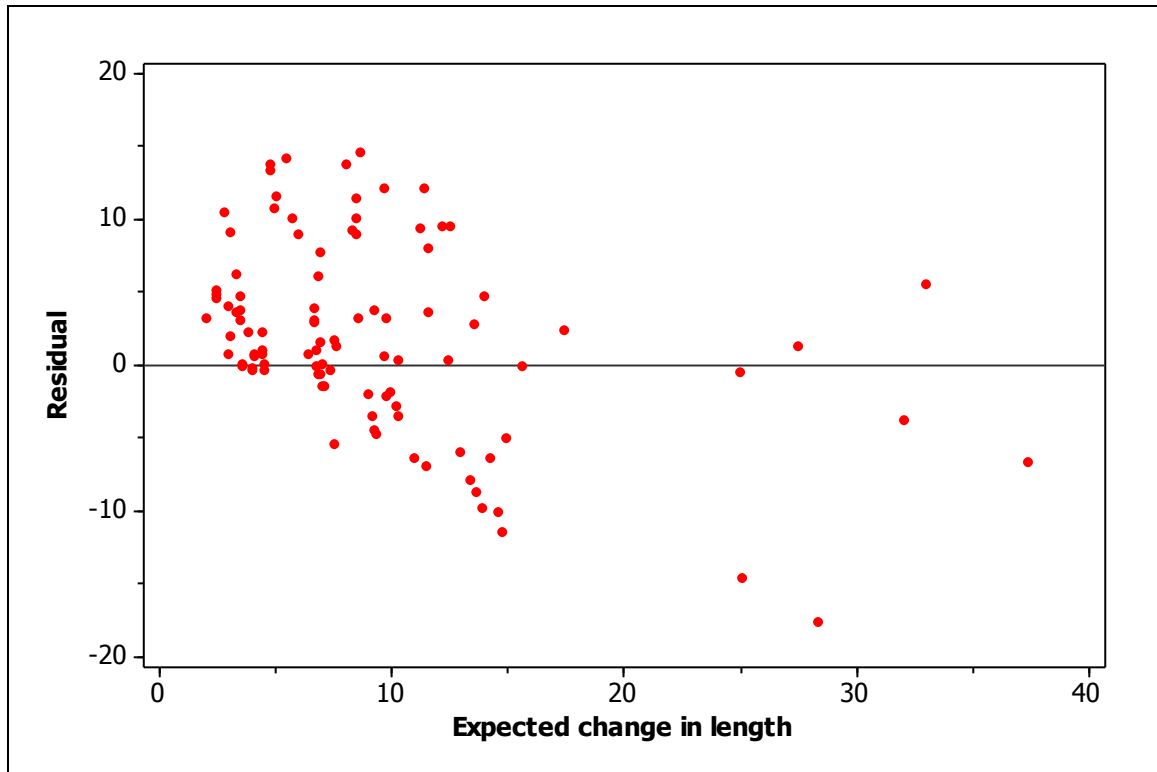


Figure 22: Residual plot of Fabens constant variance model results for *Callinectes sapidus* kept in enclosures that exhibited no limb losses.

Excel and Solver were used to fit the parameters of the Fabens inverse linear model by minimizing the negative log-likelihood estimates of L_{∞} and k , yielding values of 189.4 mm and 1.77 respectively (Figure 23). The additional model parameter ν was estimated to be 0.61. The plot of residuals for Fabens inverse linear method is shown on (Figure 24).

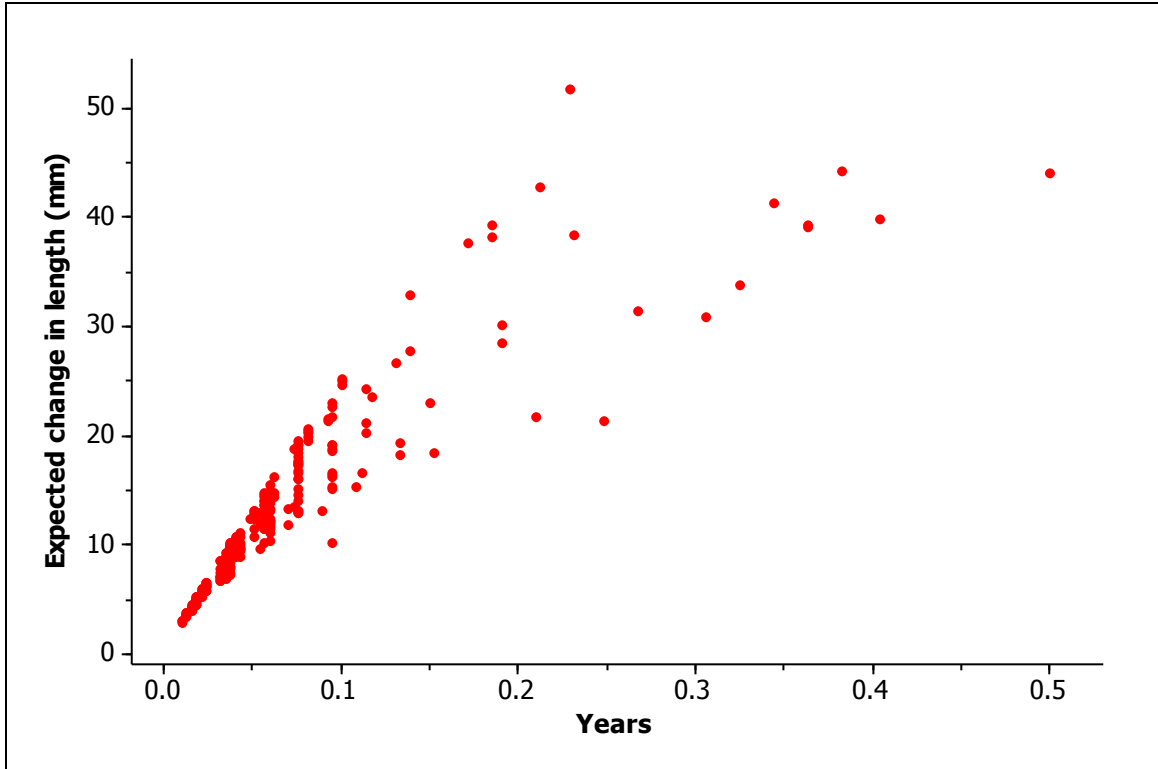


Figure 23: Fabens inverse linear model results for *Callinectes sapidus* kept in enclosures that presented no limb losses. $L_{\infty}=189.4$, $k=1.77$, $v=0.61$.

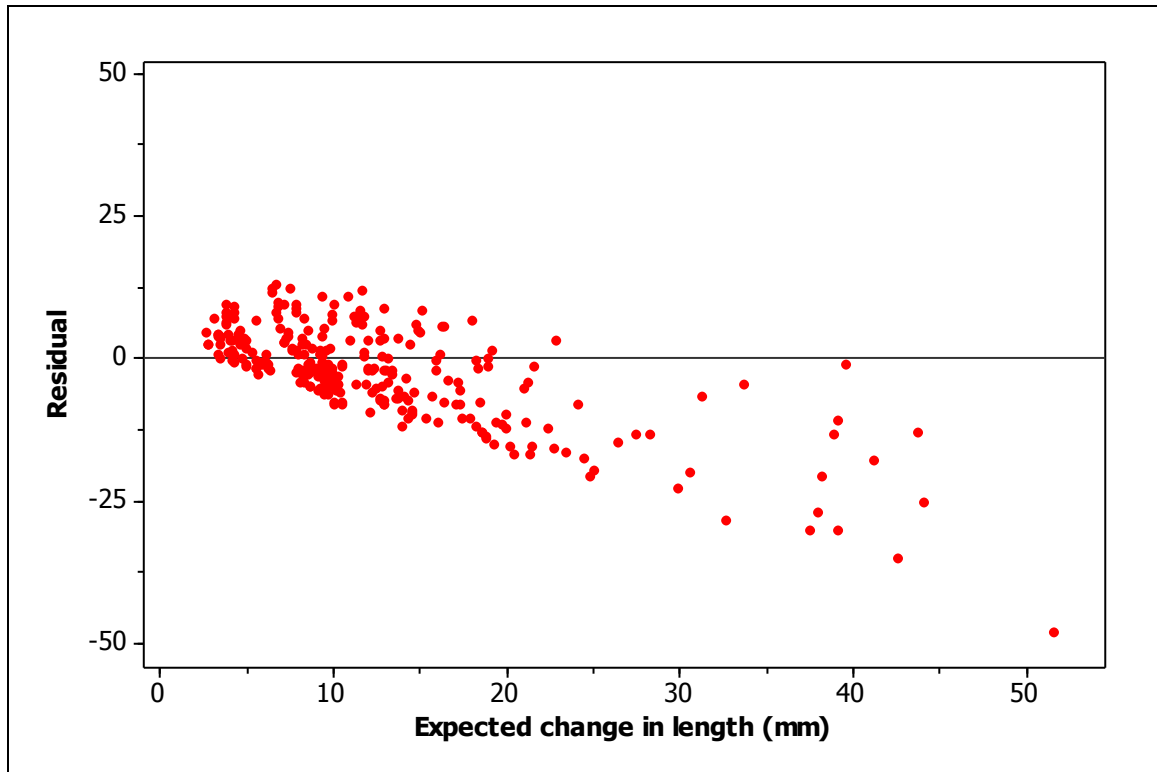


Figure 24: Residual plot of Fabens inverse linear model results for *Callinectes sapidus* kept in enclosures that presented no limb losses.

