# ABSTRACT


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| Title of Document: | A VON BERTALANFFY BASED MODEL FOR THE ESTIMATION OF OYSTER (*CRASSOSTREA VIRGINICA*) GROWTH ON RESTORED OYSTER REEFS IN CHESAPEAKE BAY |
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A model to estimate the mean monthly growth of *Crassostrea virginica* oysters in Chesapeake Bay was developed. This model is based on the classic von Bertalanffy growth function, however the growth constant is changed every monthly timestep in response to short term changes in temperature and salinity. Using a dynamically varying growth constant allows the model to capture seasonal oscillations in growth, and growth responses to changing environmental conditions that previous applications of the von Bertalanffy model do not capture. This model is further expanded to include an estimation of *Perkinsus marinus* impacts on growth rates as well as estimations of ecosystem services provided by a restored oyster bar over time.

The model was validated by comparing growth estimates from the model to oyster shell height observations from a variety of restoration sites in the upper Chesapeake Bay. Without using the *P. marinus* impact on growth, the model

consistently overestimates mean oyster growth. However, when *P. marinus* effects are included in the model, the model estimates match the observed mean shell height closely for at least the first 3 years of growth.

The estimates of ecosystem services suggested by this model imply that even with high levels of mortality on an oyster reef, the ecosystem services provided by that reef can still be maintained by growth for several years. Because larger oyster filter more water than smaller ones, larger oysters contribute more to the filtration and nutrient removal ecosystem services of the reef. Therefore a reef with an abundance of larger oysters will provide better filtration and nutrient removal. This implies that if an oyster restoration project is trying to improve water quality through oyster filtration, it is important to maintain the larger older oysters on the reef.

# A VON BERTALANFFY BASED MODEL FOR THE ESTIMATION OF OYSTER GROWTH (*CRASSOSTREA VIRGINICA)* ON RESTORED OYSTER REEFS IN CHESAPEAKE BAY

By

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Dedication

For my parents

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Table of Contents

Dedication ii
Acknowledgements iii
Table of Contents v
List Of Tables vii
List Of Figures viii
Introduction 1
CHAPTER 1: Background 4
1.1 Policy and Economic History of Oysters in the Chesapeake Bay 4
1.2 Ecology and Natural History of *Crassostrea virginica* in Chesapeake Bay 14
1.3 Modeling as a Tool for Oyster Restoration in Chesapeake Bay. 22
CHAPTER 2: Model Development 27
2.1 Assumptions and Exclusions of the Model 27
2.1.1 Food Supply 27
2.1.2 Oxygen 28
2.1.3 *Haplosporidium nelsoni* (MSX) 29
2.1.4 Recruitment 30
2.1.5 Habitat Quality 31
2.2 The von Bertalanffy Growth Function and Previous von Bertalanffy Based Models 33
2.3 Data Issues: 45
2.3.1 Diploid vs. Triploid Growth 49
2.4 A Regression Driven Approach to the von Bertalanffy Growth Model to Account for Seasonal Growth. 53
2.5 *Perkinsus marinus* Disease Impact 60
2.5.1 Time to First Infection 60
2.5.2 *P. marinus* Effect on Growth 61
Chapter 3: Model Testing 64
3.1 Calibration and Validation: Model Testing Against Observed Data 64
3.2 Model Performance with Extremely Low and High Salinity Regimes 68
CHAPTER 4: Other *Crassostrea virginica* Models 71
Chapter 5: Model Expansion: Population and Ecosystem Services Estimates 81
5.1 Mortality 82
5.2 Biomass 86
5.3 Water Filtration and Nutrient Removal 89
5.4 Modeling Multiple Oyster Plantings 94

Chapter 6: Conclusions 96
APPENDIX I: Matlab Model Code 133
Literature Cited 149

List Of Tables

Table 1: Calculated Approximate Values For The von Bertalanffy Growth Parameter K At Each Site For Each Month _____ 101

Table 2: Temperature And Salinity Threshold Values Used For Disease Mortality _____ 103

Table 3: Newell et al. (2004) Eastern Oyster Clearance Rates And Nutrient Removal _____ 104

List Of Figures

Figure 1:Maryland Oyster Harvest 1870-2003, (Maryland DNR data) _____ 105

Figure 2: Maryland Oyster Harvest 1975-2003 (Maryland DNR data) _____ 106

Figure 3: Classic von Bertalanffy Growth _____ 107

Figure 4: Oscillating von Bertalanffy function (eq 2) fit to data from Shippen Creek and Spaniard Point sites in the Chester River, using a least squares technique _____ 108

Figure 5: Regression to determine the von Bertalanffy growth constant K from mean temperature and salinity _____ 109

Figure 6: Growth Model Process _____ 110

Figure 7: Model Calibration: Growth model output compared to observed mean shell height of *Crassostrea virginica* at the Choptank river *Crassostrea ariakensis* study site_____ 111

Figure 8: Model Calibration: Growth model output compared to observed mean lengths of *Crassostrea virginica* at the Patuxent River *Crassostrea ariakensis* study site_____ 112

Figure 9: Model Validation: Model predictions using data from Chesapeake Bay Program monitoring station LE1.1 to estimate growth at Kitts Marsh (Patuxent River) compared to observed mean lengths at Kitts Marsh 113

Figure 10: Model Validation: Model predictions using data from Chesapeake Bay Program monitoring station ET4.2 to estimate growth at Shippen Creek (Chester River) compared to observed mean lengths at Shippen Creek _____ 114

Figure 11: Model Validation: Model predictions using data from Chesapeake Bay Program monitoring station ET5.3 to estimate growth at Bolingbroke Sands (Choptank River) compared to observed mean lengths at Bolingbroke Sands_____ 115

Figure 12: Model growth estimates for an extreme low salinity site: ET 4.1 in the upper Chester River _____ 116

Figure 13: Model growth estimates for a high salinity site: LE 4.3 at the mouth of the York River._____ 117

Figure 14: Model growth estimates for a high salinity site: LE 4.3 at the mouth of the York River, without disease enabled in the model _____ 118

Figure 15: Estimated mortality at ET 4.2 near Shippen Creek (Chester River) 119

Figure 16: Estimated mortality at a high salinity site LE 4.3 at the mouth of the York River. _____ 120

Figure 17: Regression of oyster shell height against oyster biomass for oysters collected throughout the Maryland portion of Chesapeake Bay from 1997 to 2004. _____ 121

Figure 18: Estimated oyster biomass per square meter at ET 4.2 near Shippen Creek (Chester River) _____ 122

Figure 19: Estimated Oyster Biomass per square meter at ET 5.3 near Bolingbroke Sands (Choptank River) _____ 123

Figure 20: Estimated monthly clearance rate (liters/month/ $m^2$) at ET 4.2 near Shippen Creek (Chester River) _____ 124

Figure 21: Estimated monthly clearance rate (liters/month/ $m^2$) at ET 5.3 near Bolingbroke Sands (Choptank River) _____ 125

Figure 22: Estimated total monthly nitrogen removal (g $N/m^2$) at ET 4.2 near Shippen Creek (Chester River) _____ 126

Figure 23:Estimated total monthly nitrogen removal (g $N/m^2$) at ET 5.3 near Bolingbroke Sands (Choptank River) _____ 127

Figure 24: Estimated monthly phosphorus burial at ET 4.2 near Shippen Creek (g $P/m^2$) _____ 128

Figure 25: Estimated monthly phosphorus burial at ET 5.3 near Bolingbroke Sands ($g/m^2$)_____ 129

Figure 26: Estimated annual nutrient removal at ET 4.2 near Shippen Creek compared to Boynton et al. (1995) Estimates _____ 130

Figure 27: Estimated annual nutrient removal at ET 5.3 near Bolingbroke Sands compared to Boynton et al. (1995) estimates. _____ 131

Figure 28: Estimated biomass per meter square for a 10 year restoration program with replanting every 2 years at ET 4.2 (Chester River) _____ 132

## Introduction

The Eastern oyster (*Crassostrea virginica (Gemlin, 1791)*) has been a part of the culture and economy of the Chesapeake Bay region since before European settlement. The oyster was a major keystone species in the Chesapeake Bay, exerting a controlling influence on the biological structure and functioning of the entire ecosystem. Scientists have been actively studying the eastern oyster for hundreds of years. However, in spite of the importance of the oyster, there is still quite a bit that is unknown about the species itself and how it interacts with its environment.

For example, not enough is known about the relationship between current standing stock of oysters and expected recruitment. That is; if we know the size of an adult population in one specific place, it is difficult to make reliable predictions about how many larvae from those oysters will settle or where they will set. Additionally, not enough is known about the dynamics of the *Perkinsus marinus* (dermo) and *Haplosporidium nelsoni* (MSX), the two major diseases that affect oysters in Chesapeake Bay. Growth rates of *C. virginica* are known to change in response to variations in temperature, salinity and other environmental factors, however the specific magnitude of these changes in growth are not known and are difficult to separate out from other effects.

This research could not attempt to address all of these problems but rather it focused specifically on oyster growth and attempted to both refine the information from previous studies in this area, and develop a new approach for future work.

As such, there were two main goals of this research project. One was the development of a variation of the classic von Bertalanffy growth model that can be used to describe dynamic seasonal growth. The second major goal was the development of a model to estimate *C. virginica* growth in the upper (Maryland) portion of Chesapeake Bay, based on the new von Bertalanffy variant.

The application of the new modeling approach to a specific oyster growth model allows for specific examples that can be used to test and demonstrate the effectiveness of the model and modeling tools. Furthermore, the modeling process itself is valuable in that it serves to refine knowledge about a subject that has been found in a wide range of other studies. Conversely, it also serves to highlight the specific areas in which knowledge about a subject is lacking.

The model developed for this project is a simple growth model of oysters planted as part of a restoration project at any given location in the upper portion of the Chesapeake Bay. The growth estimates from the model directly respond to monthly variations in temperature and salinity. Thus, the model may be useful to help determine the suitability of a given site for an oyster restoration project or reserve planting. The model stops short of being an oyster population model

because it does not incorporate annual recruitment since both the temporal and spatial relationships of parental broodstocks and recruitment are unknown in Chesapeake Bay. Modeling these relationships was not attempted due to a desire to keep this project tractable.

## CHAPTER 1: Background

### 1.1 Policy and Economic History of Oysters in the Chesapeake Bay

Early post-European settlers in the Chesapeake Bay area reported oyster reefs so numerous and large that they posed a hazard to navigation of ships in the Bay (Kennedy & Breisch 1983, Warton 1957). Since that time a massive oyster industry grew in the region and has now all but disappeared. The oyster fishery in Maryland is distinct from most of the other oyster fisheries in the world in that it remains a wild fishery, with almost no oysters in cultivation or aquaculture. The first observations that the oyster fishery should be managed and protected were made almost 200 years ago (Kennedy & Breisch 1983). Since that time, there have been many attempts to manage, restore and revitalize the oyster fishery, however the oyster population has still suffered a massive decline and the current oyster population is a fraction of what it once was.

The first law to regulate oyster harvesting in Maryland was established in 1820. This law prohibited vessels not owned by Maryland residents from dredging for oysters or transporting them out of the state. This law was established to protect the oysters in the Maryland portion of the Bay from fishermen moving out of the highly depleted oyster bars in New England. At the time it was feared that the industry from New England would move down to Maryland and over fish and deplete the stock of oysters in the Chesapeake (Kennedy and Breisch 1983).

Another early management law was passed in 1936, where Somerset and Dorchester counties prohibited burning of oysters to make fertilizer. These counties feared that this practice would overexploit the resource and not allow for more valuable uses of oysters (Kennedy & Breisch 1983). Worchester county established the first oyster season in Maryland. Legislators in this county were concerned that continuous harvesting of oysters would not allow the oyster stock to replenish itself. They hoped that a partially closed season would help to relieve fishing pressures (Kennedy & Breisch 1983).

In 1865 the state of Maryland established a statewide licensing program for oyster harvesting and established a set of regulations for oyster harvest. This state level regulatory structure superceded the local county regulations and in many cases made some significant changes. Many counties had previously prohibited the use of dredges and scrapes for oyster harvest (Kennedy & Breisch 1983). Dredges are a much more efficient method of capturing oysters, especially in comparison to hand tonging (the other main method of the day), due to the greater depths at which they can be used and due the greater area that can be effectively fished by a dredge. Thus, the use of dredges allows for a much greater possible harvest. However, dredges are more destructive to oyster reef structure and can break up the shell accumulations that form the reef. This loss of reef structure reduces the amount of area that spat can settle on and further increases the effective fishing pressures on the oyster stock (Rothschild et al. 1994).

In 1878, Winslow conducted the first oyster survey of the Tangier and Pocomoke sounds. This study showed a diminishing oyster abundance (Kennedy & Breisch 1983). Several years later, in 1882, W.K. Brooks was commissioned by Maryland to conduct a broader survey of oyster beds in Maryland, using Winslow's methods. The results of this study showed a broad decline in oyster abundance and a reduction in the ratio of live oysters to shell on each of the surveyed bars (Kennedy & Breisch 1983). Brooks recommended that the oyster resource be more actively managed, and also that when oyster bars reach a depleted state they should be closed to fishing when needed to allow for resettlement of the bars and regrowth of the reefs (Brooks 1905).

Peak harvest of oysters in Maryland was in 1885 with landings of over 15 million bushels (DNR data, 2005). The total harvest declined steadily after this point until the 1920s (figure 1). The increased capture efficiency of dredges were likely responsible for the increased harvest up until this point.

In 1890 a "cull law" was passed. This law set the minimum size for harvested oysters at 2.5 inches and required that oysters under this limit as well as oysters with spat (newly settled oysters) attached to their shells be tossed back immediately. However, this law was unpopular with watermen and was largely ignored (Brooks 1905).

In 1906, C.C. Yates began a six-year survey of the oyster bars in the Chesapeake Bay. This study mapped the distribution of oysters and natural oyster reefs in the bay and constituted the most extensive survey of the extent of oysters in the bay for almost 70 years (Kennedy & Breisch 1983).

One of the primary goals of the Yates survey was to identify the places in the bay where there were naturally occurring oyster beds, and the places where there was "barren bottom" which could be leased for use in private oyster aquaculture. Between 1906 and 1914 there were several laws passed in the Maryland legislature that represented an ongoing conflict between those trying to encourage private aquaculture and those supporting the primarily wild caught fishery.

The Haman Oyster culture Law of 1906 expanded the area of the bottom that was allowed to be leased by the state for aquaculture, however this bill included a wide range of gear restrictions and additional fees such that actually establishing an aquaculture operation was very difficult. The 1912 Price-Campbell Bill eased many of these previous restrictions, however 2 years later the Shepard bill again created many barriers to aquaculture. The Shepard Bill, established that any area fished for oysters once in 5 years could not be leased by the State for private aquaculture. This effectively prevented the granting of bottom leases for oyster aquaculture (Kennedy & Breisch 1983, Paynter 1996).

This back and fourth between the wild caught fishery and private oyster culture has been one of the characteristic issues surrounding oyster management in Maryland, and continues to be widely discussed today. Increased support for aquaculture has been repeatedly suggested since before Winslow's first survey in 1878. The debate was at its peak in the early 20th century, however even the most recent management agreements such as the 1993 "Oyster Roundtable" and the Chesapeake 2000 agreement, still actively supported oyster aquaculture in Maryland (Paynter 1999, NRC 2004). In spite of this long history of support for oyster aquaculture in Maryland, the industry remains one of the only primarily wild caught oyster fisheries in the country.

The oyster harvest in Maryland declined precipitously from the peak in 1885 to the mid 1920's. Between the mid-1920's and up until the 1980's the oyster harvest stabilized at around 2-5 million bushels per year (figure 1) (DNR 2005). This stabilization may be attributable to the introduction of shell planting, and oyster transplantation programs by the state of Maryland.

In 1916 Maryland began to establish reserve areas for oyster transplantation. Seed oysters from low salinity areas were moved into high salinity areas where they would grow faster. In 1922 the shell planting program was established. This program helped encourage spat settlement by planting shucked oyster shell from packinghouses to help restore lost structure and hard surface to depleted oyster reefs (Kennedy & Breisch 1983, Paynter 1996, NRC 2004).

In 1927 these shell planting programs became a central part of the oyster management strategy in Maryland. In order to support the program, a 10% shell tax was established. That is 10% of the shell processed by an oyster packing house in Maryland was to be supplied to the state for use in these repletion programs. In 1947 this tax was increased to 20% and then to 50% in 1953 (Kennedy & Breisch 1983). Additionally, in 1927 cull size was increased to 3 inches from 2.5 inches, and better enforcement of the cull limits meant that the law was not ignored, as it had been in the past. These changes in policy and enforcement may have helped the oyster catch remain stable.

However, during this time there was still substantial concern about overharvesting. In 1936 the Maryland State Planning Commission conducted a study of the oyster industry and noted a continued decline in harvest. This commission argued that more oyster shell needed to be returned to the oyster bars to support resettlement. Additionally, this commission argued for more support of private aquaculture of oysters in the bay and for stronger enforcement of the cull limits. In 1943 a similar commission came to similar conclusions and made similar recommendations (Kennedy & Breisch 1983, NRC 2004).

In 1961 the state began a program to dredge fossil shell from "extinct" oyster reefs. This shell was cleaned and used in the seed and shell planting programs.

Following the start of this program, fossil shell quickly became the primary source of substrate used in the state repletion programs. (Cabraal 1978).

These annual shell planting and seed transplanting programs quickly became the most important tools used to support the oyster harvest (Ulanowicz et al. 1980, Lipton et al. 1992). At this point the oyster industry in Maryland began to take on many characteristics of a "put and take" fishery. The process of planting oyster shell to capture spat in areas that were known to be productive and then moving those seed oysters into the fishing grounds successfully served to support the oyster harvest and provide significant short term economic benefits (NRC 2004).

In 1950, the oyster pathogen *Perkinsus marinus* (dermo) was first found in the Bay. *Haplosporidium nelsoni* (MSX) was found in 1959 (Andrews 1996). Both of these parasites have had a significant effect. Both MSX and dermo are more active and more lethal to oysters in high salinity (over 15) (Paynter 1996) and both can potentially kill oysters before they reach market size. In response to these diseases the repletion program was modified in the 1960s. Instead of moving oysters from low salinity areas to high salinity to promote faster growth, seed oysters were moved from moderate and high salinity areas to low salinity areas in order to reduce the effect of both oyster parasites, and allow the oysters to live long enough to reach market size. This policy helped to support the oyster harvest in the short term but had the unfortunate effect of introducing the oyster

diseases into areas of the Bay where they would not normally have been able to reach (Paynter 1996).

In the 1980s, a series of droughts raised the salinity of the Bay and allowed both MSX and dermo diseases to reach substantially higher prevalence and intensity. This increase in disease caused widespread oyster mortality (Burreson and Andrews 1988, Andrews 1996), and resulted in substantially lower harvest in 1982-1983, as well as again in 1987 to 1993 (figure 2). A similar pattern of high disease mortality and lowered harvest during droughts continues to the present (figure 2) (DNR 2005). While there have been brief periods of slight recovery, such as in 1998-2000, overall harvest continues to decline. 2003 harvest was estimated at 53,000 bushels, this is only 35% of the previous year's harvest (figure 2) (DNR 2005).

Until recently the fundamental character of the restoration efforts in Maryland has been a focus on restoring and supporting the oyster harvest, rather than a focus on restoring oysters as a functional part of the ecosystem of the Bay. (Paynter 1999) This attitude began to change around 2000. Many recent studies have suggested moving away from the focus on fishery based management and restoration towards strategies that are designed to restore the ecological role of the oyster in Chesapeake Bay (Mann 2000, Coen & Luckenback 2000, Hargis & Haven 1999, Paynter 1999, NRC 2004). One of the more recent major oyster related strategies is outlined by the Chesapeake 2000 agreement. The major goal of this agreement

is to achieve a 10-fold increase in the oyster population in the Chesapeake Bay, before 2010, relative to a 1994 baseline. This agreement intended to achieve this goal by promoting the development of management strategies that focus on the ecological benefits of oyster restoration (Chesapeake Bay Program 2000).

In order to restore the ecological role of the oyster in the Bay, many of these recent studies argue that it is very important to take a long-term focus. Success of these programs cannot simply be measured by how much fishery yield is increased but rather that the efforts would be judged on how much the project helps to support a self sustaining oyster population (Coen & Luckenbach 2000) and in its contribution to the restoration and management of the estuarine system resource as a whole (NRC 2004). This requires looking beyond the point where oysters reach market size and toward the ecological contributions of larger oysters and mature reefs.

Oyster restoration with this sort of long-term perspective may, in the end, be far more valuable. If oysters were restored to a naturally self sustaining population and if harvest from that population was managed in a sustainable way, the economic benefits from the harvest alone would likely be more valuable in the long term than the "put and take" fishery model that characterizes the industry currently. Furthermore, beyond this immediate fishery based improvement, many studies have shown that restoring the ecological role of oysters in the bay would have substantial benefits in terms of nutrient removal (Newell et al. 2004) and

will provide substantial benefits to higher trophic levels in the ecosystem through habitat enhancement and increased food production (Ulanowicz & Tuttle 1992, Rodney & Paynter 2006).

## 1.2 Ecology and Natural History of *Crassostrea virginica* in Chesapeake Bay

Oysters have the capacity to remove phytoplankton, sediment and detritus from the water column, and they can do so with astonishing efficiency. Oyster deposits of feces and pseudofeces further promote ecosystem level removal of nitrogen and phosphorus through sediment burial and bacterially mediated denitrification (Newell et al. 2004). Because of this ability, oyster restoration could play an important role in addressing the problems caused by eutrophication in the Bay (Paynter 1996). In order to properly understand many of the challenges associated with oyster restoration in the bay it is helpful to describe the natural history of *C. virginica*.

Reproduction of oysters in the Bay is seasonal, beginning in late May and can continue until late September (Thompson et al. 1996). Gametogenesis and spawning are believed to be triggered by environmental factors. In particular, increasing water temperature and food availability are believed to be the primary cues that trigger spawning behavior (Thompson et al. 1996).

Sexual maturity can be reached within 3 months of oyster setting. In southern regions such as the Gulf of Mexico the prolonged periods of high temperatures can allow juveniles to participate in reproduction. However, in more northern regions such as the Chesapeake Bay, this is less likely (NRC 2005).

During spawning, gametes are released directly into the water column. Males are believed to be more responsive to environmental cues that trigger a spawning event, and the presence of sperm in the water is believed to be a primary cue for females to release eggs (NRC 2005, Thompson et al. 1996). Fertilization occurs in the water column. Oyster density and hydrology are critical at this point. Low adult oyster density can reduce the chances of synchronous release of gametes. Furthermore, the gametes are believed to deteriorate within a few hours, so oysters being physically distant from one another or being in an area of high currents can tend to dilute the gametes reducing fertilization efficiency (Pavlos 2004, NRC 2004, Thompson et al. 1996).

Shortly after fertilization, a larva develops and it soon develops a simple swimming apparatus. This larval stage can last up to 3 weeks. During this phase two interacting factors; the estuarine currents and the swimming behavior of the larvae control movement of the oyster larvae. The swimming ability of the larvae is very limited and is believed to function primarily to adjust the larvae's position in the water column. In response to salinity changes caused by changing tides, the larvae will tend to swim upward during an incoming tide and downward during an outgoing tide, this behavior is believed to help to prevent the larvae from being flushed out of the estuary (NRC 2006, Thompson 1996). However, this swimming behavior is insufficient to fully control the position of the larvae. So, oyster larvae are transported as quasi-passive particles by estuarine currents, and

as such their movements are largely controlled by the hydrology of the estuarine system, as wells as wind and weather events.

This creates a fundamental problem for oyster restoration projects. Given the complex hydrology of the Bay, and the chaotic influence of weather and the added complexity of larval swimming behavior, it becomes very difficult to predict where spat from one oyster reef will finally settle. Similarly, if one area receives a good spat set one year, it is very difficult to tell what may have caused this. Spat settlement in one place is likely related to good fertilization success at a reef that may be many miles away from the reef that received the settled oysters. This randomness and unpredictability lends an intrinsic difficulty to planning oyster restoration projects.

In addition to creating difficulties in determining the source of spat and destination of larvae, these issues combined with the very high mortality rate of oysters in this stage (>99%, NRC 2004) make it difficult to develop a relationship between spawning stock and recruitment. While it may seem intuitive that a small standing oyster stock will lead to a small recruitment, this is not always the case. Fegley et al. (1994) and Livingston et al. (1999) reported rapid repopulation of oysters after major episodic events (MSX epizootic and hurricane) that caused significant mortality among adult oysters.

Near the end of their larval phase, oysters begin to actively seek a site to settle on. Oysters can settle on a wide variety of hard unsilted surfaces. However, they do exhibit preferences based on chemical, morphological and lighting cues (Kennedy et al. 1996). In particular, oyster larvae appear to prefer to settle on oyster shell (Kennedy et al. 1996). These preferences tend to generate large aggregations of oysters and oyster reefs. This preference has also been a key part of the oyster repletion strategies used in the Bay. As discussed in the previous section, Maryland has a long history of planting oyster shell gathered from packing houses or fossil oyster shell. Planting oyster shell provides a solid and preferred substrate for oysters to settle on. This allowed for a concentrated collection of oyster spat that was later moved to other portions of the bay to encourage better growth of the oysters (Kennedy & Breisch 1983, Paynter 1996, NRC 2004).

After settlement, oyster larvae metamorphose into juvenile oysters. Shortly after settling oysters are particularly vulnerable to predation. In the first week after settling as many as 40% of the spat can be lost to predation (Haskin & Tweed 1976, Newell et al. 2000). Size provides a substantial refuge against this predation and larger oysters suffer substantially less mortality. Oysters over about 35mm have sufficient size and shell thickness to avoid many predators. (Kennedy 1996) This high level of post-settlement mortality presents an additional challenge to restoration projects. This problem can often be minimized by choosing to plant oysters at time when the potential predators are less active, such as in the late fall,

and by using hatchery reared spat that are large enough to avoid many of the very early predators.

Adult oysters feed by capturing particles from the seston. Particles smaller than 1 µm are poorly retained. Particles larger than 6µm, up to about 300µm, are retained well (Newell & Langdon 1996). Furthermore, particles that are not consumed are rejected as pseudofeces and deposited on the bottom. This means that, even if the oyster does not consume the particle it captures, the particle does not return to the water column. That is, even if the oyster is not feeding, even if its gut is full, it will continue to remove particles from the water column (Newell & Langdon 1996). So essentially, oysters will filter a very wide range of particles from the water, not return them directly to the water column, and they will filter almost constantly while they are active. Newell (1988) reported that subtidal oysters in the Chesapeake Bay will feed for over 23 hours per day during summer months. The result of this is that a healthy oyster reef is capable of filtering a very large amount of water very quickly. Using Newell (2004) as a basis for making an estimate, a market size oyster (~75mm) that weighs about 0.8g (dry tissue weight) will filter about 7.6 liters of water each hour during the summer months. Over a total oyster reef this filtration can be very significant. As such, this is often considered to be one of the most important ecosystem services provided by a healthy oyster reef. The impact of water filtration by benthic organisms on phytoplankton and nutrient dynamics has been shown in several studies. (Cloern

1982, Cohen et al. 1984, Newell 1988, Dame et al. 1992 Ulanowicz & Tuttle 1992, Newell et al. 2004).

Newell (1988) estimated the filtering capacity of the pre-1870 oyster population in Chesapeake Bay, and determined that that the population would be able to filter the entire volume of the Bay in just over 3.3 days. For comparison, he estimated that the 1988 filtering time would have been about 325 days. Given this remarkable difference in filtering capacity, restoration of oysters to substantial populations in the Chesapeake Bay could have dramatic impacts on the ecosystem of the bay and could reduce the effects of eutrophication. Ulanowicz and Tuttle (1992) used a network analysis model to determine the impacts of restoring oysters to the Bay. Their model predicted that even a relatively modest (compared to historical levels) 150% increase in the oyster population driven by a 23% reduction in oyster exploitation, would have dramatic impacts on the Bay. They predicted a 12% decline in baywide phytoplankton production; a 29% increase in benthic production, indicating an improvement in water clarity; a remarkable 89% decrease in gelatinous zooplankton; a 5% increase in both mesozooplankton and filter feeding fish; and a 18% increase in carnivorous fish, many of which are commercially valuable. These changes in productivity at various trophic levels are the result of changes in the way that energy would cycle though the system if oysters were restored, and the impacts of these changes on various autocatalytic relationships within the system.

Additionally, Newell et al. (2002, 2004) showed that suspension feeding bivalves, and oysters in particular, due to their high clearance rates, have the potential to remove substantial amount of nitrogen and phosphorus from the water column through sediment burial and bacterially mediated denitrification. Newell (2004) argues that this net removal of nutrients from the system will result in ecosystem wide reductions in phytoplankton production.

These results suggest that oysters, at one point, must have been a critical part of the ecosystem in the Bay, and that their near absence has had dramatic effects on the system as a whole. Furthermore, it implies that oyster restoration could play a role in addressing the eutrophication problems of the Bay. It is unlikely that oyster restoration alone could solve the eutrophication problem, but, when combined with reducing the excess nutrient inputs, the results could be substantial.

It is these potential benefits that have led to the recent changes in the direction and goals of oyster management goals and policies in Maryland. As mentioned previously many studies have suggested moving away from the focus on fishery based management and restoration towards strategies that are designed to restore the ecological role of the oyster in Chesapeake Bay (Mann 2000, Coen & Luckenback 2000, Hargis & Haven 1999, Paynter 1999, NRC 2004). This approach can improve the fishery by establishing a self-sustaining population and can capitalize on the enormous filtration capacity of oyster reefs to provide

substantial ecological benefits beyond their economic benefits as a fishery resource.

## 1.3 Modeling as a Tool for Oyster Restoration in Chesapeake Bay.

The previous sections have described the history and ecological role of oysters in the Chesapeake Bay, and pointed to the changes that are happening in the practice of oyster restoration in Maryland. In order to effectively develop and implement effective oyster restoration strategies a diverse set of tools will need to be developed. One useful tool is modeling and computer based simulation.

Modeling is a process that allows us to organize information, identify gaps or strengths in knowledge and can be useful in evaluating policies or programs. It is important to view modeling as a process and not as just a way to arrive at a final answer. There are many different kinds of models and modeling approaches with some being very simple and others highly complex; some can be purely descriptive and some strive to be predictive in some way. However, the modeling process itself is a process of abstracting reality in order to simplify the interactions and relationships between different components of a system in order to make it more easily understood. It is a method for dealing with the limits of our understanding and limits of data availability.

When attempting to design a model, the first step is to identify the components of the system. Each of these components typically can be reduced into its own set of interacting components. An oyster reef can be represented as a whole reef or as individual oysters, each individual oyster can be represented as a set of tissues

(shell, adductor muscle, digestive tract, etc), each individual tissue can be described as a set of cells, and so on. Because of this, a level of analysis and complexity needs to be selected for the model, and each of these choices comes with a variety of problems and benefits.

As an example, consider attempting to build a model of the complete life of all of the oysters in the Chesapeake Bay. Attempting to model each individual oyster, and each of the individual cellular processes within each oyster is a very arduous task. The sheer number of calculations necessary to capture every interaction within each oyster and with each oyster and its environment is huge, and needlessly so. The end result of this approach would be a model that is so complex that it is difficult to work with and difficult to understand, just like reality is. In order to avoid this problem it is useful to eliminate as much needless complexity as possible and focus the model on the specific interaction that are of immediate interest. The fewer variables, and interactions that are used in a model the easier it is to understand. However, this must be balanced with the recognition that biological and ecological systems are complex and this complexity cannot be ignored.

Finding the appropriate balance between simplicity and complexity is one of the basic challenges in model design. The basic advantage of limiting complexity is that the model becomes easier to develop, easier to work and is more adaptable if conditions being examined or hypotheses being tested change (Chwif et al 2000).

In contrast the fundamental problems with developing a simple model is that more abstraction implies more assumptions and oversimplifying a model can lead to the model being less valid (Chwiff et al 2000).

Lindenschmidt (2006) explores this problem by testing a hypothesis presented by Snowling and Kramer (2001). Snowling and Kramer (2001) suggest that as the number of parameters in a model is increased the error tends to be reduced and the model sensitivity is increased. Lindenschimidt (2006) adds additional parameters to a river water quality model and finds that while the most complex model provides the least error, it is not necessarily the most useful because many of the simpler models have the nearly the same results as the more complex ones. Essentially, complexity can be added to the models, and the results can improve, but once the most important factors that influence the interaction being modeled are included the benefit of adding additional parameters decreases rapidly.

Additionally, the process of modeling and the process of determining an appropriate level of complexity can provide useful insights on its own. Modeling requires that each of the components of a system be studied, to some extent, and then abstracted in a way that preserves the relevant characteristics of that component or interaction.

While attempting to represent reality in a model it is usually necessary to compare a wide variety of previous studies on a topic and to try to reconcile the differences in results or experimental design between each of the studies to try to determine

how best to represent the interactions in the model. This can highlight potential deficiencies in knowledge or data in a particular area in the field, and often can raise even more questions about why the differences in experimental results exist. Hanon and Ruth (1997) highlight this point and argue that good models are thought-organizing devices that should produce more questions about the behavior of the system. Often it is this process of abstraction that generates the most useful and interesting results in a study. In this sense the modeling process is a useful filter for examining the extent of knowledge in a field.

Finally, the goal of most models is to be predictive in some way. If a model is found to produce results that are similar to what is observed in nature then the model may be used as a tool to help determine what an appropriate course of action might be, or what might happen in the system. In terms of oyster restoration, the applications of models could include many things. If a model is a good representation of the hydrodynamics of the bay and of oyster larval behavior then perhaps a model could be used to predict where spat will settle when they are produced from a given location (e.g. North et al. unpublished). Furthermore, a model might be used for site selection, determining what areas might have habitat suitable for a restoration project (e.g. Battista 1999). Or perhaps a model could attempt to predict the potential effects of oyster restoration on the ecosystem in the Bay in general (e.g. Ulanowicz and Tuttle 1992).

Modeling can be a useful tool for oyster restoration in the Bay. The process can highlight what areas may need more research and may be useful for developing tools that can potentially help guide the goals and design of oyster restoration projects in Maryland. For this project, I developed a simple model of individual oyster growth in the upper portions of the Chesapeake Bay that responds directly to variations in temperature and salinity on a monthly time scale. Oyster growth is a particularly interesting area to begin modeling because it can be useful in multiple ways. First, it is a gateway to estimating at the ecosystem services that can be provided by an oyster reef, because oyster filtration capacity varies by oyster size (Newell & Langdon 1996, Newell et al. 2004). Furthermore, it is broadly useful for many other oyster models, a model that estimates oyster growth may be used as a component of larger oyster models attempting to represent oyster populations on a larger scale.

# CHAPTER 2: Model Development

## 2.1 Assumptions and Exclusions of the Model

For this model the only factors that significantly influence growth rate are assumed to be temperature and salinity, and the *Perkinsus marinus* parasite. In reality, there many other environmental factors that can influence oyster growth or survival. The following factors were excluded from the model for a variety of reasons:

### 2.1.1 Food Supply

Food supply can affect oyster growth. If there is insufficient food in the water column for the oysters to eat then the will not grow as quickly as they would otherwise, since they will not have sufficient energy reserves to divert from metabolism toward growth. However, given the current state of the Chesapeake Bay, it doesn't seem likely that food generally will be limiting to growth. Several studies have argued that anthropogenic sources of nitrogen and phosphorus have enhanced the production of phytoplankton biomass in the Bay (EPA 1988, Fisher et al. 1988, Malone 1992). This excess production of phytoplankton implies that there should generally be sufficient food available to oysters in the Bay. The only periods where this may not be the case are in late December and January when phytoplankton biomass is low. However, during these times low temperatures

cause oysters to become dormant, creating a period of no growth (Loosanoff & Nomejko 1949). Therefore, even during these periods where there may be insufficient food, food cannot be considered limiting to growth.