The Fabens power model was fit to the data using Excel and Solver to minimize the negative log likelihood estimates of L_{∞} and k yielding values of 224.9 mm and 1.05 respectively (Figure 25). The additional parameters of this model, ν and τ , were estimated to be 2.88 and 0.37 respectively. The plot of residuals for the Fabens inverse linear model is shown on (Figure 26).

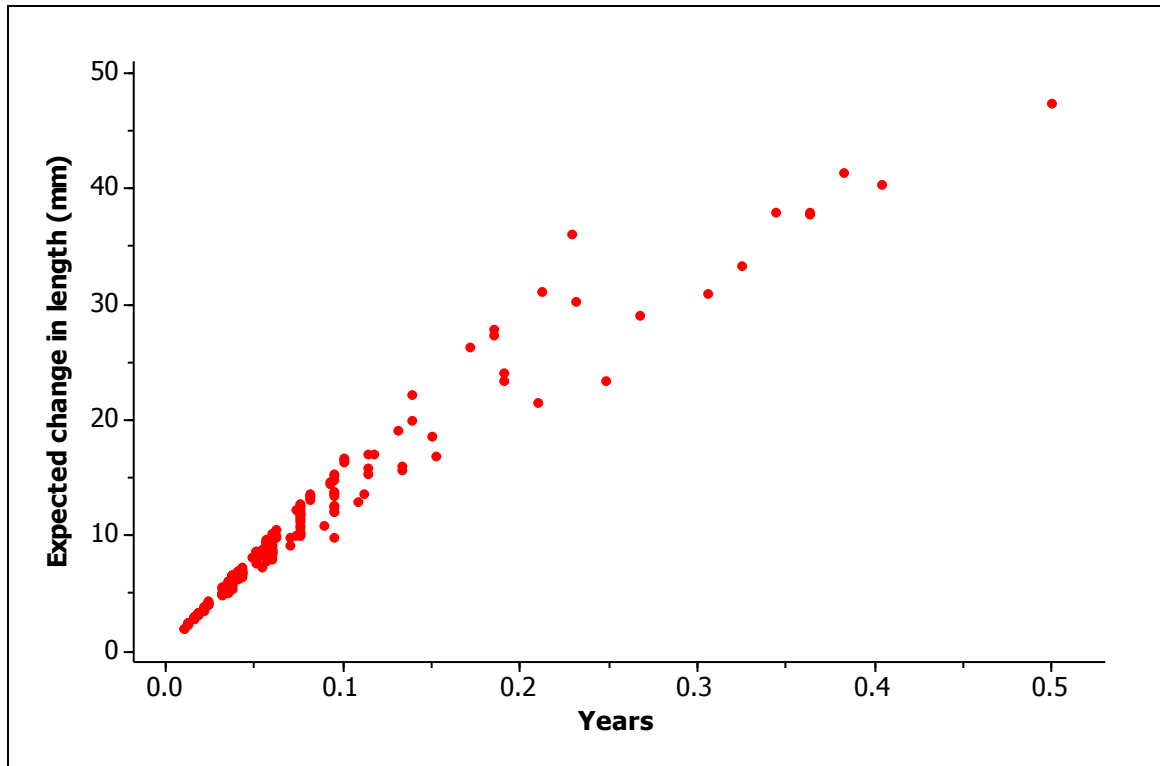


Figure 25: Fabens power model results for *Callinectes sapidus* kept in enclosures that exhibited no limb losses. $L_{\infty}=224.9$, $k=1.05$, $v=2.88$, $\tau=0.37$.

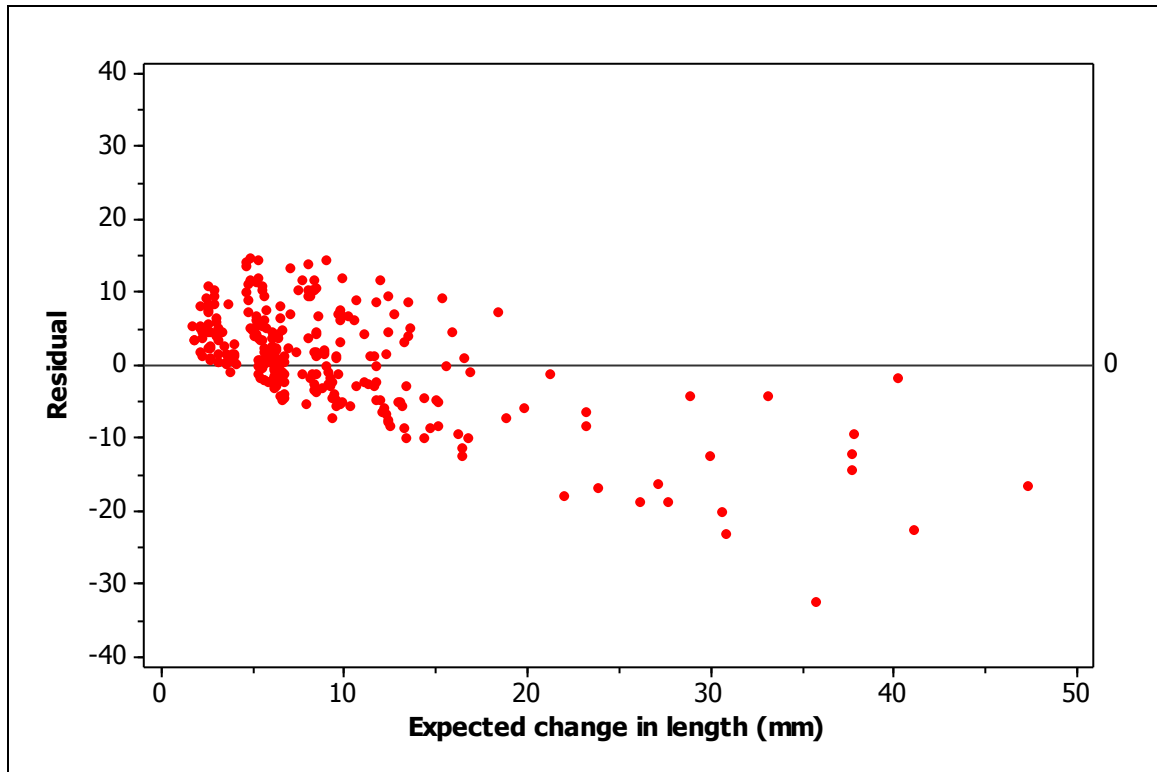


Figure 26: Residual plot of Fabens power model results for *Callinectes sapidus* kept in enclosures that presented no limb losses.

Appeldoorn's model was executed using the FISAT II software package and yielded estimates of L_{∞} and k to be 225.5 mm and 1.15 (Figure 27). The model also produced estimates of C and WP which were 0.55 and 0.63 respectively. The plot of residuals (Figure 28) suggests that the model has a good fit.