Related to this is the fact that oysters may lose biomass during the winter (Dame 1972, 1976). During winter oysters enter dormant state during which they do not feed, but respiration continues, although at a lower rate (Dame 1972, 1976). This loss in biomass is not generally reflected as a loss in shell height, and because most studies measure oyster growth in terms of shell growth this short-term loss in biomass during winter is not captured by most studies. This study assumed that this loss of biomass during the winter is relatively small compared to overall oyster growth. Therefore, oyster growth is assumed to be only oyster shell growth, as such negative biomass growth is not reflected in the model.

### 2.1.2 Oxygen

The relationship of hypoxia and anoxia to oyster growth has also been left out of this model. A few studies have found that low oxygen conditions can inhibit oyster growth during the early post settlement stages (Baker & Mann 1992, Osman & Abbe 1995). However, tolerance of these conditions increases with age, and adult oysters are able to survive for several days to weeks in low oxygen conditions (Stickle et al. 1989). However, it is reasonable to expect that these conditions will have some effect on oyster growth. It is likely that these

conditions can create significant oyster mortalities and inhibited growth, particularly in deep-water sites in the Bay where long term hypoxic or anoxic conditions may occur. The impacts of these conditions on growth were left out primarily because it would be difficult to sort out the effects of these short term low oxygen events that reduce growth, from the seasonal changes in temperature and salinity that affect growth. Periods of hypoxia and anoxia are generally seasonal with their greatest impacts being in the summer, during the periods of highest oyster growth and disease. Given that so many different factors are potentially affecting growth at these times, I decided to keep the model simple and controllable by focusing on only temperature and salinity, the environmental effects that are believed to have the most significant impacts. Additionally, since this model focuses on oysters at restoration sites, and since most restoration projects are not located in hypoxic areas, oxygen is less likely to be an issue for the oysters covered by this model.

### 2.1.3 *Haplosporidium nelsoni* (MSX)

The impacts of the oyster disease *Haplosporidium nelsoni* (MSX) were not included in the model for a variety of reasons. First, MSX behaves differently than dermo disease. While dermo is typically a long-term infection, MSX is generally a more acute disease. Oysters infected with dermo can be expected to live for several months to years as long as the infection intensity remains light (Ford & Tripp 1996). Conversely, susceptible oysters infected with MSX can be

expected to die within a few weeks to months (Ford & Tripp 1996). Second, MSX is not as tolerant of low salinities as dermo. Exposure to salinities of less than 10 for 2 weeks has been shown to remove MSX infections from oysters (Andrews 1983). For oysters in the upper portions of the Chesapeake Bay, such as the ones considered in this study, the low salinity in spring helps to eliminate the MSX problems. While MSX potentially can be a significant problem for oysters in the Bay, its most direct impact is on mortality, rather than growth, and might be better included in a model as episodic mortality event, similar to a hurricane.

### 2.1.4 Recruitment

Recruitment has been ignored in this model primarily to reduce complexity and keep the model simple and focused on growth issues. Oyster spawning and recruitment is a complex affair and can be very difficult to predict. One of the primary reasons for this is due to the long larval phase in which the oysters are moving freely in the water column. During this phase two interacting factors, the estuarine currents and the swimming behavior of the larvae control movement of the oyster larvae. The swimming ability of the larvae is very limited and is believed to function primarily to adjust the larvae's vertical position in the water column. This means that in order to predict where oyster larvae will move during their 3 weeks in the water column, one would need a very detailed hydrodynamic model of the Chesapeake Bay, running on tidal time steps, with a spatial

resolution sufficient to isolate at least a single oyster bar. Building a model of this sort is an extremely complex project and would require a substantial amount of computing power and model design time. This effort is well beyond the scale and scope of this project. However, there are projects such as the North et al. (unpublished) model that focuses specifically on modeling oyster larval movement. Also, the models by Cerco et al. (2005) and, the Powell, Klinck, and Hoffmann, Galveston Bay model use this approach (Hoffman et. al. 1992, 1994, 1995; Powell et al. 1992,1994,1995; Dekshenieks et al. 1993, 2000).

### 2.1.5 Habitat Quality

Habitat quality is another major parameter that has been left out of this model. Oyster larvae require a hard substrate to settle on, and muddy bottom conditions can inhibit oyster growth. Furthermore oysters can sink into soft bottom areas and be suffocated. Therefore, proper habitat conditions are very important to the growth and survival of oysters. Rothschild et al. (1994) point to the loss of good quality oyster habitat as one of the major factors contributing to the decline of oysters in the Chesapeake Bay. For this study we assume that the oysters are planted as part of an oyster restoration project. Site selection for this kind of project will need to consider the habitat quality of each site. It is assumed that the restoration projects represented by this model plant the site with sufficient oyster shell to improve the habitat quality or select sites with good habitat. Battista

(1999) developed a GIS based model for determining habitats suitable for *C. virginica* growth that addresses these site selection issues.

## 2.2 The von Bertalanffy Growth Function and Previous von Bertalanffy Based Models

The primary goal for the project was to develop a model of oyster growth that can easily be applied to examine issues related to developing oyster restoration strategies. Furthermore, the model was designed to be modular. If a simple, easily adaptable model for oyster growth is developed, then it can be used readily in larger, more complex, models that could examine oyster dynamics on a larger scale.

In order to achieve this goal of modularity, the model had to be developed such that it could be used on a wide variety of time and spatial scales. This implies that the growth model should be built on a fairly short time scale. Oysters have a highly seasonal component to their growth. Low temperatures in winter will cause the growth of oysters to slow dramatically or stop. Conversely, growth will increase at higher temperatures, during the summer (Paynter & DiMichele 1990, Shumway 1996). Because of this seasonal component to growth, the model will have to estimate growth at a sub-seasonal levels in order to be able to be used for a model or project that is interested in growth on short time scales.

There are a wide variety of classical growth models that can be used to describe the growth of an organism or a population. In order to find a good starting point

for developing a model of *Crassostrea virginica* growth it was useful to examine the set of possibilities and to find one that in general matches observed oyster growth post settlement.

Simple linear models that use a constant growth rate or exponential growth models that use a constantly increasing growth rate are not appropriate as they have no inherent limit to growth. After settling, oysters grow rapidly early in their life but tend to slow their growth rates as they age (Paynter & DiMichele 1990, Shumway 1996). This suggests that a logistic function is more appropriate. However, many logistic type functions will show an s-shaped curve. This implies that growth will be very slow at the beginning of life and also at the end of life, when an upper limit is reached, with a period of rapid growth in the middle. While this type of function had been applied to a population, and to individual growth in applications such as the Gompertz curve, it does not adequately match observed oyster growth. The von Bertalanffy Growth model (von Bertalanffy 1938) is another variant of logistic growth that does not have an initial period of slow growth, and as such was a good candidate to serve as a starting point for this model.

The von Bertalanffy growth model describes growth toward a maximum asymptotic size limit, with the rate of growth decreasing as the size approaches the maximum limit. Figure 3 shows a picture of the shape of an ordinary von Bertalanffy function. A standard formulation of this model is:

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

Where $L_t$ is length at time t; $L_\infty$ is the asymptotic length; K is a growth constant; and $t_0$ is the initial time, that is, the time of oyster settling or planting. This model has been used extensively to model the growth of a very wide range of fish species. (Fortoura & Agostinho 1996, Xiao 2000, Pauly et al. 1992, Pitcher & MacDonald 1973, Cloern & Nichols 1978, and others) Additionally, it has been used in a variety of applications, such as determining age from size and for estimating fishery yield (Pauly et al. 1992, Pitcher & MacDonald 1973). Christman et al. (unpublished), Mann et al. (2003), Mann and Evans (2004) and Rothschild (1994) also use a von Bertalanffy based approach to estimate annual oyster growth in Chesapeake Bay.

Since its original development in 1938, the von Bertalanffy model has become a standard growth model and has been modified many times and used for a very wide variety of purposes, including things ranging from human growth to growth of tumors. Of the many variations on the von Bertalanffy function, several have modified the basic function to incorporate seasonal effects on growth. For fish species this has been incorporated as both a simple seasonal effect and as a direct incorporation of temperature changes. (Pauly et al. 1992, Pitcher & MacDonald 1973, Somers 1988) These modifications introduce a seasonal oscillation that will slow or stop growth in winter months. This allows the model to account for

seasonal variations in growth rate at the sub-annual level and is intended to predict growth during different seasons.

Cloern and Nichols (1978) developed one of the first of these variants of the von Bertalanffy model to account for seasonal oscillations in growth. They applied their model to the growth of both the Baltic Tellin (*Macoma balthica*) a bivalve mollusc species and a fish species, the flathead sole (*Hippoglossoides elassodon*). In order to add their seasonal response to the von Bertalanffy function Cloern and Nichols include a set of time varying parameters that adjust the growth rate on a periodic basis (eq 2)

$$L(t) = L_{\infty}\left(1 - e^{-K\left[(t-t_0) + \frac{C\sin(2\pi(t-t_s))}{2\pi} - \frac{C\sin(2\pi(t_0-t_s))}{2\pi}\right]}\right) \qquad (2)$$

Two new parameters control the oscillation: $t_s$, the time between $t_0$ and the start of the first seasonal oscillation, and C, the amplitude of the oscillation. This represents the degree of response to the seasonal effects so that if C=0 there is no seasonal oscillation and the equation reduces to equation (1). When C= 1 then growth stops at the minimum point of the oscillation in winter and will grow in summer at double the rate in equation (1) at the maximum point of the oscillation in summer. Intermediate values represent a degree of variation between these two

extremes. Values of C > 1 in this function will cause a loss of length (L) during the winter months (Pauly 2006) and a very rapid growth in summer months.

This variant of the von Bertalanffy growth model provides several advantages in that it is able to represent a seasonal change in growth rate, and can offer improvements in estimates of biological growth on seasonal scales. One problem that this approach has is that growth will only be zero instantaneously. Many species, including oysters, can have an extended period of no growth during winter. Pauly et. al. (1992), addressed this problem by introducing another parameter to the function that represents this period of no growth. This allowed the model to respond appropriately in the winter, and to capture the effective reduction in total growth that occurs from this cessation in growth.

When working with von Bertalanffy models (e.g. equations 1 or 2), several important issues arise. Primarily, it becomes difficult to relate the estimated parameters of the von Bertalanffy function to the actual environmental conditions that are in reality driving the seasonal changes in oyster growth.

The way in which the von Bertalanffy model is typically applied uses a curve fitting approach to determine the parameters of the von Bertalanffy growth function. That is; growth data for a species is collected over time and a statistical approach (typically least squares) is used to determine the set of von Bertalanffy parameters that will produce a growth function that is most similar to the

observed data. This approach has some real value in studying the growth of an organism in general, however it suffers some serious limitations. Figure 4 highlights one of these limitations. This figure shows oscillating von Bertalanffy growth functions for two oyster restoration sites in the Chesapeake Bay, Shippen Creek and Spaniard Point (data from ongoing monitoring projects by Paynter et al.). These sites are very close to each other in the Chester River. The observed shell heights for these sites were used to determine the best-fit parameter set for the oscillating von Bertalanffy growth function, equation 2. The resulting function using these parameters is used to make this graph. For Shippen Creek K= 0.237 and for Spaniard Point K= 0.396. It can be seen from the graph that the oysters at Spaniard Point grew faster over 5 years than the ones at Shippen Creek did, and this is reflected in the difference in the growth parameter.

The basic problem with this approach is illustrated when we start to consider why the growth is different. It is reasonable to assume that the difference in growth rate is due to differences in environmental conditions at each of the sites. Temperature, salinity, substrate, and other factors are believed to influence the rate of oyster growth, and each of these factors is in some way represented in the differences in the von Bertalanffy parameters that the curve fitting approach gives. However, it is difficult to understand the direct impact of these environmental effects on the von Bertalanffy parameters. The growth parameter chosen by curve fitting is a single parameter that describes growth over the entire 5-year sampling period. Seasonal and inter annual variations in environmental

conditions that are expressed in the best-fit growth parameter are essentially aggregated together. Furthermore, the relative contribution of each of the environmental factors is impossible to determine as these impacts are also aggregated into the single parameter set. Finally, and most importantly, the impact of these environmental conditions on the growth parameter is expressed only through the observed oyster growth; the environmental parameters themselves were never used in the calculation of growth or size estimates. Thus the relationship is not clear.

A study by Coakley (2004) also provides some interesting insight into these problems. Coakley took data from the annual state of Maryland dredge survey of 64 sites in the Chesapeake Bay, and used a shell height based modal analysis technique to attempt to identify various age cohorts at each site, and then used these age cohorts to fit a standard von Bertalanffy function (equation 1) to them to attempt to determine the von Bertalanffy parameters for each site. For the twenty-three sites in where Coakley was able to find sufficient age classes to fit a von Bertalanffy function, she found that the average asymptotic shell height ($L_\infty$) of oysters at these sites was 90.85mm, with some sites as low as 77mm. This size is interesting because it is very close to the legal harvestable size limit in Maryland (75mm), and is well under the maximum lengths that have been reported historically and under the size that can be found in sanctuary sites (200mm-230mm as reported by Rothschild et al. 1994). This remarkable difference in the apparent von Bertalanffy parameters is likely due to the intense fishing pressures

on oysters in the Bay, and may be confounded by the presence of oyster diseases such as dermo (Coakley 2004). This possibility is further supported by Coakely by the observation that in her data the distribution of mean shell lengths for older age classes shifted from being normally distributed to a lognormal distribution, suggesting a higher mortality for larger oysters (Coakley 2004).

Furthermore, Coakley attempted to identify a relationship between oyster growth and temperature and salinity as is suggested by many previous studies (Ingle & Dawson 1952, Loosanhoff 1953, Shaw 1966, Paynter & Burreson 1991, Paynter et al., 1995). However, Coakley was unable to identify this relationship in her study at the site-specific level. The analysis only revealed a weak relationship between the growth parameter K and salinity when data was aggregated across 3 broad salinity regimes (Coakley 2004).

This study further highlights a fundamental problem with this traditional approach to the von Bertalanffy growth function. Estimates of von Bertalanffy growth parameters may be highly site specific, and may be very highly influenced by the presence of external pressures such as fishing or disease. The effect can be so predominant in many cases that the influence of environmental factors of interest such as temperature and salinity may be completely overwhelmed by these site specific pressures.

This presents a fundamental problem if a model is to predict growth at any given site. We can develop several sets of von Bertalanffy parameters, each of which can be accurate at estimating the growth of oysters at specific sites where oyster growth has been measured before. However, since it is often difficult to relate the von Bertalanffy parameters to any specific environmental conditions, it becomes difficult to say anything in a specific functional way about why the parameters are different at each of the site. Also, any predictions made with the model will have the intrinsic assumption that the environmental conditions and site-specific pressures such as fishing will remain relatively constant year to year at the modeled site. Furthermore, we cannot predict how oysters might grow at a site for which there is not a set of observed oysters from which to derive a set of von Bertalanffy parameters, because there is no way to relate these environmental and site specific parameters to the growth parameter. Thus, we cannot determine them without site specific growth observations.

There are further problems that arise when one is trying to work with an oscillating variant of the von Bertalanffy growth function in order to represent the seasonal component of growth. Essentially, the parameters that were added to introduce a seasonal oscillation define a sine function with amplitude C and a period of one year, beginning at $t_s$. Thus, while this sine function may mimic the general shape of seasonal changes in growth rate, the real thing driving these changes, temperature, is irrelevant to the function.

The parameter C, the amplitude of the seasonal oscillation, has definite impacts on growth throughout the entire modeled year. Since the oscillation is regular there is an implicit assumption that if growth slows to near zero during the winter there will be a symmetric doubling of the mean growth during the summer months. This means that the model cannot accommodate a particularly warm winter, with subsequently higher growth, followed by an average summer, with normal growth. Similarly, it implies that if the winter is particularly cold, the summer must be particularly hot.

Furthermore, since the period of the oscillation is defined as one year, the point of maximum growth must always be exactly six months from the point of minimum growth. This requires that summer conditions cannot come early in any year, and winter conditions cannot come late in any year,

Because all of the parameters that are used describe the nature of the sine wave over the entire year, it becomes difficult to use this function to describe sub-annual variations in environmental conditions. In order to attempt to estimate any of these parameters from actual environmental data, it is necessary to understand growth as it relates to patterns of temperature and salinity over the course of at least an entire year. This does not allow for estimation on timescales less than a year. Furthermore, if this function is used for multiple years, it assumes that there is not any year-to-year variation in temporal effect. The oscillating function will

produce the same seasonal variations in growth for every year that the model is run.

Further problems arise, if one considers the oscillating form of the von Bertalanffy function (eq. 2) and compares it to the standard form (eq. 1), it can be seen that the mean annual growth from both the models will be the same. The sine function serves to modify K over the course of one year, and during that year a full period of the sine wave will occur, and there will be no net change in annual growth. Thus, both functions will produce the same result if used at 1-year interval due to the symmetry of the sine function. Effectively, equation 2 produces an average growth estimate with an average estimate of seasonal effects. However, since the sub-annual effects that drive the seasonality are all aggregated together into the set of von Bertalanffy parameters, it is impossible to discuss growth on a sub annual scale with the oscillating model. Which is, in fact, the only point of including the oscillation in the function in the first place!

The Pauly et al. (1992) variant addresses this problem somewhat, in that it removes the symmetric nature of the sine function by forcing extended periods of no growth. However, during the periods of growth the original sine function is used to represent growth. So, while the sub-annual symmetry is removed, the inter-annual symmetry remains the same.

Because of these issues, it was necessary to develop an alternative approach to the von Bertalanffy function that allows for the development of an oyster growth model that is directly influenced by the environmental factors of interest, such as temperature and salinity, while at the same time is less affected by site-specific concerns such as fishing.

**2.3 Data Issues:**

It has been shown in several studies that the growth rate of the eastern oyster will change in response to changes in temperature and salinity (Kennedy et al. 1996, Paynter & DiMichele 1990, Paynter & Burreson 1991, Dekshenikes et al. 2000, Shumway 1996). Examples in Kennedy et al. (1996) show that oyster activity, including growth, will slow dramatically or stop at lower water temperatures (5°C-8°C) and will increase at higher temperatures. Salinity also has been shown to affect oyster growth (Paynter & Burreson 1991, Paynter et. al. 1995, Shumway 1996). Lower salinities are associated with lower growth rates and, therefore, seasonal and inter-annual variations in the salinity of the Bay due to weather can affect growth in a dynamic way. This study focused on attempting to capture these seasonal changes in growth directly from changes in temperature and salinity values.

Previous sections describe why it was necessary to develop an alternate approach to the von Bertalanffy growth model in order to estimate oyster growth on a monthly timescale so that it is possible to capture the seasonal oscillations in growth. Furthermore, it was intended to have these short-term variations in growth rate be driven by a temperature and salinity time series, not a simple aggregation of inter-annual effects. In order to develop a model to achieve this goal it was necessary to have a data set that included at least monthly shell height

observations of planted hatchery reared *C. virginica* oysters at as many sites as possible, with various salinity regimes.

The data needed to be from planted, sites so that the specific age of the oysters in the sample would be known, so that average growth of the oysters could be calculated.

Data from sites that were heavily fished could not be used because fishing pressures are a size dependent mortality and as such right-truncate the size distribution of live oysters and so depresses the apparent growth rates of oysters (Christman et. al unpublished, Coakley 2004).

Additionally, because *P. marinus* has been shown to affect growth (Andrews 1961, Paynter & Burreson 1991) and the apparent von Bertalanffy parameters (Christman et al., unpublished), sites with high prevalence or severity of could not be used in developing the growth section of the model. Furthermore, the restoration sites used needed to be from hatchery-reared seed to insure that the oysters were not infected prior to planting. The effect of temperature and salinity on growth needs to be isolated from the effects of disease on growth. If measurements of diseased oysters are used it will be difficult to determine which effect is actually driving the changes in growth rate.

Finally, temperature and salinity observations needed to be paired with the growth information. Since temperature and salinity can vary even on relatively small spatial scales, the environmental observations needed to be paired closely with the growth observations.

Unfortunately, a data set that meets these criteria without other possibly confounding issues was not available. Most of the data sources for oysters at restoration sites only observe oysters on a quarterly or annual basis. Also, many do not provide observations in midwinter due to the expectation that the oysters will not grow significantly in winter. Furthermore, due to the prevalence of *P. marinus* in the Chesapeake Bay it is very unlikely that any planted oysters will remain disease free for several years, making it difficult to separate out the disease impacts on growth from temperature and salinity impacts on growth.

Essentially, there are very few data sets that can be used due to the infrequency of data observations, and due to disease pressures in the Bay, so that it is unlikely that any long-term observations of disease free oysters can be made.

In order to proceed with model development at all, several compromises in data quality had to be made. This allows for the development of a model framework, and a preliminary model that could be improved if data quality improves.

The data used in this research comes from two datasets collected by Paynter et al. (unpublished), in an ongoing effort. One data set is used for model development and the second is used only for model testing.

The data set used for model development comes from a monitoring project conducted by Paynter et al.(unpublished), designed to compare the growth of *C. virginica* and *C. ariakensis* in the Chesapeake Bay. (Paynter et al. 2007 in press) In this study triploid *C. virginica* was planted at four sites in the tributaries of the Bay (Choptank, Patuxent, Severn, and York rivers) and sampled monthly. Shell height, temperature, salinity, and *P. marinus* incidence was observed. The preliminary model was developed using data from these sites excluding all observations after *P. marinus* infection was found. This provides only about one year of observations at each site. This dataset is largely inadequate for the development of a robust model due to the limited number of observations and the possible confounding factor of using triploid *C. virginica*. Triploid oysters are sterile and thus will not devote energy towards reproduction. For *C. virginica* this is a significant energy savings, and triploid oysters have been shown to grow faster than the fertile diploid oysters (Stanley et al 1984, Barber and Mann 1992, and Mattheissen and Davis 1992). These differences between diploid and triploid growth are discussed below.

The second data set is from the longer term monitoring projects of the Paynter labs. These data include several dozen restoration sites that have been monitored

for up to 7 years and have been sampled a various irregular intervals, typically quarterly. Several sites from this data set were chosen for use in model testing only. Mean monthly temperature and salinity data from nearby Chesapeake Bay Program monitoring stations were used to drive the preliminary model. The model output was compared to the growth observations at each of the selected sites.

### 2.3.1 Diploid vs. Triploid Growth

Several studies have examined the differences in growth between diploid and triploid *Crassostrea virginica* (Stanley et al 1984, Barber and Mann 1992, and Mattheissen and Davis 1992). The results of these studies vary on the extent of the growth difference.

The Stanley et al (1984) study shows a very small, but statistically significant difference in growth. They reported a 3-4 mm difference in shell height over 53 days for 3 year old oysters. Interestingly, Stanley et al examined 2 types of triploids, one made by inhibiting meiosis I and another made by inhibiting meiosis II. The group made by inhibiting meiosis II showed no significant difference in growth from the diploid group. Stanley et al suggested that the difference in growth might depend more on heterozygosity than on ploidy specifically. Regardless, the difference in growth between diploids and triploids was limited in this study.

Barber and Mann (1991) also showed a small but statistically significant difference is growth between diploid and triploid *C. virginica*. Over 1 year of growth this study reports that the triploid oysters grew about 5% more than diploids. This study also reported that there was no apparent difference in susceptibility to *P. marinus* infection between diploid and triploid oysters. Myers et al 1991 also reported equal susceptibility to dermo.

Finally, Mattheissen and Davis (1992) compared the growth of diploid and triploid *C. virginica*, however they found a more substantial difference in growth than either of the previously mentioned studies. Across 3 sites they report a 17%-24% difference in growth during the first growing season and a 14%-21% difference in growth over the second growing season.

Two studies based on *Crassostrea gigas* triploids (Allen and Downing (1986) and Wang et al (2002)) highlight a seasonal component to the difference in growth rates. During spawning diploid oysters will divert a good deal of metabolic energy towards spawning. The sterile triploids will grow faster during these periods because they are not expending their energy in this way. (Allen and Downing 1986) Shell height will increase slightly faster in triploids during this period, however the more pronounced effect is seen in weight of the oysters. After spawning, diploid oysters will have a much lower weight, higher water content and a lower glycogen content compared to triploid oysters. (Wang et al 2002).

Wang (2002) further suggests that a creating triploid oysters by breeding diploids and tetraploids causes even higher levels of heterozygosity, and reports that triploids created this way have higher growth than triploids created by Meiosis inhibition.

Essentially, these studies have shown that triploid oysters will grow faster than diploid oysters, but the extent of the difference in growth rate can vary across a wide range. Barber and Mann (1991) reported a small difference in growth while Mattheissen and Davis (1992) reported a substantial difference in growth. Furthermore, the difference in growth rate is seasonal, linked to spawning, and may also be affected by the age of the oyster (Stanley et al 1984), and site specific environmental conditions (Mattheissen & Davis 1992). Finally, differences in growth rates may be affected by the way in which the triploid oysters were made.

Given this complexity, it becomes very difficult to estimate and predict specifically the difference between diploid and triploid growth will be in any given situation. Because of this impact of using data from triploid oysters for the development of the model is difficult to correct for. For this reason I assume that the differences in triploid and diploid growth will be small (Stanley et al 1984, Barber & Mann 1991). Furthermore, I assume that triploid oyster growth can serve as a sufficient proxy for diploid growth for the purposes of this model, and accept that the model results may overestimate total growth. This issue could be

addressed in the model by either recalibrating the model using data from disease-free diploid *C. virginica* or by developing a reliable method for determining the differences in diploid an triploid growth.

For reference, The oysters used for this study were made by breeding diploids with tetraploids potentially increasing the growth rate difference. However, the growth measurements come from the first 15 months of the oyster's life, where the differences in growth rate are expected to be lower.

## 2.4 A Regression Driven Approach to the von Bertalanffy Growth Model to Account for Seasonal Growth.

In order to adapt the von Bertalanffy model to present a more dynamic variant of oyster growth I focused on the growth response to changes in temperature and salinity. Both of these environmental factors have been shown to have a significant impact on oyster growth. Temperature has been shown to be the major contributor to seasonal variations in growth, with growth stopping in winter (Newell et al. 1996). Lower salinities will tend to lead to lower growth rates, and higher salinities are expected to result in higher growth rates (Paynter & Burreson 1991, Paynter et al., 1995). For the model to attempt to capture these short-term variations in growth, and to actually allow for useful modeling and predicting of sub-annual effects, two fundamental changes in mindset were needed. First, instead of attempting to model the entire lifespan of an oyster with a single function, it is more accurate to model growth on smaller growth increments. Second, and most significantly, the idea that the growth constant K is, in fact, a constant needs to be abandoned.

Focusing the model on incremental growth avoids the need for a rigid oscillating function as in equation 2 and allows for seasonal oscillations to be induced by varying environmental conditions. Fabens (1965) provides a variant of the von Bertalanffy function that is suitable:

$$L_2 - L_1 = (L_\infty - L_1)(1 - e^{-K(t_2 - t_1)}) \quad (3)$$

$L_2$ is the length after the time interval $t_2$-$t_1$ and $L_1$ is the length at the beginning of this time interval.

In most applications of the von Bertalanffy function the growth parameter, K, is typically considered to be a constant value. However, von Bertalanffy (1938) developed the model using a foundation of physical chemistry, and adapted functions for modeling chemical reactions to the growth of organisms. In the original chemical models the rate constants (the analogs of K) are constants that are determined by physical constraints in the system and do not change over the course of the reaction, unless the physical constraints change. However, when looking at growth of organisms over the short term, and in particular changes in growth as a response to short term changes in environmental conditions, it may not be reasonable to assume that the growth parameter should be considered to be a constant over the lifespan of the organism. In fact, oyster growth will slow dramatically or stop as water temperature drops below 8$^{o}$C (Shumway 1996). Essentially, this means that as temperatures drop, the growth constant that best represents oyster growth is changing.

Using a single von Bertalanffy constant to model the entire lifespan of an organism is a simplification that treats growth as if it were a single, simple

chemical reaction. However, growth is clearly a more complex affair. Organisms respond dynamically to changing environmental pressures and this response needs to be included in any growth model that would hope to accurately represent sub annual oyster growth. Previous models such as equation 2, present the illusion of a seasonal effect, but the forced symmetry of the sine function and the constant growth parameters mean that the model cannot have any predictive power.

In order to adapt the von Bertalanffy model to present a more dynamic variant of oyster growth we will focus on the growth response to changes in temperature and salinity. Both of these environmental factors have been shown to have a significant impact on oyster growth. Temperature has been shown to be the major contributor to seasonal variations in growth with growth stopping in winter (Newell et al. 1996). Lower salinities will tend to lead to lower growth rates, and higher salinities are expected to result in higher growth rates. (Ingle & Dawson 1952, Loosanhoff 1953, Paynter & Burreson 1991, Paynter et al., 1995) As such, seasonal and inter-annual variations in the salinity of the bay due to weather have an impact on the growth factor K that best represents oyster growth at any given time.

Because we know that oyster growth rates are changing on a sub annual level, we know that the effective growth constant K should be changed on a sub annual level as well. Therefore, it is necessary to develop a method to determine an

independent value of K based on temperature and salinity, for each time step of the model.

On a typical von Bertalanffy curve, defined by a single set of parameters such as in equation 1, the value of K can be estimated at any given point on the curve from:

$$K = \left( \frac{\left( \frac{dL}{dt} \right)}{L_\infty - L} \right) \qquad (4)$$

Determining a value for $L_\infty$ presented a challenge because an actual value for this number is very hard to determine. Studies by Christman, et al. (unpublished) and Coakley (2004) have shown that the apparent value of $L_\infty$ estimated with field data is confounded with harvest, predation, disease, or other size dependent mortalities. Furthermore, due to the prevalence of oyster disease and harvest in Chesapeake Bay, few if any, oysters have recently been observed to die of senescence. Coakley (2004) estimated values for $L_\infty$ for twenty-three sites in the Chesapeake Bay and found values for $L_\infty$ that ranged between 77mm and 152mm. Rothschild (1994) also encountered this problem and examined reports and studies dating back to 1884. He reported observations of maximum size ranging between 120 mm and 230 mm. An inspection of the data from reserve and sanctuary sites collected by Paynter et al. (unpublished) used in this study

revealed a large number of oysters observed at with lengths over 150 mm with a few even well above 200 mm.

Essentially, there is a wide range of potential values for $L_\infty$. All of the observations of oysters that are available represent conditions in the Bay where there were heavy pressures due to harvesting or disease. Additionally, all of the reported observations (where age was known) were of oysters that were 5 years old or younger. Therefore, since a value needed to be chosen for this study, and in the absence of specific information about the maximum shell height of oysters; and because many of the pressures on oysters in the bay are known to depress their growth and shorten their life span, a high value of 250 mm was chosen. I believe that this represents a value close to the potential maximum growth of *Crassostrea virginica* under optimal conditions, although this value clearly is up for debate. Analysis by Christman et al. (unpublished) has shown that the $L_\infty$ value chosen does not have a major impact for the first few years of estimated growth, although it does have a significant impact as shell height approaches the potential values of $L_\infty$. For a lower value, such as 150 mm, oysters under good conditions could be expected to reach this asymptotic limit in about 5 years or so, higher values might not be reached by oysters for 10 or more years. As such if a lower value were chosen for this project it would have a more significant effect because oysters would be more likely to reach the asymptotic limit and stop growing within the time horizon of some of the model runs. Choosing a larger

value essentially assumes that the oyster will continue growing throughout the modeled period, but the rate may slow in later years.

The next step that is needed is to determine a set of monthly values for K from each of the four sites in the Paynter *C. virginica* and *C. ariakensis* growth comparison study. For each month, at each site, a mean shell height was calculated and this mean shell height was used to calculate a mean change in shell height for each month at each site. Finally, a linear approximation of equation 4 (equation 5) was used to estimate a value for K for each month at each site (Table 1).

$$K(approximate) = \left( \frac{\left( \frac{(L_2 - L_1)}{(t_2 - t_1)} \right)}{L_\infty - \left( \frac{L_2 + L_1}{2} \right)} \right) \qquad (5)$$

These approximate values for K were used in a linear regression with the mean temperature and salinity measurements at each site for each monthly time interval. A cross product term of temperature and salinity was also used, due to the seasonal covariance of temperature and salinity. This yielded the regression equation (6). Figure 5 shows details of this regression.

$$\hat{K} = (-0.43427) + (0.02539 * \text{mean temp.}) + (0.01762 * \text{mean sal.}) + ((\text{mean temp.} - 17.72692) * ((\text{mean sal.} - 9.40128) * 0.00312)) \qquad (6)$$

$R^2$=0.726 p<0.0001

It is worth noting that the individual t tests for each parameter show that there is a much stronger relationship between temperature and K than there is with salinity and K (figure 5). Suggesting that with this model we would expect the variations in temperature will have a more significant impact on growth than variations in salinity.

This relationship allows for an estimate of the growth parameter K for each month given a monthly estimate of mean temperature and salinity. This function was implemented in a MatLab 7 model that takes a monthly temperature and salinity time series and an initial mean oyster shell height as the base input. For each month in this time series, a value for K is determined using equation 6 and the estimated oyster growth is determined by equation 3. This model was run using environmental data from the four sites used to develop the regression function (eq. 6) as well as against several sites that were part of separate ongoing monitoring projects (data from Paynter unpublished). The results of this are discussed below in the model testing section.

By substituting equation 6 back into equation 3 for the growth constant K, we can write a form of the von Bertalanffy growth function that explicitly uses temperature and salinity to determine a mean growth increment (equation 7).

$$L_2 - L_1 = (L_\infty - L_1) * (1 - e^{-((-0.43427) + (0.02539 * \text{mean temp.}) + (0.01762 * \text{mean sal.}) + ((\text{mean temp.} - 17.72692) * ((\text{mean sal.} - 9.40128) * 0.00312)))*(t2-t1)}) \quad (7)$$

## 2.5 *Perkinsus marinus* Disease Impact

*P. marinus* has been shown by several studies to reduce the growth rate of oysters after infection (Paynter & Burreson 1991, Paynter et al. 1995, Dittman et al. 2001). Due to the prevalence and extent of *P. marinus* disease in oysters in the Chesapeake Bay, it is difficult to compare the results of a model based on uninfected oysters to the growth of infected oysters in the bay without some method to adjust the model results to account for the reduction in growth rate due to *P. marinus* infection.

Rather than attempting to directly model the dynamics of the interaction between the oyster and the parasite, a more simplified approach was taken. I assumed a series of temperature and salinity based threshold values drawn from existing literature to reduce the incremental growth predicted by the model described above. This approach is used to find a time to first infection for each modeled oyster bar, and once this time has been passed in the model run; the model calculates a reduction in incremental growth.

### 2.5.1 Time to First Infection

Initially, a simple regression model to predict the time to first infection using disease, temperature and salinity data from restoration monitoring projects was

tried. These regressions, not surprisingly, yielded no relationship. However, several studies have shown that the parasite is sensitive to variations in temperature and salinity and that there are minimum threshold values that are needed for the parasite to function properly (Ford & Tripp 1996, Chu & La Peyre 1993, Ragone & Burreson 1993, Ragone Calvo & Burreson 1994, Bushek et al. 1994 Mackin 1951, Ray 1987, others). A salinity of at least 12 (Ford & Tripp 1996) and temperatures of at least 16˚C (Chu & La Peyre 1993) are required for the parasite to be sufficiently active to induce a full epizootic stage. Hence, it is assumed that a planted oyster bar becomes infected when the mean temperature for a month is above 16˚C and the salinity is also above 12. After this threshold is reached the bar is considered to be in an infected state, and will not return to an uninfected state. This may be a lower threshold than was observed at the data sites. These oysters survived for about a year before dermo was detected, however it is possible that these oysters were infected at a low intensity and prevalence and this infection was not detected for several months.