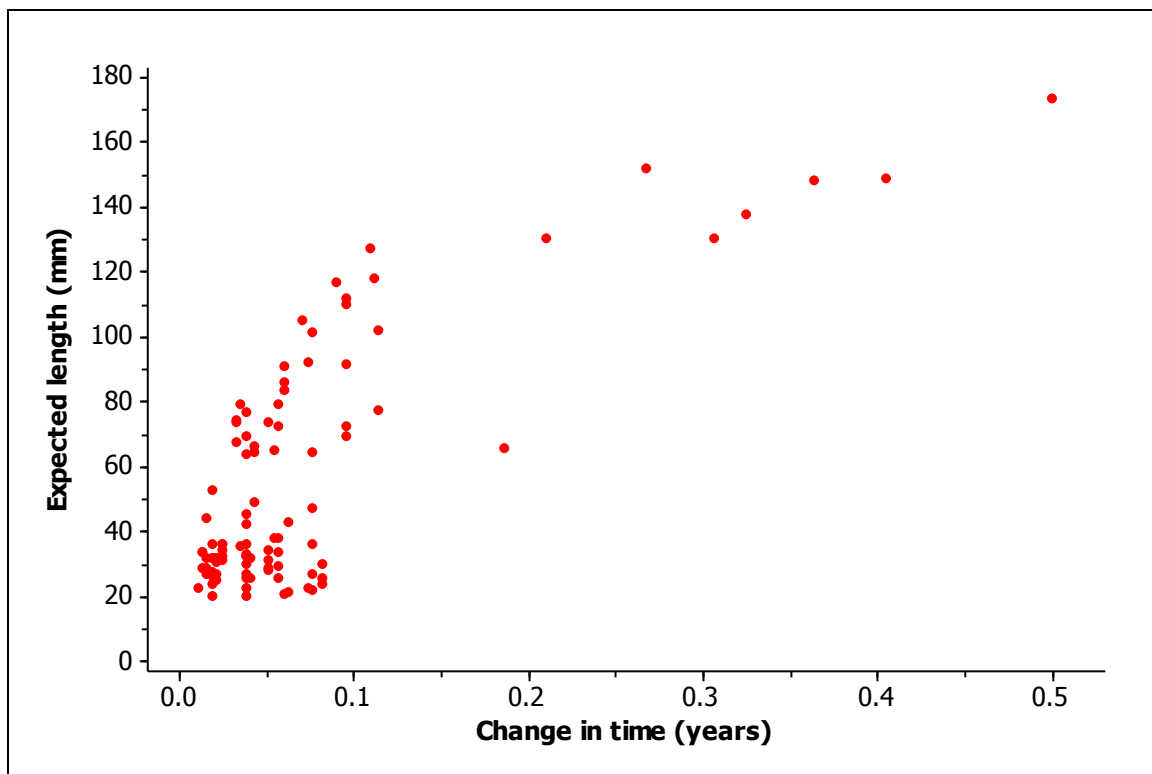


Figure 27: Appeldoorn's growth curve (FISAT II) for *Callinectes sapidus* kept in enclosures that were not missing any limbs. $L_{\infty} = 225.53$, $K = 1.15$, $C = 0.55$, $WP = 0.63$.

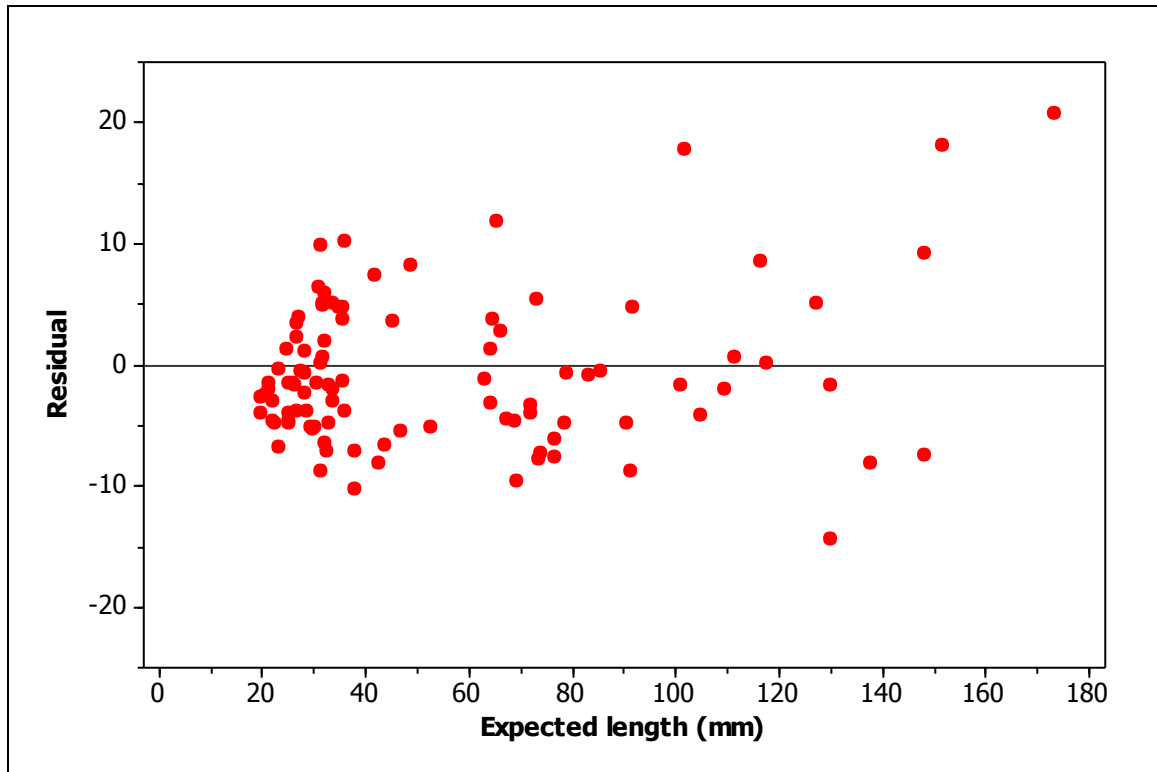


Figure 28: Residual plot of Appeldoorn's model using FISAT II for *Callinectes sapidus* kept in enclosures that presented no limb losses.

The Appeldoorn's model derived using Excel Solver had well distributed plot of residuals suggesting that it is a good fit (Figure 29). The parameters L_{∞} , and K were estimated to 204.90 and 1.3 respectively. The additional parameters C and WP were estimated to 0.37 and 0.42. A list of calculated parameters, R^2 and AIC values for all used models are shown on Table 8.

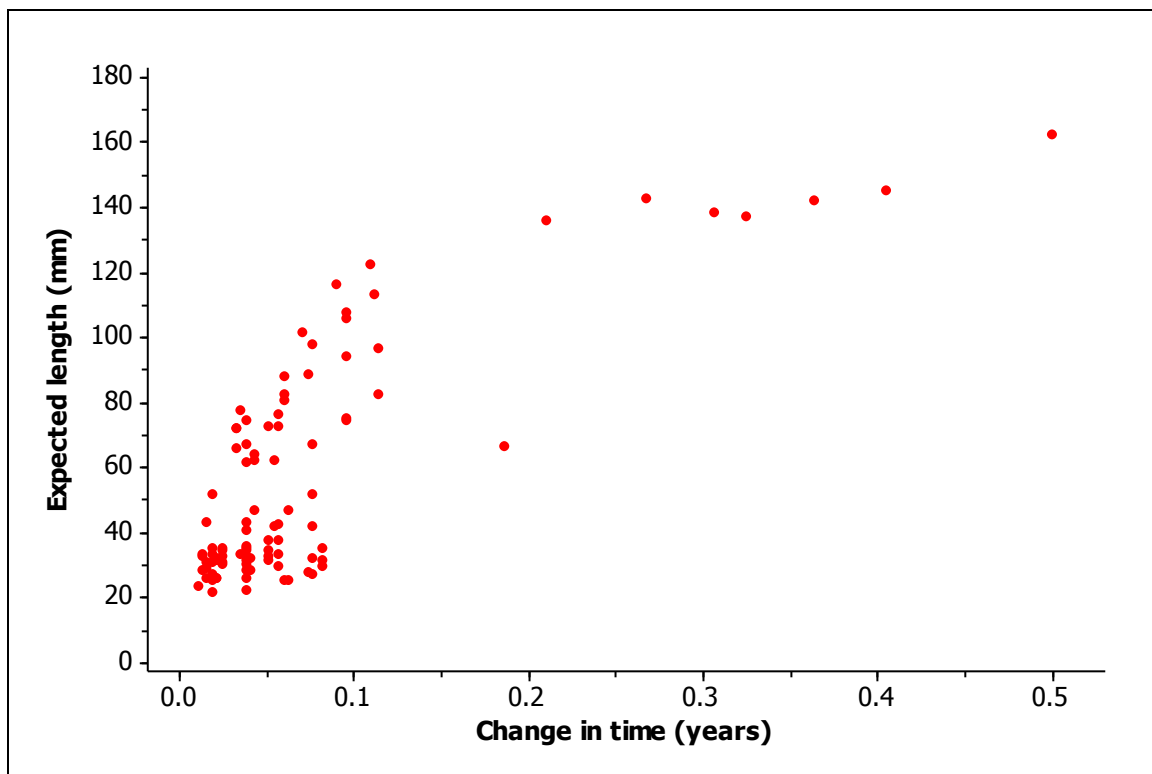


Figure 29: Appeldoorn's growth curve calculated using Excel and Solver for *Callinectes sapidus* kept in enclosures that were not missing any limbs. $L_{\infty} = 204.9$, $K = 1.3$, $C = 0.37$, $WP = 0.42$.