### 2.5.2 *P. marinus* Effect on Growth

Several studies have shown that at higher salinities and temperatures the *P. marinus* parasite becomes more active and higher infection prevalence occurs. (Andrews 1965, Fisher et al. 1992, Chu & La Peyre 1993) Similarly, at lower temperatures and salinities the parasite has been found to be less active and lower

infection prevalences are found (Ray 1987, Craig et al. 1989, Ragone Calvo & Burreson 1994, Bushek et al. 1994, Chu et al. 1993, Chu & La Peyre 1991).

*Perkinsus marinus* has also been shown by several studies to reduce the growth rate of oysters after infection (Paynter & Burreson 1991, Paynter et. al. 1995, Dittman et. al. 2001). This effect is modeled using threshold values from Paynter and Burreson (1991). For salinities over 16 after the bar has been infected growth is reduced by 80%. For salinities between 12 and 16 growth is reduced by 60%. For salinities lower than 12 no impact on growth is used. These reductions in growth are applied in the MatLab model as direct reductions in the incremental growth calculated each month as described above. These reductions are applied only after the bar has entered a disease state by reaching the temperature and salinity threshold values described above.

As mentioned above, temperature has been shown in several studies to have an effect on parasite activity. It is reasonable to assume that this will affect the growth rate reduction caused by infection, however since there is not, to my knowledge, a study that focuses on this effect, salinity is the only factor that is used to adjust the estimated growth. Using threshold values from existing literature in this way provides a simple method for adjusting the estimates from the model to account for disease impacts in a general way

Figure 6 is a flow chart showing the order of operations for the growth model. Appendix 1 is the MatLab code for the model itself.

## Chapter 3: Model Testing

### 3.1 Calibration and Validation: Model Testing Against Observed Data

For a simple model calibration, figures 7 and 8 compare the model output of predicted mean shell height to 2 of the 4 sites that were used to develop the relationship between the growth factor K and temperature and salinity (equation 6). The disease component was not included in these model runs because these sites were not observed to be infected during this time period. These figures are intended to show that the model can closely reproduce the data that was used to develop it.

The results from the Patuxent River site (figure 8) show the model results overestimating the observed shell height at the later dates. This may be partly due to the loss in mean shell height that was observed at the site after late November. This small loss in length over the winter is believed to be the due to sand and wave action eroding the edges of the oyster shells during the winter months. The model as currently written does not allow for a loss in shell height.

The dynamics of the model over a longer term can be seen by comparing the model predictions to observed growth at nearby sites where oyster growth has been measured for several years. This can also serve as a simple model validation technique.

Monthly salinity and temperature time series are not typically available at sampled oyster bars, so data from the closest water quality monitoring stations maintained by the Chesapeake Bay Program (CBP) were associated with the bars (http://chesapeakebay.net/data).

Estimates for oyster growth at three additional sites not used for model development are also presented. These sites are part of ongoing monitoring projects conducted by Paynter et al. (unpublished) and have been sampled at least three times each year for up to five years. The Shippen Creek site is moderately close to the CBP monitoring station ET4.2 in the Chester River. Similarly, the LE1.1 site is close to the Kitts Marsh restoration site in the Patuxent River and the ET5.2 site is close to the Boling Broke Sands site in the Choptank River.

For each of these sites monthly mean temperature and salinity time series were constructed from the water quality monitoring station data. These environmental data were used as an input to the MatLab model to provide an estimate of oyster growth at each of the sites. The model was run both with the disease effect on growth and without, for each site. Figure 9 compares modeled output using data from LE 1.1 to Kitts Marsh. Figure 10 shows the results for ET 4.2 compared to Shippen Creek. Figure 11 shows ET 5.3 compared to Bolingbroke Sands.

Primarily, the results from the model runs over a longer term show that this approach to dynamically changing the growth parameter K can induce seasonal

oscillation in growth without the need for the extraneous parameters and the sine function used in equation 2. In each of the model runs the periods of most rapid growth occur during the summer months when highest growth would be expected. Similarly, little growth occurs over the winter months.

Additionally, when disease effects were excluded from the model, the model consistently overestimated mean oyster shell height. However, including the *P. marinus* effects depresses the mean shell height prediction such that the estimates are close to the observed lengths. Estimates from Shippen Creek shows this effect particularly well (figure 10).

When disease effects on growth are included in the model there is a much better agreement between the predicted and observed growth at each site. At the Shippen Creek site the root mean squared error (RMSE) between the model estimation and the observed shell height is 7.53 mm. Indicating a fairly good fit. At the Kitts Marsh site the RMSE is 5.75 mm and at the Bolingbroke Sands site the RMSE is 6.7 mm.

It should be noted that a part of the overestimation is likely due to the use of data from triploid *C. virginica*. As discussed above, these oysters have been shown grow at a faster rate than natural oysters, however the extent of this difference and the interaction of this effect with *P. marinus* infection is unknown. The model estimates match the observed data fairly well, but it may be that the disease

estimate of the model is actually overestimating the disease effect on growth since the model estimate would be expected to be slightly higher than the observed growth due to the triploid effect.

Evaluation of the model's predictive ability remains difficult due to the lack of restored oyster bars in the Chesapeake Bay that have remained free of *P. marinus* exposure for several years. However, this model presents a good starting point for the estimation of the growth of planted oysters in the upper portion of the Chesapeake Bay. Even though the model development and evaluation of the model's results are hampered by a lack of data, a relationship between short-term temperature and salinity measurements and the von Bertalanffy growth parameter can be developed. Additionally, this relationship can be used to develop a model that can capture the seasonal oscillations in oyster growth. Further model development will focus on developing a better way to dynamically estimate *P. marinus* impacts on growth.

### 3.2 Model Performance with Extremely Low and High Salinity Regimes

The model is intended to function best in the moderate salinity regions of the upper Chesapeake Bay. Also since most of the data the was that was used to develop the model comes form the moderate to low salinity areas in the Chesapeake Bay it is useful to test the limits of the model by running it using data from a high salinity region and an extremely low salinity region.

For the low salinity site I used data from the Chesapeake Bay Program monitoring station ET 4.1 in the Chester River. This site is located far up river. Salinities there ranged between 0 and 4 for the modeled time period between August 1999 and August 2004. This salinity range is near the lower limit of oyster tolerance (Shumway 1996). The model output for this time period show that the site has very low growth (figure 12). Over five years the mean shell height only reaches 60mm, compared to the other sites described above where shell height reached 60 mm in one to two years. However, even this slow rate of growth is a slightly higher than would be expected at a site with this low salinity. The site modeled never becomes infected with dermo because the temperature and salinity threshold values are never reached.

For a high salinity site we use the Chesapeake Bay Program Monitoring Station LE 4.3, at the mouth of the York River in Virginia. This site has consistently

higher salinities than any of the sites used to develop this model. The model development did use one site in the York River. However, this site was farther up river and at lower salinity than the LE 4.3 site at the mouth. Also, since the model development used a regression technique that did not weight the one high salinity site any more than the 3 other low salinity sites, the result would likely be skewed towards the low to moderate salinity sites.

For the same 5-year period used for the low salinity site above, August 1999 to August 2004 the lowest salinity recorded at this the LE 4.3 site was 17, with typical salinities ranging between 20 and 26. Oddly, the model estimated growth at this site is substantially less than what would be expected. Over the 5-year period the shell height only reaches 94mm (figure 13). This is likely do to problems in estimating the disease impact on growth at high salinities. As described above, the disease impact on growth, estimated from Paynter and Burreson (1991), uses a two-tiered system. For most of the moderate salinity sites used in this study the second tier of growth reduction (for salinities over 16) is used only for short periods in the model. However, for this site, the lowest observed salinities are above the threshold for the second tier of growth reduction. Indeed, if we turn off the disease component of the model estimation the total estimated growth is rapid (figure 14). Without disease enabled the estimated shell height reaches 87mm in the first year, and at the end of the 5-year model run the estimated shell height is over 200mm. This result implies that the disease

component of the model will over estimate the growth reduction due to disease for high salinity areas.

This may represent a weakness in the model and suggests that the disease impact on growth, especially at high salinities is something that needs to be examined in more detail. However, this is fundamentally problematic because at these high salinities dermo infection tends to produce substantial mortality, making it difficult to specifically isolate the growth effect in an experiment.

## CHAPTER 4: Other *Crassostrea virginica* Models

Several other models have been applied to oyster populations. The model developed here differs significantly from other major models of oyster dynamics in Chesapeake Bay, primarily in scale and scope. The most significant difference is that most previous models have focused on modeling oyster dynamics in a broad geographic area or at a population scale. This model is intended to estimate the growth of oysters in a single location in the upper Chesapeake Bay.

The EPA Chesapeake Bay Program model, developed by Cerco and Noel (2005) was adapted from several previous models (Bicknell et al. 1996, Johnson et al. 1993, Cerco & Cole 1993, DiToro & Fitzpatrick 1993, Wang & Johnson 2000, Myers et. al. 2000, Cerco & Meyers 2000, Cerco & Moore 2001), and is primarily a nutrient transport and hydrodynamic model.

The EPA model is primarily a bottom up design. It focuses on modeling the specific individual components of the ecosystem and then relating these components rather than starting at a highly generalized level and adding detail when it is explicitly needed.

The model itself focuses on the movement of water, nutrients and sediments from the watershed and into the Bay itself. From these components the model

calculates algal growth, nutrient cycling and estimates dissolved oxygen levels throughout the Bay. This model has also undergone several revisions and expansions to include estimates and interactions between the basic nutrient and sediment loading and zooplankton, submerged aquatic vegetation and benthic species (Cerco & Noel 2005). Oyster dynamics were explicitly added to this model in an attempt to estimate the impact of the "Chesapeake 2000" agreement between Pennsylvania, Maryland, Virginia, District of Columbia and the US EPA which calls for the native oyster biomass in the Chesapeake Bay to be increased by 10 fold by 2010, based on a 1994 baseline.

In the EPA model, oysters are modeled primarily using a mass balance function. Individual oysters are not modeled; rather the population within a model cell is aggregated together into a single function. Oyster growth is controlled by several estimates of oyster feeding rates and estimates of nutrient assimilation efficiency. As a result this model establishes a direct link between nutrient dynamics and the increase in oyster biomass. The parameters used for this model come from a large number of previously published studies. (including Meyers et. al 2000, Cerco & Meyers 2000, Cerco & Moore 2001, Jordan 1987, Newell 1982, Westrich and Berner 1984, DiToro 2001) This model represents oyster mortality as a direct loss in oyster biomass. The rate of mortality is determined primarily through a constant, user controllable, mortality term. Mortality from hypoxia is also explicitly included in the model. This provides a link to oyster mortality to the

nutrient and hydrodynamic model that is driving the estimates from the EPA model.

There are few similarities between the EPA model and the model that was developed for this project. The models take such different approaches and have such different focuses that it is difficult to make even general comparisons. The EPA model does not model individual oysters, but rather estimates total biomass directly, using a carbon content as the measure of biomass, and distributes this biomass spatially across all of the known historical locations of oyster reefs (the 1906 Yates survey was used). The EPA model was applied to oysters in an attempt to measure the ecosystem service benefits of achieving a 10-fold increase in the oyster population. In order to model this increase in population Cerco and Noel (2005), reduced the mortality rate of oysters in their model until they achieved a stable population of oysters with at total biomass 10 times larger than the estimated 1994 levels. This approach allows for a reasonable estimate of the potential Bay-wide ecosystem services that could be achieved with this sort of increase, but does not provide any real insight into how the increased population goal might be achieved. Further, estimates of annual recruitment of oysters and the relationship between standing stock and annual recruitment are not well understood. Because of this uncertainty about the spatial distribution of oyster recruitment in the Bay, it is difficult to make any estimates of Bay wide ecosystem services that depend on the spatial distribution of the Chesapeake oyster population, without explicitly modeling larval transport and recruitment.

The model developed for this project takes a different approach. This model avoids many problems by limiting the scope of the model. By focusing on a single restored bar, a simple model can be developed that could potentially be scaled to larger geographic areas simply by replicating the model for multiple locations in the Bay. Estimates of biomass from a single restored oyster reef can be determined through a shell height to weight relationship. These biomass estimates can in turn be used to provide estimates of local scale ecosystem services. This is discussed in the model applications and ecosystem services section in chapter 5.

Powell, Klinck, Hoffmann, and Deksheniks (Hoffman et. al. 1992, 1994, 1995; Powell et al. 1992,1994,1995; Dekshenieks et al. 1993, 2000) developed another commonly used model of *Crassostrea virginica* in Galveston Bay, Texas and Delaware Bay, DE. This model takes an energy-based approach. Energy flow through the ecosystem is used to estimate oyster growth and reproduction, based on estimates of oyster metabolism. Similar to the EPA model, the Galveston Bay model takes a bottom up approach that begins with a detailed hydrodynamic model. It relies on estimates of food concentrations and other environmental conditions such as temperature and salinity to determine filtration rates and subsequent metabolic and assimilation rates.

The Galveston Bay model is an interesting contrast to the model that was developed for this project in that it essentially takes a directly opposite approach to estimating oyster growth. In the Galveston Bay model, the rate of oyster growth is controlled by the amount of food that the oyster consumes. The energy of the food is converted into oyster growth through a metabolic equation. However, in many places, particularly in Chesapeake Bay, food availability is not limiting to oysters. There is far more food available to the oysters than they are able to consume. Because of this, the factor that most directly determines oyster growth in the Galveston Bay model is the estimated oyster filtration rate (Powell et al. 1992). This model uses previously published lab studies to provide information about oyster filtration rates under various conditions. Temperature and salinity are the primary environmental factors that are included in the model, however other factors such as particle density in the water are also included. The effects of these environmental factors on filtration rates, respiration, and reproductive effort are the main factors influencing oyster growth in this model (Powell et al. 1992, Hoffmann et al. 1994).

In the von Bertalanffy based model developed for this project, temperature and salinity are the main factors that determine oyster growth rates, however I do not integrate the physiological and metabolic factors that are causing these differences in growth rates. Instead, I attempted to develop a relationship directly between observed values. The Galveston Bay model represents temperature and salinity effects through a series of threshold values from previously published studies and

expresses these environmental factors through the estimated filtration rate. However, the approach used in the von Bertalanffy based approach represents a simpler and easier to use approach and represents a continuous estimate of oyster growth response to temperature and salinity.

The other fundamental difference between the Powell, Klinck, Hoffman and Deksheniks approach and the approach used here is that their model measures oyster growth in terms of dry tissue weight, rather than shell height. This provides their model with a way to capture smaller variations in oyster growth and variations in oyster health. The fundamental difference is that shell height is never reduced, whereas tissue weight has been observed to decrease, particularly in winter. This approach is a strength because it is a somewhat better measure of oyster size, however it comes with some difficulties. Tissue weight in oysters will vary dramatically in response to seasonal changes, reproductive effort, disease challenges and a variety of other factors. Electing to model tissue weight necessitates that all of these factors be explicitly included in the model, adding a substantial layer of complexity. This high level of complexity, and the reliance on a feeding rate mechanic for estimating oyster growth, requires a substantial number of assumptions and introduces a large number of sources of potential error. The Galveston Bay model is a far more ambitious model than the one developed for this project, however the approach that they have, particularly for oyster growth, provides an interesting contrast to the simplified approach taken in this project.

The Jordan and Coakley (2004) model is also primarily concerned with oyster dynamics on a Bay-wide scale. It does not attempt to estimate individual oyster growth on an individual reef, but instead uses a logistic growth function to estimate the changes in Bay-wide oyster population in response to various management strategies. The model does not attempt to represent the oyster dynamics at the individual bar level, but rather divides the Maryland portion of the Bay in to 3 salinity zones and calculates the population dynamics of oysters in each of those areas. This model uses a top down approach, which makes it more similar to the model developed for this project than most of the other models discussed here which use a bottom up approach.

The Jordan and Coakley model has very different methods and goals from the model presented here. The main focus of the Jordan and Coakley model is to evaluate the potential impact of reducing fishing pressures on the total oyster population over the period of the Chesapeake Bay Program's 10-year management goals (Chesapeake Bay Program 2002). Whereas the model developed for this project is focused on oyster growth and survival at one specific location, over short periods of time, and explicitly ignores fishing pressures and recruitment.

The Jordan and Coakley model is a dynamic model using randomly generated values for fishing mortality, natural mortality and recruitment that are constrained

by the observed means and standard deviations. This allows the model to evaluate potential management strategies on the basis of a likelihood of a desired outcome.

The Jordan and Coakley model is often criticized because its results present a very optimistic outlook for the status of oysters in the Bay. Specifically that a 40%-50% reduction in fishing pressures would result in substantial oyster stock restoration and fishery enhancement within 10 years (Jordan & Coakley 2004). This potential overestimate appears to come from 2 parts of the model. Primarily, the estimates for recruitment are not related to standing stock of oysters but rather an average annual value is calculated based on landings from the oyster fishery. Jordan and Coakley clearly take this approach in an attempt to simplify the model, because annual recruitment in of oysters in Chesapeake Bay is largely unknown due to the complexity of both the temporal and spatial relationships of parental broodstocks to recruitment. However, given the put and take nature of the current fishery, the state of Maryland's ongoing repletion program affects the results of this kind of fishery based estimate of oyster standing stock. As was discussed above in the management history section, this repletion program largely determines the amount of oysters that can be caught in the Bay and determines the fishing effort. Essentially, harvest is artificially supported and may bear little relationship to the actual natural oyster population.

The second significant problem with the Jordan and Coakley model is that it assumes logistic population growth, which may not be appropriate for very small populations. Any overestimates in recruitment can easily inflate the total population estimates very quickly. Given the current state of oysters in the Bay this assumption may also have some further problems. Because oysters rely on aggregating in dense assemblages for reproduction, any location in the bay where oysters are found, but are at very low density are likely to have very poor fertilization efficiency (Pavlos 2004) and thus may contribute very little to overall natural recruitment.