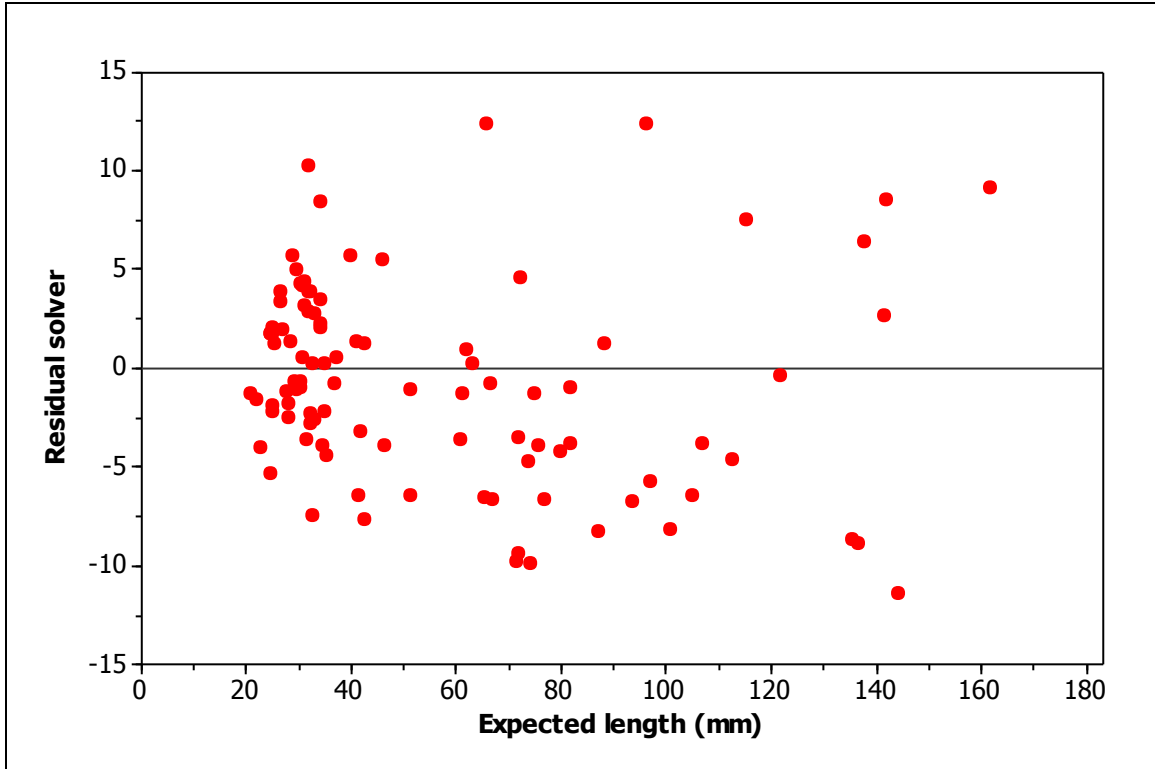


Figure 30: Residual plot of Appeldoorn's model using Excel and Solver for *Callinectes sapidus* kept in enclosures that presented no limb losses.

Table 8: Calculated model parameters, sum of square residuals (SS), R^2 and adjusted Aikike Information Criterion (AICc) for Fabens constant variance model, Fabens inverse linear variance model, Fabens power law variance model, Appeldoorn FISAT model, and Appeldoorn Solver model.

Model	L_∞	K	σ	ν	τ	C	WP	SS	R^2	AICc
Constant variance	223.8	0.92	6.67	-	-	-	-	4399	0.04	167.4
Inverse linear variance	189.4	1.77	-	0.61	-	-	-	6344	0.00	183.1
Power law variance	224.9	1.05	-	2.88	0.37	-	-	4653	0.73	170.9
Appeldoorn FISAT	225.5	1.15	-	-	-	0.55	0.63	3811	0.97	162.4
Appeldoorn Solver	204.9	1.30	-	-	-	0.37	0.42	2555	0.98	145.2

Mark-Recapture Study

A total of 2600 crabs were tagged as part of the mark-recapture portion of this study and 245 crabs were recaptured. Of the 245 recaptured crabs, 222 had molted at least once between tagging and recapture time.

Statistical Analysis

Growth rate of crabs used in mark-recapture study did not follow normal distribution (Figure 31, $P < 0.005$) so it was log-transformed for data analysis (Figure 32, $P = 0.132$).

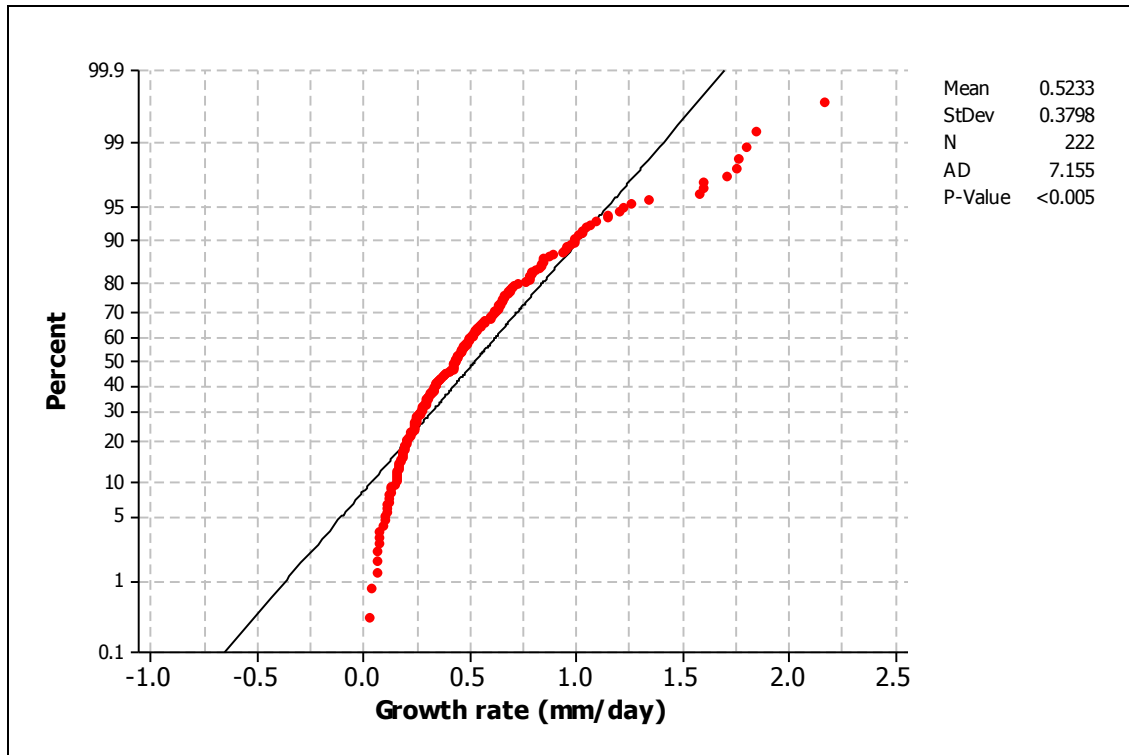


Figure 31: Normal probability plot of growth rate for *Callinectes sapidus* from mark-recapture study.

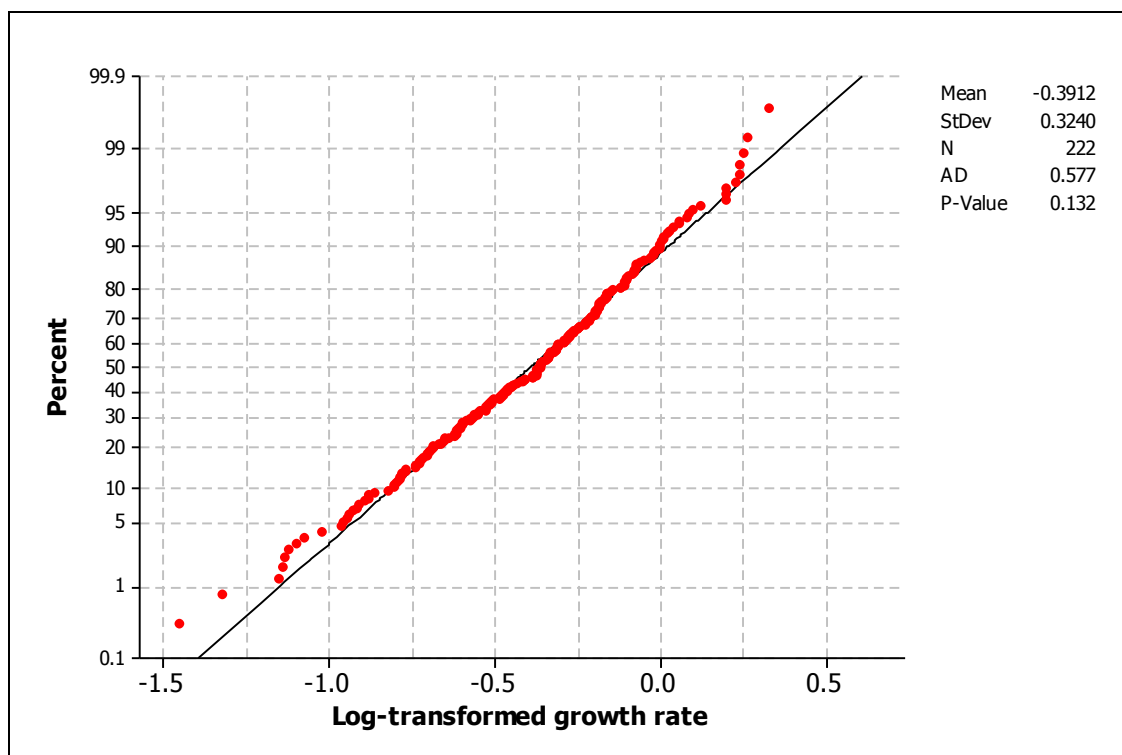


Figure 32: Normal probability plot of log-transformed growth rate for *Callinectes sapidus* from mark-recapture study.

GLM analysis of sex and missing limbs as variables and temperature and initial size as covariates indicated that only sex did not appear to have an effect on log-transformed growth rates of blue crabs in the wild (Table 9).

Table 9: General linear model (GLM, Minitab) results for log-transformed growth rate of *Callinectes sapidus* from mark-recapture study

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Initial carapace size (mm)	1	1.08	1.43	1.43	26.13	0.00
Average temperature	1	9.76	9.22	9.22	168.21	0.00
Sex	1	0.00	0.00	0.00	0.05	0.83
Missing limbs	1	0.46	0.46	0.46	8.39	0.00
Error	217	11.89	11.89	0.05		
Total	221	23.20				

A multiple regression analysis of growth rate as a function of initial size and temperature was performed to better visualize the effects of covariates. The slope of growth rates with respect to both initial size and average temperature were significantly different from zero (Table 10). Most of the crabs tagged in the mark-recapture study were between 18 to 40 mm CW. Growth rates amongst crabs in that size group seemed to be variable. The linear regression indicates that growth rates increase with increasing in initial size, which is not common, but the regression model does not explain the variation in growth (Figure 33, $R^2=6.2\%$). The linear regression of growth rate as a function of average temperature also indicates that growth rates increase as temperatures increase (Figure 34, $R^2=33.3\%$).

Table 10: Regression output (Minitab) for mark-recapture growth rate of *Callinectes sapidus* as function of temperature and initial carapace width.

Predictor	Coef	SE Coef	T	P
Constant	-0.60	0.09	-6.44	0.00
Initial size	0.01	0.00	5.42	0.00
Average temperature	0.04	0.00	11.40	0.00

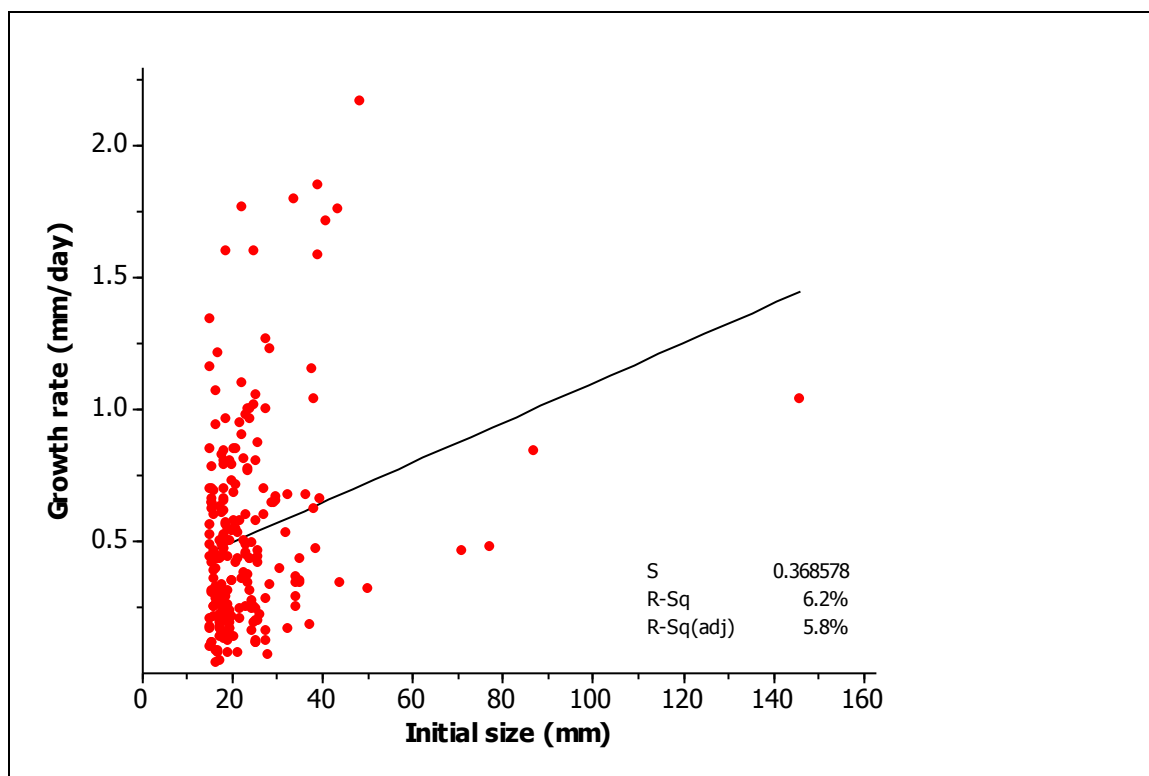


Figure 33: Linear regression of growth rate as a function of initial size. $R^2=6.2\%$.