Christman et al. are also currently developing a model in conjunction with the Maryland Department of Natural Resources to predict the impact of introducing an exotic species of oyster into the Chesapeake Bay. This model remains unpublished so discussion of it must be necessarily limited. The main goal of the Christman model is not to represent oyster dynamics on an individual bar, but to represent oyster dynamics across a hydrodynamic region.

These other models of oysters are more complex than the model that is developed in this research. However, this complexity comes at a cost. As the number of parts to a dynamic model grows, more and often non-linear, interactions between various parts of the system come into play. As a result, it may become more difficult to understand each of these individual interactions, as each one becomes obfuscated by all the other interactions. Alternatively, one interaction might have

an unexpectedly high impact on the results of the model. An example of this is in the Galveston Bay model. (Powell et al. 1992) It is an energy flow model, yet in many situations, especially in Chesapeake Bay, the parameter that has a controlling effect on the model results is filtration rate.

It can be beneficial to strive to keep a model as simple as possible so that the interactions between the various parts of the model are readily apparent, and so that the interactions, and environmental conditions that are of most interest can be isolated and their impact highlighted. By using a simple, classic growth model such as von Bertalanffy growth we can develop the relationship between growth and the specific environmental parameters that are of most interest. Furthermore, once growth is known, it is possible to make a wide variety of other estimates, such as total oyster biomass, which in turn allows for the estimation of the benefits of a variety of ecosystem services. Essentially, the approach of using a simple general model enables us to develop an easily understood model that can represent the relationships of interest. However, it will not provide any detail on the physiological or energetic processes that underlie those relationships.

## Chapter 5: Model Expansion: Population and Ecosystem Services Estimates

The von Bertalanffy based growth model developed here is a simple tool that provides an estimate of mean size and disease status for oysters on a restored reef at any given point in the bay. This provides the foundation upon which a broader model of an individual restoration site can be constructed. By including an estimate of initial oyster planted population and mortality over time, the model can be used to provide a simple analysis of the ecological services that potentially could be provided by an oyster reef. Once oyster population and mean size is known, an estimate of oyster biomass can be made. Once biomass has been determined, estimates of water filtration by oysters and subsequent nutrient reduction can be made. These estimates of ecosystem services are significant because they demonstrate the usefulness of the model as a tool for oyster restoration projects in general, and also they help to demonstrate the value of the restored oyster reefs. In discussions about oyster restoration, water filtration and nutrient removal are always at the center of the discussion, and restoration is often justified on the basis of potential nutrient reductions.

## 5.1 Mortality

There are 2 types of mortality implemented in the model, natural mortality and disease related mortality. Natural mortality represents mortality due to all causes other than *Perkinsus marinus*. This is modeled as a constant annual rate that is applied evenly across all monthly timesteps. As a default value this rate is 15%, however the user can change it to any value that is deemed appropriate. The value was chosen as a general estimate based on data from the ongoing monitoring projects conducted by Paynter et al. (unpublished), however this value can be difficult to estimate properly due to confounding effects from disease mortality. However, since this value is user configurable it is possible to test a range of natural mortality rates that suit a variety of scenarios.

Disease mortality is the second type of mortality included in the model. The estimation of disease mortality starts with a base annual rate of 15% (estimated from Andrews & Hewatt 1957, Ford & Trip 1996) that is added to the natural mortality rate after the model puts the bar into a disease state. This base mortality rate is then modified by several factors. The first factor is the time since infection. Several studies have shown that the longer an oyster bar has been infected with the dermo disease the higher the observed mortality rate (Andrews & Hewatt 1957, Ford & Tripp 1996). Unfortunately, there is very little specific data on this effect; therefore the effect is estimated primarily from data from Andrews and Hewatt (1957). In the model, this effect is represented as a simple

multiplier to the base rate of disease mortality based on the number of years since infection. The number of months since the time of first infection is calculated. This value is converted into years and this number is multiplied by the base rate of mortality. That is, independent of other factors the base rate of dermo mortality will be twice as high 12 months following infection and 3 times as high 24 months following infection.

After this base rate is calculated, it is modified based on temperature and salinity threshold values. At very low temperatures and salinities the parasite becomes fairly inactive and produces very little mortality. For winter temperatures below $10^{o}$C the parasite becomes inactive and very little mortality is observed (threshold estimated from Paynter monitoring data and Ford & Tripp 1996). For months in the model where temperatures are below this threshold disease mortality is reduced to zero. A minimum salinity threshold of 9 is also used. Mackin, (1956) has reported that *P. marinus* appears to be intolerant of very low salinities and that the development of lethal infections are severely reduced below this threshold. For months where the salinity is below 9, disease mortality is reduced to zero.

Conversely, high salinities and high temperatures can greatly increase the pathogenicity of the disease and greatly increase mortality rates. Several studies have shown this temperature effect on mortality (Mackin 1951, Andrews 1965, Burreson & Ragone Calvo 1993, Fisher et al. 1992). This model uses a

temperature threshold estimate based primarily on Mackin (1951), Andrews (1965), and Chu & La Peyre (1993). These studies reported significantly higher mortality and disease prevalence at temperatures above 25°C. Makin (1951) reported a six fold increase in disease mortality for oysters at temperatures above 25°C this study was used as the primary basis for the effect of increased disease intensity at high salinity on mortality because it had the clearest results of the limited set of sources. For months in which the temperature is above 25°C the annual dermo mortality rate, determined by the base rate and the time since infection, is multiplied by a factor of 6. High salinities also have been shown to increase dermo mortality rates (Fisher et al. 1992, Ragone Calvo & Burreson 1993, others). However, it appears that the effect of high salinity alone is not as significant as the effect of high temperature. To incorporate a high salinity effect, an estimate was made from data presented in Fisher (1992) and Ford and Tripp (1996). These studies show increased mortality at salinities above 24. In the model this is incorporated as a 2 fold increase in the annual dermo mortality rate. This increase is applied after the time since infection effect, and other temperature and salinity threshold effects. Table 2 summarizes the temperature and salinity threshold values used and the sources for them.

After these threshold multipliers modify the base annual dermo mortality rate, it is converted to a monthly rate assuming an even distribution of mortality across the year. This monthly rate is added to the monthly natural mortality and the

population of oysters on the bar is reduced by this percentage. Total monthly mortality is capped at 100% in the model.

Figure 15 shows the estimated population of oysters at the Shippen Creek site. The actual planted population for this site is unknown, so a density of 200 oysters per square meter is assumed and with a total area of 4000 square meters (about 1 acre).

For comparison, figure 16 shows the estimated survival of oysters at an extreme high salinity site, LE 4.3 at the mouth of the York River. This graph shows that that at these salinities the effect of dermo would be sufficiently large that the oyster reef would be expected to be essentially extinct within 3 years.

## 5.2 Biomass

Total biomass on the reef was estimated from the mean shell height calculation and a total population calculation. The mean shell height is calculated as described above, and population is calculated initially from the area and density of planting numbers that are provided by the user as model inputs. Subsequently, population is reduced every timestep by the mortality rates calculated as described above. A shell height to biomass conversion (kg total weight) from Paynter et. al. (unpublished) is used. (eq. 9)

$$\text{Weight} = ((0.001 * (\text{shell height}^2)) + (0.0045)(\text{shell height})) \quad (9)$$

This relationship gives the weight of the average oyster on the bar and is then multiplied by population to determine total biomass on the bar.

However, for purposes of additional analysis, primarily the filtration and nitrogen removal discussion below it is more convenient to discuss biomass in terms of dry tissue weight rather than total animal weight. For this value I use a different conversion from (Paynter et. al. unpublished):

$$\text{Dry weight} = 0.00003 * (\text{Shell height})^{2.3512} \quad (10)$$

Figure 17 shows the regression used to determine this relationship. The model results showing estimated dry weight biomass per square meter at the Shippen Creek and Bolingbroke Sands sites are shown as figures 18 and 19.

These biomass estimates produce an interesting result. Jordan et al. (2002) estimates the total 1994 oyster biomass as approximately 2.41 $x10^8$ g. Using the Shippen Creek site as an example, the peak biomass at the site is 35g/$m^2$. This biomass peak occurs 2 years after planting. From this we can calculate that the total oyster biomass in the Bay in 1994 would represent 6.89$x10^6$ square meters of similar oyster reef, approximately 1742 acres. To put this into perspective, the total biomass 1994 biomass would represent about 0.06% of the total Bay surface area as moderately healthy oyster reef. It is also worth noting at this point that the Shippen Creek site is less productive than the Boilingbroke sands site that has a peak biomass of 80 g/$m^2$. This implies that in order to achieve the 10-fold increase in oyster biomass called for by the Chesapeake 2000 agreement, an area of less than 17,000 acres of moderately healthy oyster reef needs to be maintained.

It is also important to note, that this represents the peak biomass at the site, about 3 years after planting. By this time there has already been significant mortality at the site, but oyster growth was able to maintain an increasing biomass as the larger oysters make a more substantial contribution to total biomass. In fact, oyster density at Shippen Creek had declined from 200 oysters /$m^2$ to only 60

oysters /$m^2$ at the time of peak biomass. This suggests that in order to maximize the potential returns from a restoration project and in order to maximize oyster biomass in general, maintaining larger oysters is important.

### 5.3 Water Filtration and Nutrient Removal

One of the most prominent ecosystem services provided by oyster reefs is that of water filtration. A large healthy oyster reef has the potential to remove large amounts of phytoplankton and particulate matter from the water column.

Newell (1988) reported that subtidal oysters in the Chesapeake Bay will feed for over 23 hours per day during summer months. The result of this is that a healthy oyster reef is capable of filtering a very large amount of water very quickly. As such this is often considered to be one of the most important ecosystem services provided by a healthy oyster reef. The impact of water filtration by benthic organisms on phytoplankton and nutrient dynamics has been shown in several studies. (Cloern 1982, Cohen et al. 1984, Newell 1988, Dame et al. 1992 Ulanowicz & Tuttle 1992, Newell 1988, Newell et al. 2004).

Two potential estimates of this service can be analyzed. One method is to estimate total water filtered, and another to estimate nutrient removal.

Newell et al. (2004) provides conversion factors that allow for estimating clearance rates for the eastern oyster, as well as a method for estimating the rate of nitrogen and phosphorus biodeposition due to oyster feces and pseudofeces as well as the amounts of this nitrogen and phosphorus that are denitrified or buried.

These rates vary by month and can be applied to the model output to determine a monthly amount of nutrients removed by the bar being modeled. Table 3 shows these values, taken from table 2 in Newell et al. (2004).

Figure 20 and 21 show the monthly rates of water filtration at Shippen Creek and the Bolingbroke Sands sites. Figures 22 and 23 show the rates of nitrogen removed at the Shippen Creek and Bolingbroke Sands sites. Phosphorus removal for these sites is shown in figures 24 and 25. These results are based on model output and calculations using parameters from Newell et al. (2004). The total filtration rate increases for the first 3 years at both sites. During this time the oyster growth allows for more filtration, until after the 3$^{rd}$ year when mortality catches up and filtration rates begin to decline.

Filtration is highest in the summer, when water temperatures are highest and when oysters are the most active. This puts filtration slightly out of phase with the nutrient inputs into the Bay. Nutrient inputs are greatest during the spring and serve to stimulate phytoplankton production, during the summer. $NO_3$ inputs used by diatoms in the spring are recycled as $NH_4$ and this supports summer phytoplankton production (Fisher et al. 1998). While oyster filtration activity is not in phase with nutrient inputs, it is in sync with the periods of highest phytoplankton production.

These results highlight the important role that larger oysters play in providing ecosystem services. If we compare the model results from Shippen Creek for July 1999 (shortly after planting in fall 1998) to the model results from July 2001 we can see some interesting differences. In July 1999, the estimated density was 162 oyster/$m^2$, with a mean shell height of 34 mm. At this population and size, an estimated 2.9 g N/mo $m^{-2}$ was removed by denitrification and 1.4 g N/mo $m^{-2}$ was buried. A total of 4.3 g N/mo $m^{-2}$ was removed. In July 2001, the estimated density was only 47.6 oyster /$m^2$ due to significant mortality. However, the mean shell height at this time was up to 70mm. As a result an estimated 4.6 g N /mo $m^{-2}$ was removed by denitrification and 2.3 g N /mo $m^{-2}$ was buried. A total of 6.9 g N /mo $m^{-2}$ was removed. Although the modeled population of oysters at the site had dramatically decreased in that two-year period, the total filtration services of the oyster reef was still increasing due to oyster growth. Figure 18 shows the modeled biomass at the Shippen Creek site, and this too highlights the value of larger oysters. The peak filtration is at the point of highest biomass. The sharp loss in biomass after July 2001 was due to disease losses. There are fewer oysters remaining at that time, but they are all of significantly higher biomass. Losing larger oysters to disease represents a larger loss of total biomass. Growth rates can outpace mortality, and biomass can increase or be maintained up until a certain point. Figure 18 shows this, total population is constantly decreasing (figure 11) but up until August 2001 biomass is increasing or constant. After this point, there is a more rapid loss in biomass and in ecosystem services provided as

mortality outpaces growth. This period of rapid loss in biomass is not seen in figure 15, which only shows the number of oysters surviving.

Furthermore, the relative scale of nitrogen removal at restored oyster bars is significantly higher than the average rates of nitrogen removal. Boynton et al. (1995) estimated nutrient loss rates on an areal basis for several parts of the Chesapeake Bay. His estimates for denitrification ranged between 4-5 g N $m^{-2}$ $yr^{-1}$, and nitrogen burial rates ranged between 2-12 g N $m^{-2}$ $yr^{-1}$. For Shippen Creek and Bolingbroke sands sites denitrification ranged between 8 and 24 g N $m^{-2}$ $yr^{-1}$ and nitrogen burial ranged between 5 and 12 g N $m^{-2}$ $yr^{-1}$. Similarly, Boynton et al. estimated phosphorus burial to range between 0.4 and 3.9 g P $m^{-2}$ $yr^{-1}$, and for the oyster restoration sites, phosphorus burial rates ranges between, 4.4 and 13.6 g P $m^{-2}$ $yr^{-1}$. This implies that oyster reefs can contribute very substantially to the removal of nitrogen and phosphorus from the system. Figures 26 and 27 compare the annual nitrogen removed for the Shippen Creek and Bolingbroke Sands sites with the Boynton et al. estimates for the Choptank River and the mainstem of the upper Chesapeake Bay. These charts show not only the large difference in nitrogen removal rates between oyster bars and average bottom area, but they also again highlight how these nutrient removal rates at the oyster bars increase as the oysters grow.

These results show that oyster reefs can greatly enhance nutrient removal in the Chesapeake Bay, and furthermore that because larger oysters will filter more than

smaller oysters, they are particularly valuable for nutrient removal. From this it can be inferred that one possible way to try to maximize the filtration and nutrient removal benefits of an oyster restoration project would be to focus on maintaining the survival of larger oysters over longer periods of time. However, given the current prevalence of disease in the Chesapeake Bay this may be difficult. However, and alternative approach could be to replant the bar on a regular basis, this would help to maintain the ecosystem services by replacing the oysters lost to mortality.

### 5.4 Modeling Multiple Oyster Plantings

In order to represent a restoration strategy that replants the oyster bar on a regular basis, we can use the current model and simply run it multiple times to represent multiple plantings. This approach assumes that there are no interactions between the plantings. However, this simple approach can provide some insight into using a multiyear approach to oyster restoration projects.

As an example, temperature and salinity data from the Chesapeake Bay Program monitoring station ET 4.2 in the lower Chester River for August 1995 to August 2005 was used to run the model. Five plantings in these ten years were simulated; the initial planting in 1995, with replanting every 2 years.

The results of these model show that the biomass and related services at this site will be maintained through the ten years and slightly increase by the end (figure 28). Figure 28 also shows that the performance of the different plantings is apparent. Lower salinities and in the late '90s allow for low disease mortality and allow the initial plantings to grow well. Higher salinities in 1999 to 2003 cause high mortalities in plantings two, three and four. However, even with high mortality, growth from these plantings is able to maintain the overall biomass on the reef, suggesting that a strategy of multiple plantings can serve to provide continued ecosystem services even with high levels of mortality (figure 28). As

salinity reduces in 2003, planting 5 becomes successful and the total biomass on the reef increases significantly.

## Chapter 6: Conclusions

This project had two main goals: 1) adapt the von Bertalanffy growth function so that it is able to capture sub annual effects in growth in a meaningful way by developing a dynamic relationship between the growth constant K and environmental conditions, and 2) apply that adapted model to developing a model of oyster growth in the Chesapeake Bay that can accurately predict growth from actual restoration sites.

The approach to the von Bertalanffy growth function that is described here has several significant advantages over previous attempts to model seasonal growth. Previous attempts to incorporate seasonal effects (Pauly et al. 1992, Pitcher & MacDonald 1973, Cloern & Nichols, 1978, Somers 1988) were inherently limited. These approaches could provide an estimate of seasonal changes in growth rates, but they were limited by the fact that their approach forced both sub-annual and inter-annual symmetry in the seasonal oscillation due to their use of a single set of von Bertalanffy constants. This meant that the sub-annual effects that previous approaches estimated were not directly affected by the seasonal changes that caused these effects. As a result the estimates that these previous approaches make simply represent an aggregated seasonal effect, and in the end provide no more information than the simple annual model.

Furthermore, since previous models have not attempted to tie the von Bertalanffy constants to specific environmental conditions, such as temperature and salinity, it becomes difficult for the models to predict growth in conditions that are different from where the model was developed.

The original von Bertalanffy model was derived from techniques used to model physical and chemical reactions. However, for organisms, growth over time is a dynamic response to a variety of environmental conditions. Thus, for many situations where these dynamic changes are important, the original model, and many variants of it, lose a great deal of predictive power. The approach developed for this model assumes that the von Bertalanffy growth constant K, can be changed at every model timestep in direct response to changes in environmental conditions. This allows for a much more useful estimate of growth on short time scales.

The results of the initial modeling effort support the idea that this new approach to the von Bertalanffy function is useful. For oysters, a relationship was developed between temperature, salinity and the growth constant K. This relationship was then used in a model to estimate growth of oysters. The growth predicted by this model does respond to changes in temperature and salinity. The seasonal oscillation in growth that has been observed in *C. virginica* is clearly evidenced in the model output. In each of the model runs, the periods of most rapid growth occur during the summer months when highest growth would be expected.