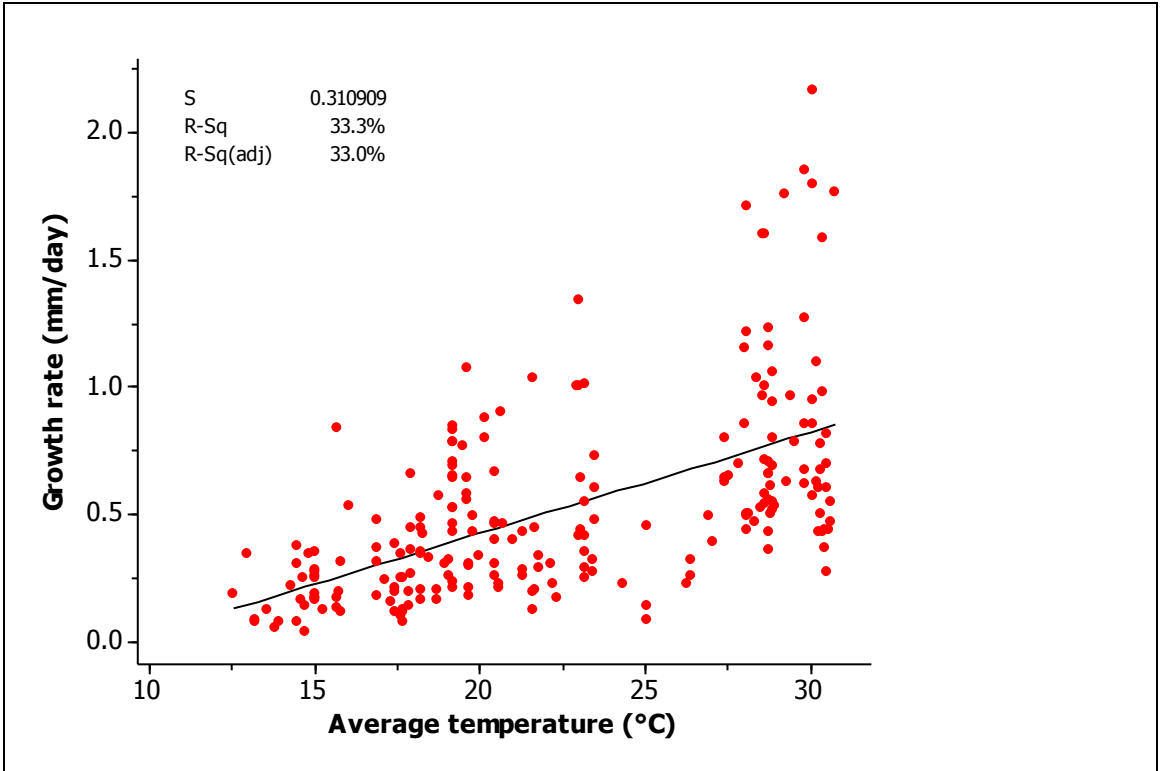


Figure 34: Linear regression of growth rate as a function of average temperature. $R^2=33.3\%$

Most of the crabs recaptured were not missing any limbs (n=150) or were missing one to three limbs (n=70). Very few crabs were missing four to six limbs (n=2) and none were missing more than six limbs. Growth parameters were estimated using only crabs that were not missing limbs.

Growth Models

A discontinuous model for mark-recaptured crabs could not be parameterized due to unknown IMP. Problems associated with this approach and possible solutions will be presented in the discussion section.

The Gulland-Holt plot used to obtain initial estimates of growth parameters K and L_{∞} for blue crabs from the mark-recapture study showed an unusual positive slope (Figure 35). Therefore, to remedy this, I fixed L_{∞} to 175.9 mm CW using published data from Louisiana and obtained an estimate of K of 1.40 (Figure 36). The plot of residuals showed a significant but small oscillation of data points ($C < 0.4$), indicating that data might be seasonally influenced (Figure 37).

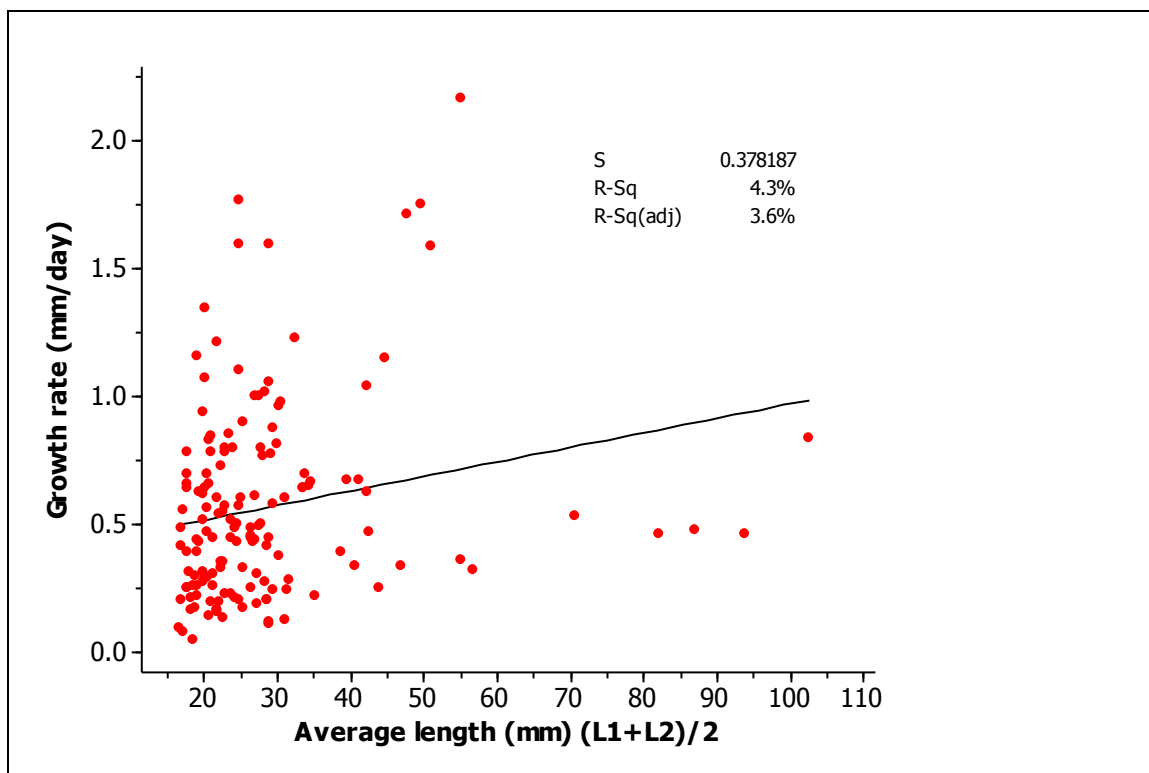


Figure 35: Gulland-Holt plot for *Callinectes sapidus* from mark-recapture study data that had no limb loss. R^2 : 4.3%.

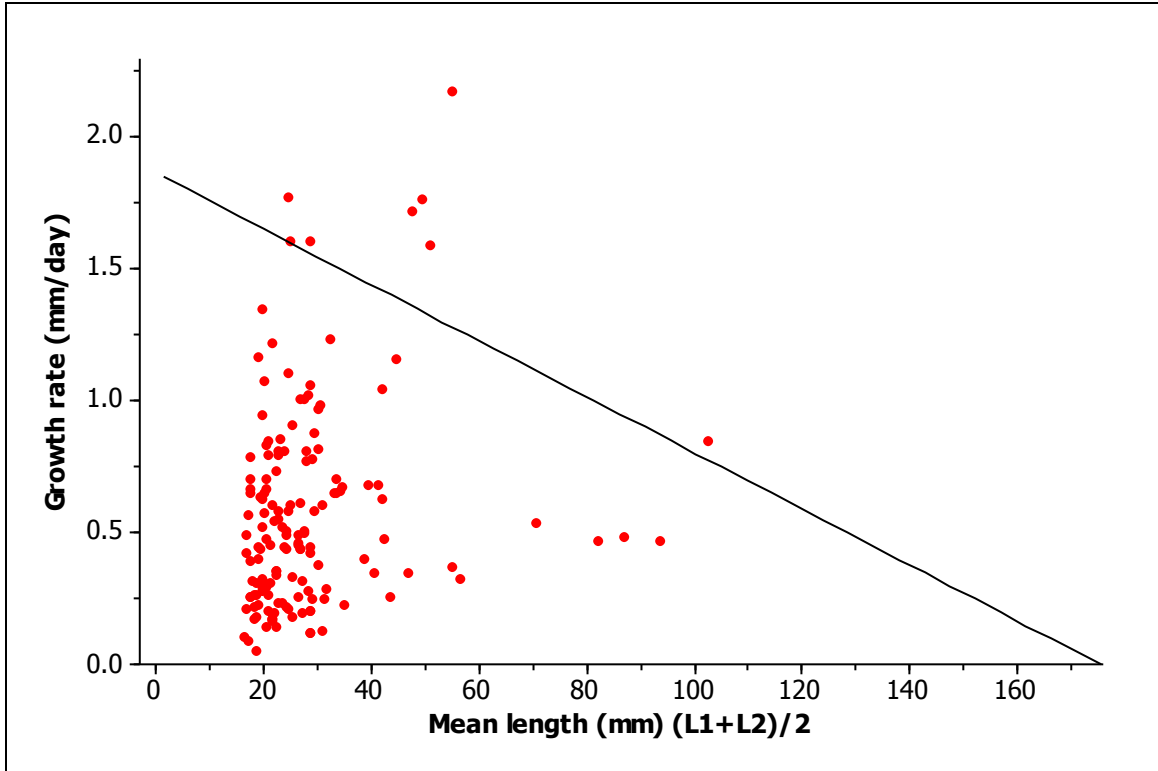


Figure 36: Forced Gulland-Holt plot of *Callinectes sapidus* from mark recapture study using a fixed L_{∞} value of 175.9 mm. Estimated value from model $K=1.29$.