Similarly, little growth occurs over the winter months. This shows that seasonal growth dynamics can be represented in a von Bertalanffy based model without the need for the extraneous parameters and the sine function used in previous approaches.

Model results show that when disease effects are not included in the model, the model consistently overestimates mean oyster shell height. However, including an estimate of *P. marinus* effects depresses the mean shell height prediction such that the estimates are close to the observed lengths. Estimates from Shippen Creek show this effect particularly well. The full model was tested with results from 3 actual restoration sites and the model predictions matched the observed growth from these sites fairly well.

Unfortunately, however, data issues prevent us from making any strong statistical statements about the accuracy of this model, and therefore an evaluation of the model's predictive ability remains difficult. Fundamentally, data for this model would need to be from observations of planted, hatchery reared, diploid, *C. virginica* oysters at as many sites as possible, in various salinity regimes. The observation sites would have to be observed at least monthly in order to capture the seasonal effects and the sites would have to remain disease free for several years. A data set that meets these criteria is currently unavailable. Furthermore, given the prevalence of *P. marinus* in the Chesapeake Bay it may be impossible to plant test oysters in a variety of salinity regimes and ensure that they will be

unchallenged by disease. Hence, the only way to get appropriate data may be through multi-year laboratory studies. Even then, the differences between laboratory and field conditions may significantly impact the results.

Despite these limitations in data quality, the results of the model appear to be useful. At each of the sites that were used for testing, the growth estimates predicted by the model with disease estimates included are close to the actual values observed at those sites. This suggests that the model can be used to give a useful growth estimate. This growth estimate itself is valuable because it allows us to apply a series of other published relationships to the model output to give estimates of the ecosystem services that an oyster reef can provide.

The examples of ecosystem services estimation presented here highlight the important role that oyster size plays in providing ecosystem services. Even with a constant high level of mortality on an oyster reef, growth rates can outpace mortality, and biomass and the resulting ecosystem services can increase or be maintained for several years. This implies that in order to maximize filtration and nutrient removal services from a restored oyster reef it is important to maintain the larger older oysters on the reef.

Finally, the model developed here focused on a single cohort of planted oysters at an oyster restoration site. However, this model can be readily applied to multiple

cohorts and multiple plantings at the same site, simply by running the model independently for each planting. Mean size, mean survivorship and water filtration and nutrient removal totals can be generated for each cohort, and these values added together to produce and estimate of the total ecosystem services. The example of this approach above demonstrates that even if larger oyster cannot be maintained on a reef, additional plantings at a site can also serve to maintain ecosystem services even if the larger oysters are being lost to disease mortality.

In summary, the model developed for this project demonstrates an alternative approach to the von Bertalanffy function that moves away from previous assumptions that the parameters of the function need to be considered constants. Developing the model in this way allows for the construction of a simple model that can actually capture seasonal changes in growth rates rather than simply providing an aggregated estimate of the effects. Furthermore, once the effects of *P. marinus* disease are included, the model itself appears to provide a reasonable tool for predicting the mean growth of oysters at sites in the upper Chesapeake Bay where a temperature and salinity time series can be estimated. Finally this project further develops the model predictions by incorporating estimates of some important ecosystem services that would be provided by an oyster restoration project at that site.

*Table 1: Calculated Approximate Values For The von Bertalanffy Growth Parameter K At Each Site For Each Month*

| Date | Site | **Mean Shell Height** | **Change in Mean Shell Height** | **K (approximate)** | **Temp ($^{o}$C)** | **Salinity** |
|---|---|---|---|---|---|---|
| 05/18/04 | Choptank | 35.875 | | | 23.6 | 8.3 |
| 06/16/04 | Choptank | 43.600 | 7.725 | 0.441 | 24.8 | 10.6 |
| 07/20/04 | Choptank | 51.654 | 8.054 | 0.478 | 27.3 | 9.1 |
| 08/17/04 | Choptank | 61.629 | 9.975 | 0.619 | 25.2 | 9.7 |
| 09/13/04 | Choptank | 61.075 | -0.554 | -0.035 | 24.4 | 10 |
| 10/20/04 | Choptank | 63.203 | 2.128 | 0.136 | 15.8 | 9.6 |
| 12/08/04 | Choptank | 65.921 | 2.718 | 0.176 | 9.5 | 9.4 |
| 01/10/05 | Choptank | 64.698 | -1.222 | -0.079 | 5.5 | 7.3 |
| 02/15/05 | Choptank | 63.348 | -1.350 | -0.087 | 6.3 | 7.8 |
| 04/13/05 | Choptank | 61.906 | -1.442 | -0.092 | 15.9 | 5.2 |
| 05/19/05 | Choptank | 66.324 | 4.417 | 0.285 | 19.7 | 5.2 |
| 05/17/04 | Patuxent | 35.063 | | | 23 | 9.6 |
| 06/15/04 | Patuxent | 42.906 | 7.844 | 0.446 | 24.8 | 10.6 |
| 07/22/04 | Patuxent | 52.194 | 9.288 | 0.551 | 29 | 11.6 |
| 08/16/04 | Patuxent | 56.493 | 4.299 | 0.264 | 25.3 | 11.3 |
| 09/10/04 | Patuxent | 61.576 | 5.083 | 0.319 | | 11 |
| 10/18/04 | Patuxent | 67.183 | 5.608 | 0.363 | 18.6 | 10.6 |
| 11/30/04 | Patuxent | 67.587 | 0.404 | 0.027 | 17.6 | 12.2 |
| 01/11/05 | Patuxent | 63.634 | -3.953 | -0.257 | 6 | 7.3 |
| 02/11/05 | Patuxent | 63.719 | 0.085 | 0.005 | 2.1 | 9 |
| 04/18/05 | Patuxent | 66.426 | 2.707 | 0.176 | 14.3 | 5 |
| 05/24/05 | Patuxent | 68.500 | 2.074 | 0.136 | 17.8 | 4.7 |
| 04/22/04 | Severn | 32.680 | | | | |
| 05/20/04 | Severn | 33.844 | 1.164 | 0.064 | 22.4 | 4.3 |
| 06/18/04 | Severn | 35.065 | 1.221 | 0.068 | 27.2 | 6 |
| 07/19/04 | Severn | 45.553 | 10.488 | 0.600 | 27.2 | 8 |
| 08/19/04 | Severn | 51.909 | 6.356 | 0.379 | 26 | 7.4 |
| 09/22/04 | Severn | 54.921 | 3.012 | 0.184 | 21.9 | 2 |
| 10/19/04 | Severn | 53.250 | -1.671 | -0.102 | 17.3 | 7.2 |
| 12/02/04 | Severn | 55.794 | 2.544 | 0.156 | 10.6 | 7.9 |
| 01/04/05 | Severn | 52.565 | -3.229 | -0.198 | 5.8 | 5 |
| 02/22/05 | Severn | 52.288 | -0.277 | -0.017 | 3.8 | 5.7 |
| 04/15/05 | Severn | 53.806 | 1.519 | 0.093 | 13.3 | 2.6 |
| 05/23/05 | Severn | 50.167 | -3.640 | -0.221 | 18.4 | 4.5 |
| 05/19/04 | York | 39.156 | | | 21.7 | 19.3 |
| 06/17/04 | York | 50.400 | 11.244 | 0.657 | 24.9 | 18.9 |
| 07/21/04 | York | 64.000 | 13.600 | 0.846 | 28.3 | 19.8 |
| 08/18/04 | York | 76.413 | 12.413 | 0.828 | 26.5 | 16.4 |

| Date | Site | **Mean Shell Height** | **Change in Mean Shell Height** | **K (approximate)** | **Temp ($^{o}$C)** | **Salinity** |
|---|---|---|---|---|---|---|
| 09/15/04 | York | 73.493 | -2.920 | -0.200 | 25 | 15.2 |
| 10/22/04 | York | 81.159 | 7.666 | 0.533 | 17.9 | 17.6 |
| 12/07/04 | York | 85.500 | 4.341 | 0.313 | 13.4 | 12.8 |
| 01/06/05 | York | 81.923 | -3.577 | -0.258 | 11 | 15.4 |
| 03/04/05 | York | 83.541 | 1.618 | 0.116 | 6.5 | 8.7 |
| 04/22/05 | York | 84.817 | 1.276 | 0.092 | 15.6 | 8.3 |
| 05/26/05 | York | 87.350 | 2.533 | 0.185 | 19.3 | 15.7 |

*Table 2: Temperature And Salinity Threshold Values Used For Disease Mortality*

| **Threshold Parameter** | **Estimated Value** | **Source** |
|---|---|---|
| Temperature Threshold for Initial Infection | 16$^{o}$C | Chu & LaPeyre 1993 |
| Salinity Threshold for Initial Infection | 12 | Ford and Tripp 1996 |
| Default Non Disease Mortality | 0.15 /year (user configurable) | Paynter Monitoring Data |
| Base Rate of Disease Mortality | 0.15/year | Andrews & Hewatt 1957, Ford and Tripp 1996 |
| Low Temperature Threshold for *P. marinus* activity | 10$^{o}$C | Paynter Monitoring Data, Ford and Tripp 1996 |
| Low Salinity Threshold for *P. marinus* activity | 9 | Mackin 1951 Ford and Tripp 1996, Ray 1987, Soniat 1985 |
| High Temperature Threshold for increased disease mortality | 25$^{o}$C | Mackin 1951, Andrews 1965, Chu and LaPeyre (1993), Ford and Tripp 1996 |
| High Salinity Threshold for increased Disease mortality | 24 | Fisher 1992, Ford and Tripp 1996 |

*Table 3: Newell et al. (2004) Eastern Oyster Clearance Rates And Nutrient Removal*

| Month | Mean Water Temp $^{o}$C | Clearance Rate (L /h /g DW) | Monthly mg N Denitrified /g DW | Monthly mg N Buried /g DW | Monthly mg P Buried /g DW |
|---|---|---|---|---|---|
| Jan | 3 | 0 | 0 | 0 | 0 |
| Feb | 3 | 0 | 0 | 0 | 0 |
| Mar | 6 | 0.45 | 4.08 | 2.04 | 2.21 |
| Apr | 11 | 0.9 | 8.69 | 4.35 | 4.71 |
| May | 17 | 1.72 | 21.2 | 10.6 | 11.5 |
| Jun | 23 | 3.74 | 46.35 | 23.17 | 25.13 |
| Jul | 27 | 9.62 | 149.26 | 74.63 | 80.92 |
| Aug | 27 | 9.62 | 155.08 | 77.54 | 84.08 |
| Sep | 25 | 7.46 | 89.52 | 44.76 | 48.53 |
| Oct | 19 | 2.34 | 17.25 | 8.62 | 9.35 |
| Nov | 11 | 1.38 | 8.36 | 4.18 | 4.53 |
| Dec | 6 | 0.44 | 2.52 | 1.26 | 1.37 |

**Figure 1:Maryland Oyster Harvest 1870-2003, (Maryland DNR data)**

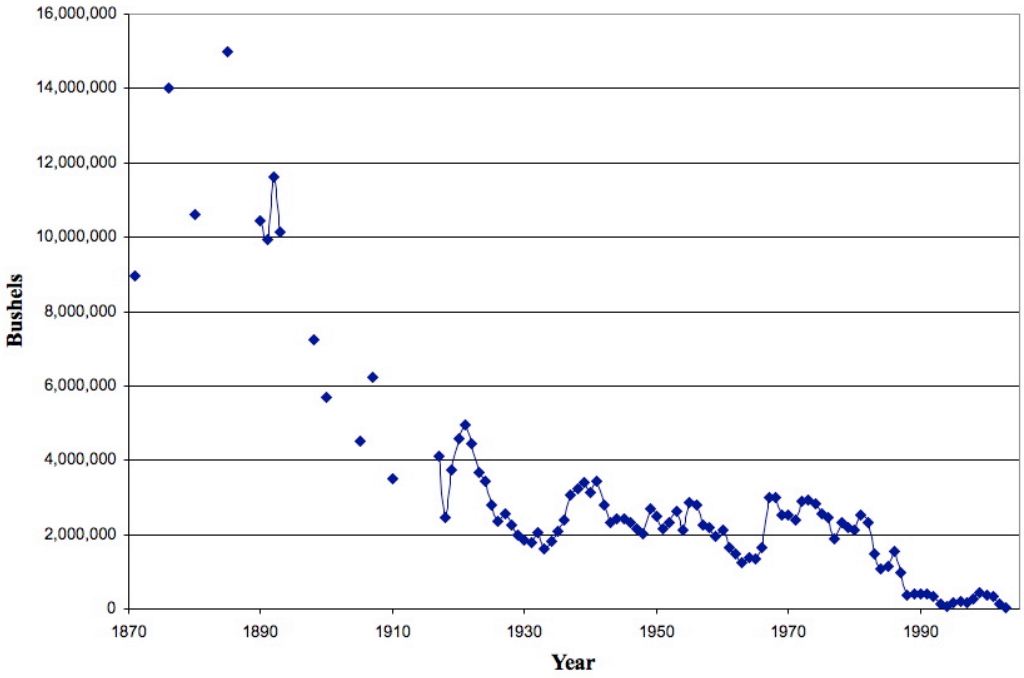


**Figure 2: Maryland Oyster Harvest 1975-2003 (Maryland DNR data)**

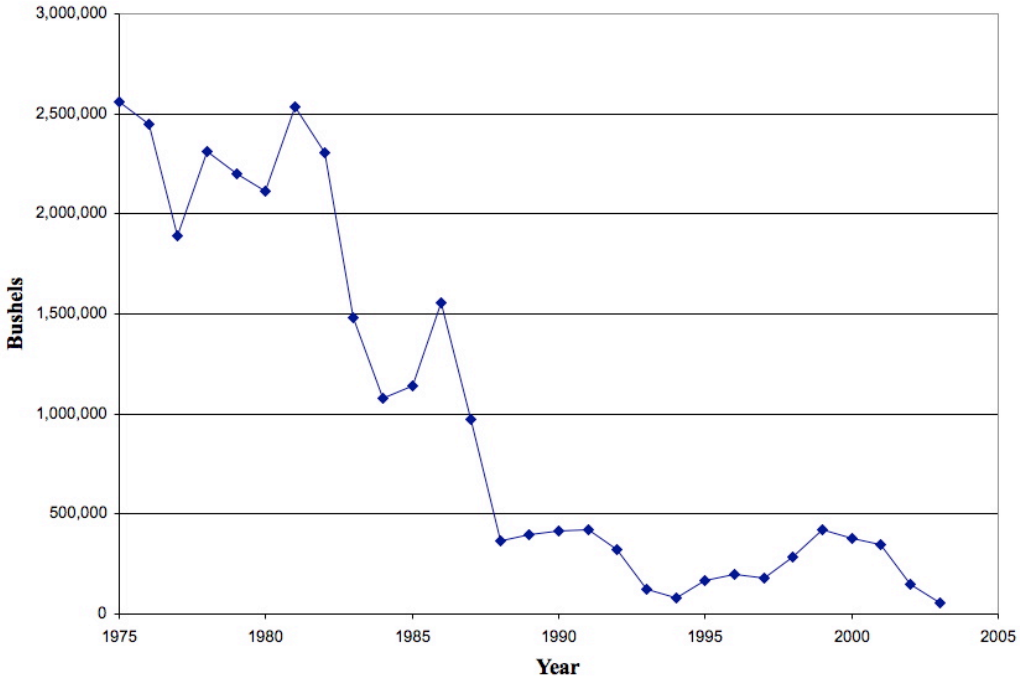
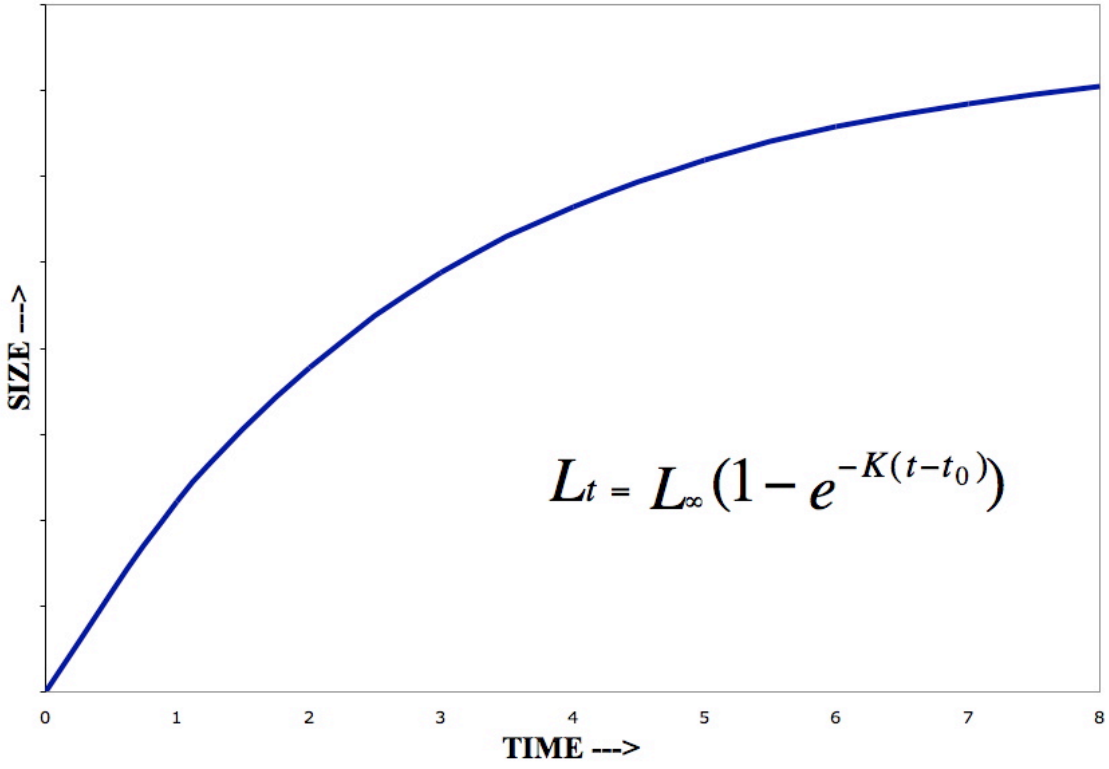