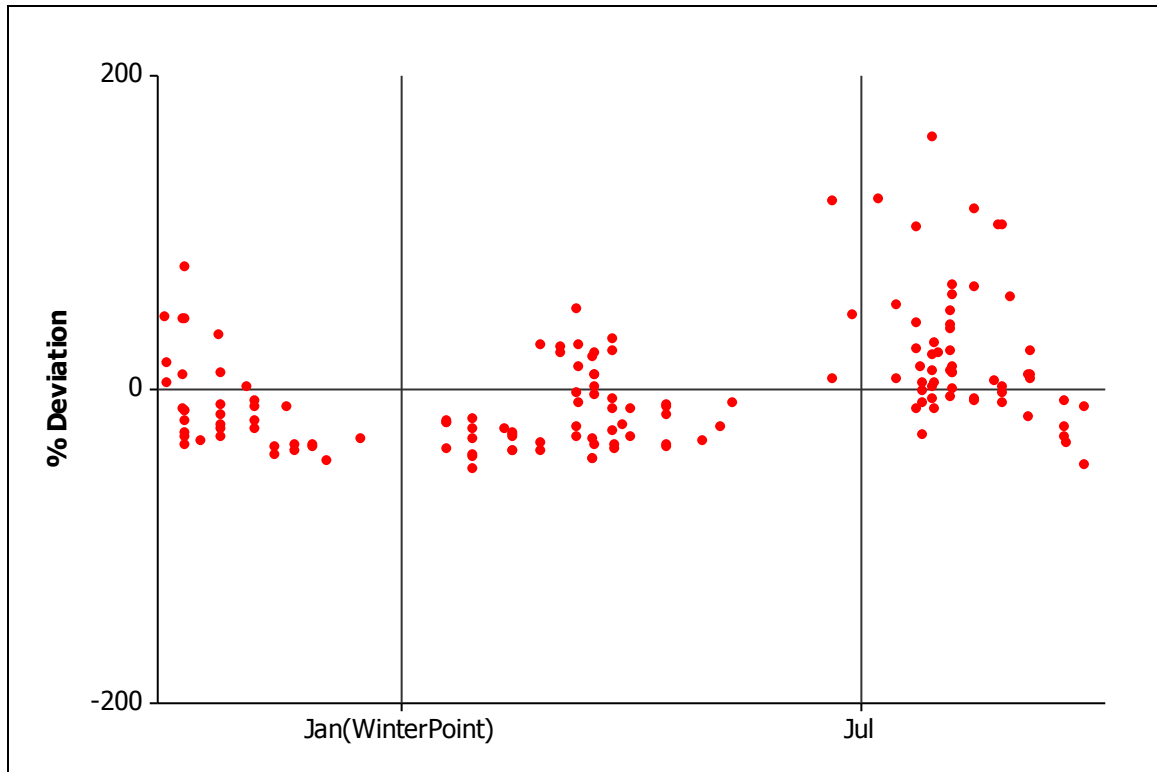


Figure 37: Forced Gulland-Holt plot of residuals for *Callinectes sapidus* from mark-recapture study. Note: The analysis indicates a strong oscillation of data points indicating seasonality on the growth of specimens that were significant but small ($C < 0.40$).

Faben's model using Excel and solver returned unrealistic results for all variations of the model. The constant variance method returned values of L_{∞} and K of 17,326.4 mm and 0.01. The inverse linear relationship method estimated L_{∞} and K to 16041.2 mm and 0.01. Finally, the power method estimated L_{∞} and K parameters to 2,974.1 mm and 0.05. The lognormal method also did not correctly calculate the parameters and yielded computational errors when using mark and recapture data.

Appeldoorn's method using FISAT II also returned unrealistic values for the estimated parameters. For example, L_{∞} was estimated to be 1,786.8 mm when using a minimum constraint for K of 0.10. The additional parameters WP and C were estimated to 0.45 and 0.54 respectively. When not setting a minimum constraint for K ($K=0.00$), L_{∞}

jumps to a number greater than 2 million, while WP and C maintain their values of 0.45 and 0.54 respectively. Using a fixed value of L_{∞} of 175.9 mm, K was estimated to 1.21 and WP and C were estimated to 0.46 and 0.54 respectively ($r^2=0.6882$).

When Excel and Solver were used to execute the Apeldoorn model, more unrealistic estimates of L_{∞} and K were obtained, that is 12500.8 mm and 0.01 respectively. The additional parameters C and WP were calculated to be 0.24 and 0.00 respectively.

Since all results for the mark-recapture study yielded unrealistic values, none of the models were graphically represented.

DISCUSSION

The main objective of this study was to parameterize growth of blue crabs in Galveston Bay, Texas. Due to the lack of a reliable way to obtain growth estimates of blue crabs from direct age estimates, mathematical calculations from growth increment data provide an alternative to model growth of these individuals.

Growth parameters were successfully estimated using both discontinuous and continuous approaches when using crabs kept in enclosures. A total of 284 growth per molt (GPM) field enclosure data points were initially available for data analysis, but after eliminating molt events with limb losses, only 99 data points were available to estimate model parameters. Based on these 99 molt events, GPM was estimated to increase blue crab's pre-molt CW size by $122.0\% \pm 6.8\%$. The physiological zero or T_{\min} was calculated to be 6.1 ± 0.05 °C, which was then used to estimate the average IP to 554 ± 53 degree-days.

Discontinuous growth of blue crabs in the Chesapeake Bay has been previously parameterized by Brylawski and Miller (2006). Their study used a combination of laboratory and field enclosure experiments to estimate parameters. Brylawski and Miller (2006) estimated GPM to $119.5\% \pm 7.5\%$, which is comparable with my estimates. Similar to my study, Brylawski and Miller (2006) found that sex did not influence GPM. They also found that pre-molt CW had an influence on GPM while temperature did not influence GPM of lab reared blue crabs (Brylawski and Miller 2006). In my study, I found that neither temperature nor pre-molt CW had an effect on GPM, which agrees

with the previous observations that GPM is remains unchanged over varying temperatures and pre-molt CW size (Smith 1997).

Tagatz (1968) performed an enclosure study similar to the current study in the St. Johns River, Florida. In his study, blue crabs were divided into 10 mm size classes and had highly variable mean GPM, from 120.9 to 134.2 percent. The average GPM of all size groups combined was 125.3 percent, which is also comparable with results obtained in my study. Tagatz (1968), however, found that GPM is higher in females, which contradicts the findings of the current study and Brylawski and Miller (2006). GPM of blue crabs have been estimated under lab conditions to be 122% (Leffler 1972) and 120.9 (Fitz and Wiegert 1991).

Although GPM results estimated in my study are comparable with results obtained by others, it is important to acknowledge constraints inherent in my experimental design that could possibly affect the physiological process of molting and GPM estimates. Limited space is a known factor to halter or slow growth of crustaceans and fish (Barton and Iwama 1991; Cheng and Chang 1994). My enclosures were only 7 percent of the volume of the enclosures used by Brylawski and Miller (2006) and 68 percent of the volume of the enclosures used by Tagatz (1968). However, the flow through design with ambient water would minimize any water quality concerns. In addition, the traps were at least 8 times larger than the average size (54.7 mm CW) of adult blue crabs. Energy input prior to molting is crucial for molting success and increase in body mass of crustaceans (Catacutan 2002; Sulkin 1975). Even though my results suggest that there were no difference in means of GPM of caged crabs that were being weekly fed or not, lack of food available could have affected the results I obtained.

However, it would be necessary to compare GPM of crabs being fed ad-libitum versus crabs only eating what is available in enclosures before making any final assumptions. Other factors known to affect GPM are limb injuries or losses (Smith 1990) and salinity (Van Engel 1958). The first I remediated by not including data points that fit this criteria. I could not determine if salinity had any effect in my analysis of GPM since the daily salinity data collected was compromised by instrument error. However, salinity did not appear to change significantly based on my weekly measurements in the field. Tagatz (1968) found no difference between GPM in crabs kept in freshwater (less than 1 p.p.t.) and brackish (7.5 to 25.8 p.p.t.) conditions. All of my observations were made in water ranging in salinity from 12 to 25 p.p.t.

The T_{\min} for blue crabs has been estimated by Smith (1997) and Brylawski and Miller (2006) by using Curry and Feldman (Curry and Feldman 1987) back calculation methodology. Smith's estimate of T_{\min} for blue crabs was calculated by using past studies from Tagatz (1968) and Fitz and Wiegert (1991) and was estimated to 9.8 °C (Smith 1997). Brylawski and Miller (2006) estimated T_{\min} by using their own laboratory reared crab data in temperature controlled tanks and estimated T_{\min} to be 10.8 °C. My estimate of T_{\min} , 6.9 °C, was much lower than those estimated by other studies. Whether T_{\min} for blue crabs in Galveston Bay is actually lower than those calculated in previous studies can only be confirmed if further experiments and comparisons are performed in the future.

Chronological IP for blue crabs have been mostly observed under laboratory conditions, making it easier to determine the exact date of and to control the effects of temperature on IP (Brylawski and Miller 2006; Leffler 1972; Van Engel 1958). Smith's

methodology of calculating IP in degree-days makes it easier to estimate IP of blue crabs in the wild, where temperature cannot be controlled, but can be easily monitored (Smith 1997). Brylawski and Miller (Brylawski and Miller 2006) used Smith's methodology to estimate molt-process parameters combining laboratory data and field enclosure data of crabs in the Chesapeake Bay, obtaining a physiological IP of 536 ± 231 degree-days.

When using IP and temperature data from field enclosures, I calculated physiological IP to be 568 ± 31 degree-days, which is higher than Brylawski and Miller (2006) previous study. Conversely to GPM, IP did not appear to be affected by limb losses. The same results were observed by Smith (1990). The effects of quantitative feeding on intermolt-period of blue crabs have not been previously described, only the effects of diet quality (Winget et al. 1976). Most of the studies on IP of blue crabs that I reviewed fed blue crabs ad libitum, daily, or every other day (Brylawski and Miller 2006; Cadman and Weinstein 1988; Leffler 1972; Smith 1990; Tagatz 1968). Even though I only fed crabs with one medium size shrimp weekly, it appears that the extra feeding had an impact on IP. Therefore, it is possible that IP was underestimated in previous assessments.

In this study, I was hoping to estimate molt-process parameters for blue crabs of Galveston Bay by comparing and possibly combining results from field enclosures and mark-recapture studies. Estimates of IP for mark-recapture crabs could not be calculated due to an error in sampling that was only brought to my attention after most of the sampling had already been performed. It is not possible to know exactly when molting occurred in the wild when recapturing a crab, unless it has a soft shell. Hoening and Restrepo (1989) developed a method to estimate IP of crustaceans using mark-recapture data. Their methodology uses a maximum likelihood approach to estimate IP by

calculating the probability of molting in proportion to the time at liberty and initial size (Hoenig and Restrepo 1989). However, to successfully calculate IP using this methodology, one must also consider recaptured crabs that did not molt over a Δt time, which I did not do. I marked crabs externally to assure that I only retrieved crabs that had molted for the analysis because for the analysis of growth rates of various models in FISAT, it requires that all data points have a change in length. I was still able to get estimates of GPM and physiological IP using field enclosed crabs, which has not been estimated for Galveston Bay or Texas blue crabs thus far.

Many authors have estimated the VBGF parameters L_{∞} and K for blue crabs of the Chesapeake Bay (Ju 2000; Rothschild et al. 1992; Rugolo et al. 1998; Smith 1997), Delaware Bay (Helser and Kahn 2001), North Carolina (Eggleston et al. 2004), Florida (Pellegrin et al. 2001) and Louisiana (Smith 1997). For comparison purposes, the results obtained in these studies are listed in Table 11.

Table 11: Different estimates of the von Bertalanfy growth function (VBGF) parameters for *Callinectes sapidus*

L_{∞}	k	Location	Reference
234.7	0.75	Delaware Bay	Helser and Kahn (1999)
200.6	0.62	Delaware Bay	Helser and Kahn (1999)
200.3	0.93	Delaware Bay	Helser and Kahn (1999)
187.0	0.51	Chesapeake Bay	Rothschild et al. (1992)
191.9	0.64	Chesapeake Bay	Smith 1997
262.5	0.59	Chesapeake Bay	Rugolo et al. (1998)
180.9	0.49	Chesapeake Bay	Ju (2000)
240.0	1.09	Chesapeake Bay	Ju (2000)
207.5	1.71	Chesapeake Bay	Ju (2000)
207.5	1.19	Chesapeake Bay	Ju (2000)
218.4	0.66	North Carolina	Eggleston et al. (2004)
175.9	1.45	Louisiana	Smith (1997)
276.0	0.66	Florida	Pellegrin et al. (2001)
223.8	0.92	Galveston Bay	Pronker (2014)
189.4	1.77	Galveston Bay	Pronker (2014)
224.9	1.05	Galveston Bay	Pronker (2014)
225.5	1.15	Galveston Bay	Pronker (2014)
204.9	1.30	Galveston Bay	Pronker (2014)

My estimates of the VBGF were within range of the results obtained by other studies cited on Table 11. Of the three Fabens variations that I calculated, the constant variance method yield the lowest AIC value of 171.1, suggesting that this is the best fit model. However, the low R^2 value (0.04) and the plot of the residuals (Figure 22) with most of the points concentrated in the top left of the plot, indicated that the model suffered from a poor fit. The constant variance model estimated L_{∞} and k to be 223.8 and 0.92 respectively.

When analyzing the plot of residuals from the forced Gulland-Holt plot (Figure 20), it is evident that the data points follow a seasonal pattern. The low AIC and high R^2 results obtained from the Appeldoorn model using both FISAT (AIC=169; $R^2=0.97$) and Excel Solver (AIC=1498. $R^2=0.98$) confirm the seasonal trend of data points. Based on my results, it is evident that the Appeldoorn model best represented the growth of the blue crabs kept in field enclosures. The growth parameters L_{∞} and K were estimated to be 225.5 and 1.15 when using FISAT and 204.9 and 1.30 when using Excel and Solver.

The vast use of the VBGF in literature to estimate growth of many different fisheries species should not bring the assurance that this is the best approach to model the growth of blue crabs. One of the main assumptions of the VBGF is that growth is continuous (von Bertalanffy 1938). The growth of blue crabs does not agree with this assumption, occurring only during a molt event. Additional problems arrive when considering that blue crab growth with cease during cold months and that they reach a terminal molt (Churchill 1919), none of which are characterized in the VBGF and its variations. The molt process approach using Smith's (Smith 1997) methodology to calculate physiological IP is able to target all these issues associated with blue crabs

growth. The molt process approach, however, does not provide the growth parameters L_{∞} , K , and t_0 , which are essential to in stock assessment and species management. Combining both molt-process and VBGF models appears to be a great solution to fit growth of blue crabs (Smith 1997).

Unfortunately, I was unable to obtain any parameter estimates for blue crabs from the mark-recapture study. That does not mean that this method should be discarded in future studies. I believe that estimates could not be calculated due to the lack of data points for blue crabs over 40 mm CW. Larger blue crabs prefer to inhabit deeper channels of the estuary (Van Engel 1958). The collapsible traps I was using were located near shore in depths between 1 to 3 feet and were attracting mostly juveniles between 15 to 40 mm CW. Towards the end of the study, I noticed the lack of data point in the higher size classes and the implications those were causing in my preliminary data analysis. Therefore, I started using larger crab pots and locating them in deeper parts of the study area, attracting the few larger crabs I was able recapture.

Studies show that although blue crabs tend to migrate between lower and upper estuary, they usually do not migrate out of estuary, showing trends of site fidelity (Aguilar et al. 2005; Fischler and Walburg 1962), making it attractive to perform mark-recapture studies using blue crabs. To target blue crabs of different size classes, an extensive mark-recapture study must be executed using different active and passive gears in different depths and areas of the estuary. This kind of study would require extensive time and effort, but would provide valuable data needed to estimate accurate and unbiased growth parameters for blue crabs in the wild.

FUTURE RECOMMENDATIONS

Despite the amount of time and effort spent in mark-recapture studies, this is still the best way to estimate true growth parameters of individuals that are hard to age, like the blue crab. In addition to an extensive mark-recapture study, a combination of laboratory and field enclosure studies would be of great reference to measure how reliable those results are when compared to results obtained in wild.

A direct way to determine length at age is still preferred when possible to estimate growth parameters. Even though the reliability of lipofuscin ageing technique for blue crabs (Ju et al. 1999; Ju et al. 2001) is still under questioning (Sheehy 2008), it would be interesting to compare results obtained through this method with results from field enclosures. In a recent publication, Kilada et al (2012) provided a novel way to age decapod crustaceans by counting growth bands in calcified body structures of the eye stalk and gastric mill. This new technique seems promising to obtain accurate length and age estimates for blue crabs to be used in future stock assessments.

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