**Figure 3: Classic von Bertalanffy Growth**




$$L_t = L_\infty (1 - e^{-K(t-t_0)})$$

**Figure 4: Oscillating von Bertalanffy function (eq 2) fit to data from Shippen Creek and Spaniard Point sites in the Chester River, using a least squares technique**

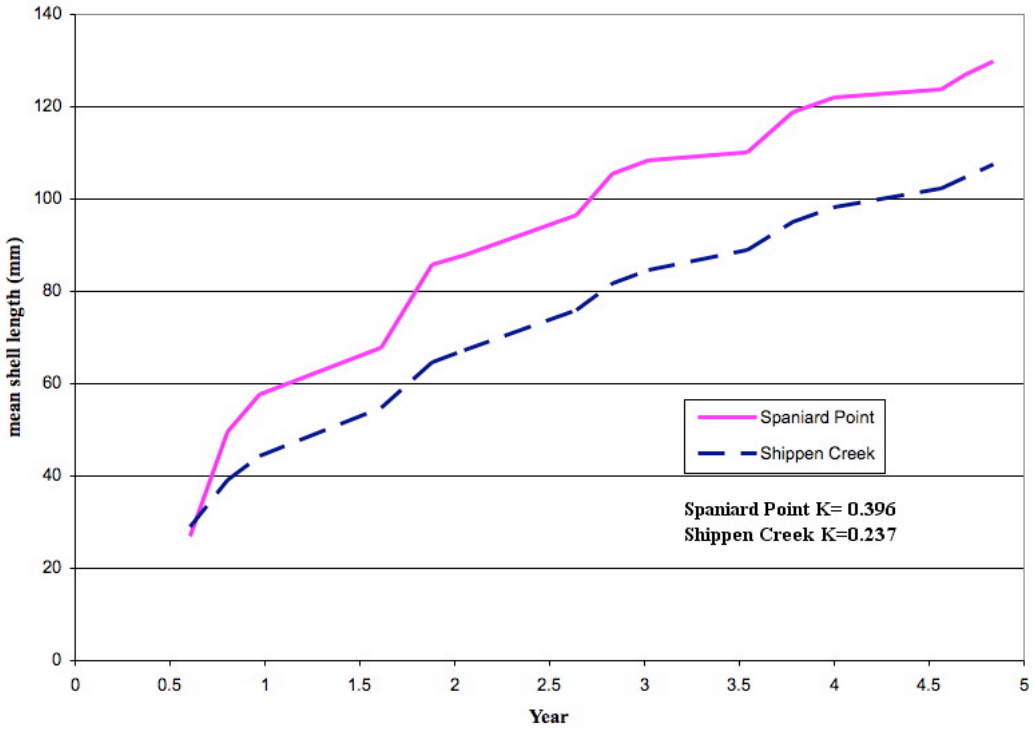
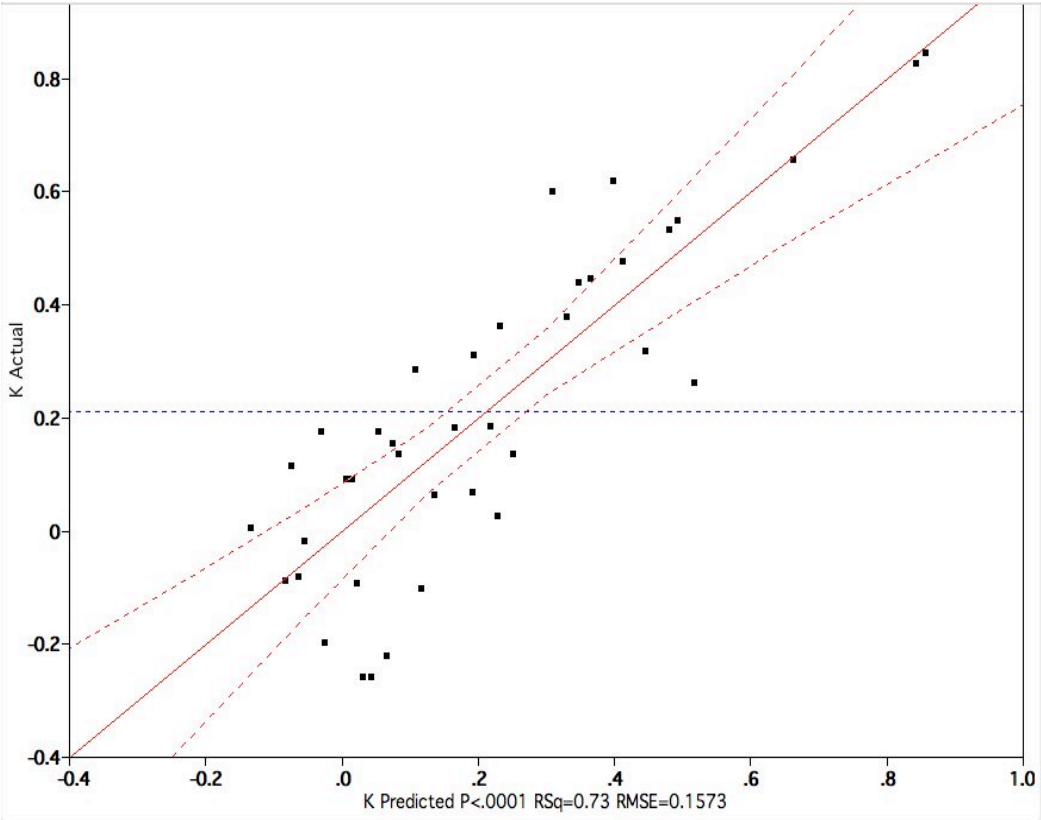


**Figure 5: Regression to determine the von Bertalanffy growth constant K from mean temperature and salinity**




**Summary of Fit**

| | |
|---|---|
| RSquare | 0.726355 |
| RSquare Adj | 0.7029 |
| Root Mean Square Error | 0.157267 |
| Mean of Response | 0.210883 |
| Observations (or Sum Wgts) | 39 |

**Analysis of Variance**

| Source | DF | Sum of Squares | Mean Square | F Ratio |
|---|---|---|---|---|
| Model | 3 | 2.2977643 | 0.765921 | 30.9677 |
| Error | 35 | 0.8656525 | 0.024733 | **Prob > F** |
| C. Total | 38 | 3.1634168 | | <.0001 |

**Parameter Estimates**

| Term | Estimate | Std Error | t Ratio | Prob>\|t\| |
|---|---|---|---|---|
| Intercept | -0.43427 | 0.077789 | -5.58 | <.0001 |
| mean temp | 0.0253856 | 0.003698 | 6.86 | <.0001 |
| mean sal | 0.0176236 | 0.007331 | 2.40 | 0.0216 |
| (mean temp-17.7269)*(mean sal-9.40128) | 0.0031161 | 0.001059 | 2.94 | 0.0057 |

**Figure 6: Growth Model Process**

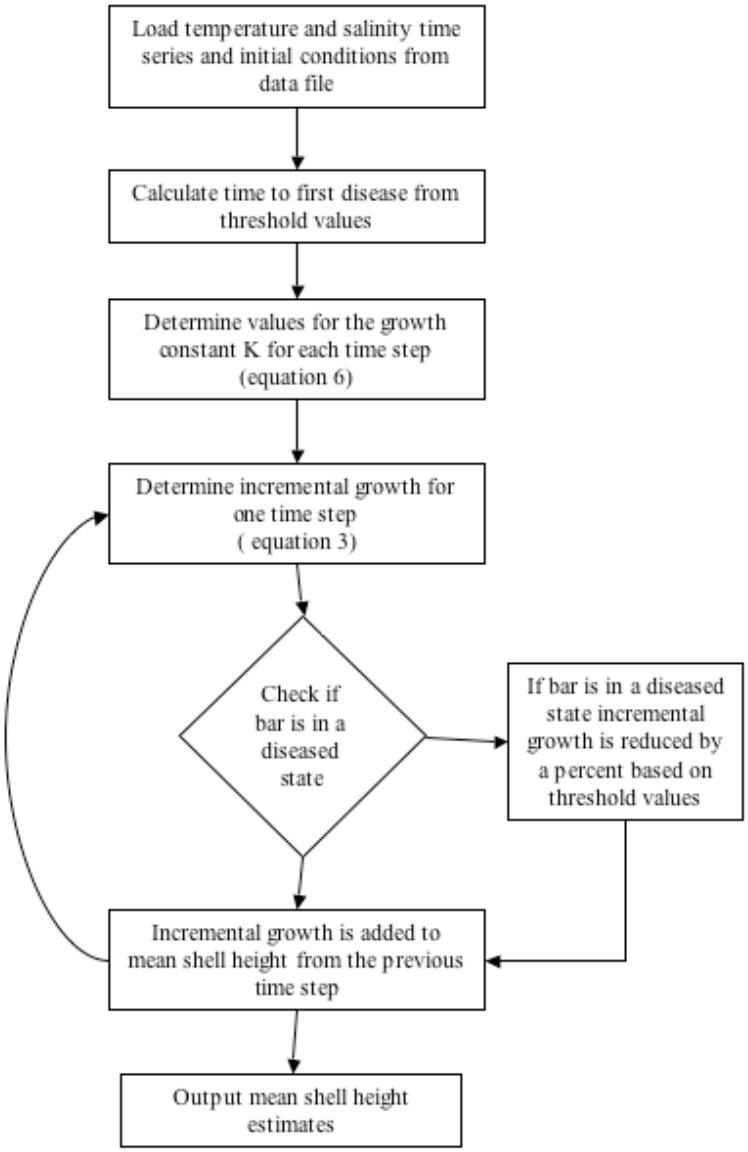


**Figure 7: Model Calibration: Growth model output compared to observed mean shell height of C*rassostrea virginica* at the Choptank river *Crassostrea ariakensis* study site**

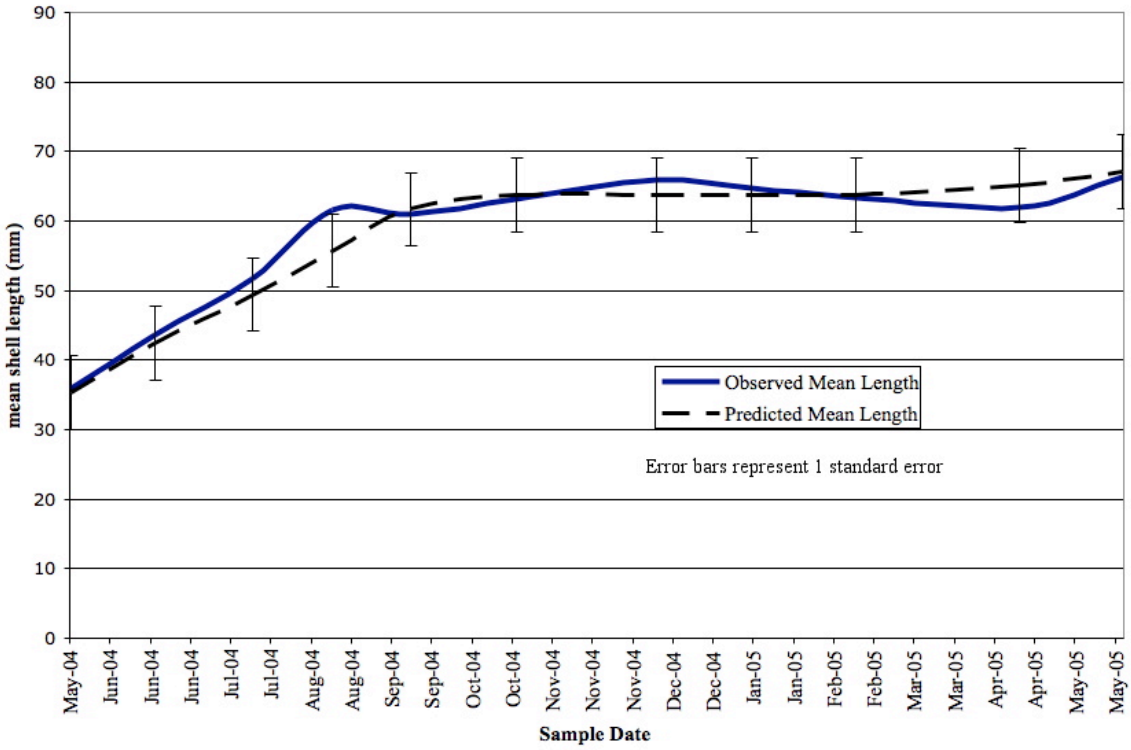


**Figure 8: Model Calibration: Growth model output compared to observed mean lengths of *Crassostrea virginica* at the Patuxent River *Crassostrea ariakensis* study site**

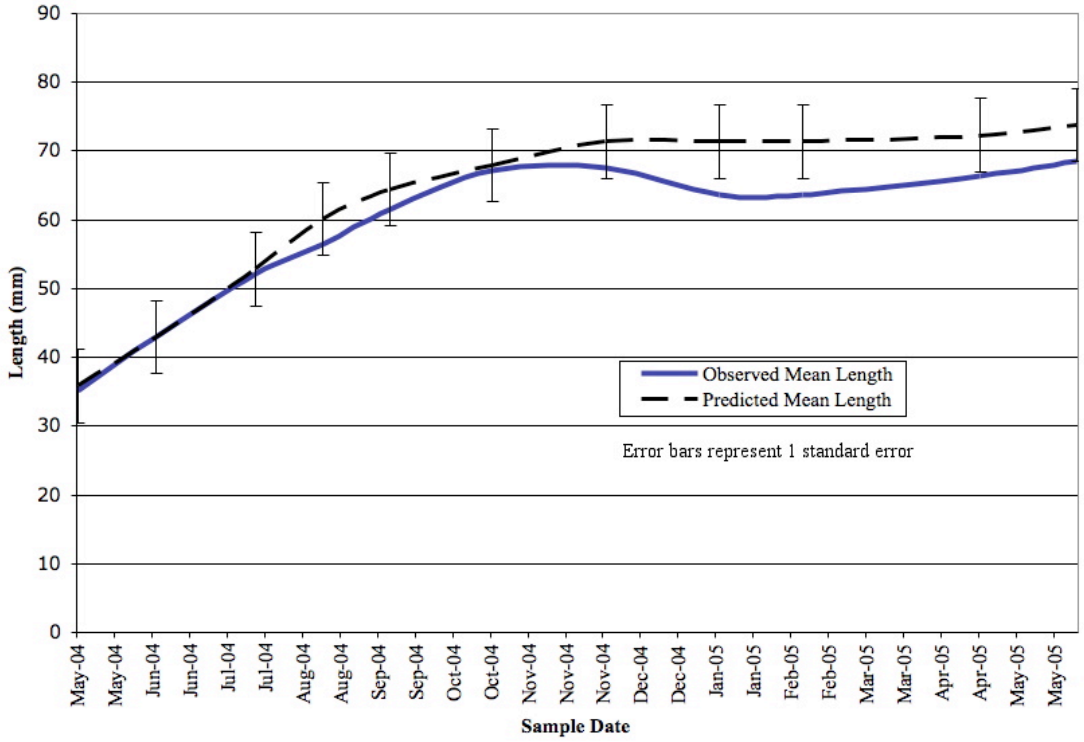
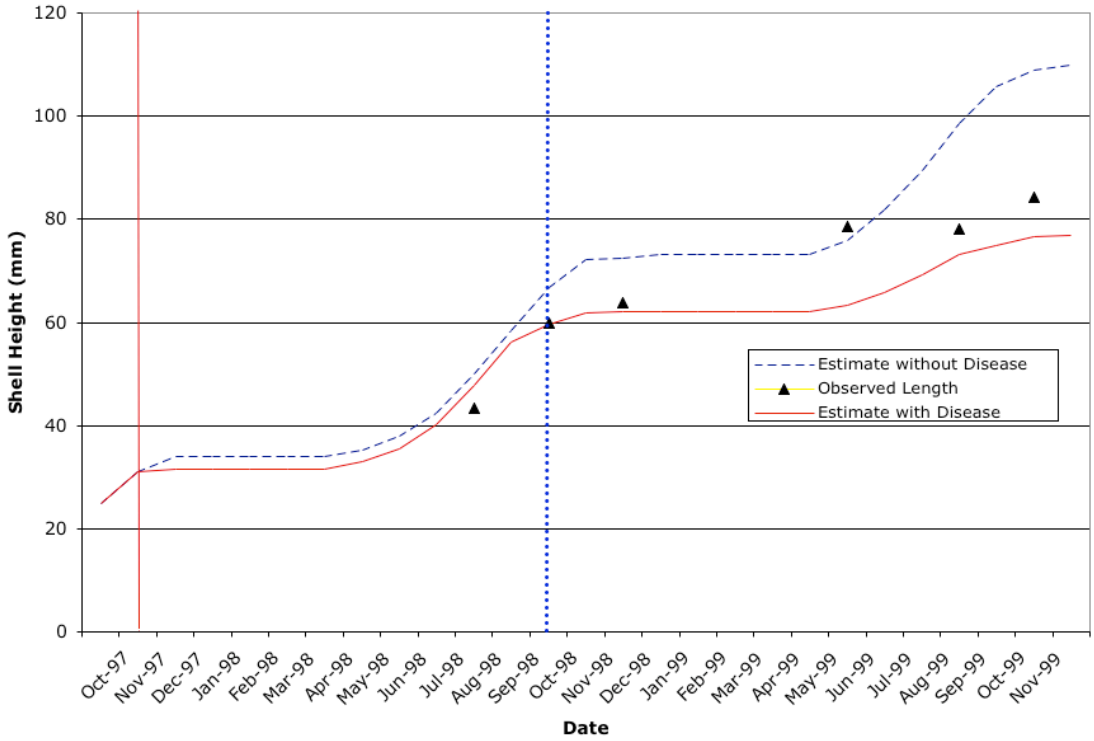


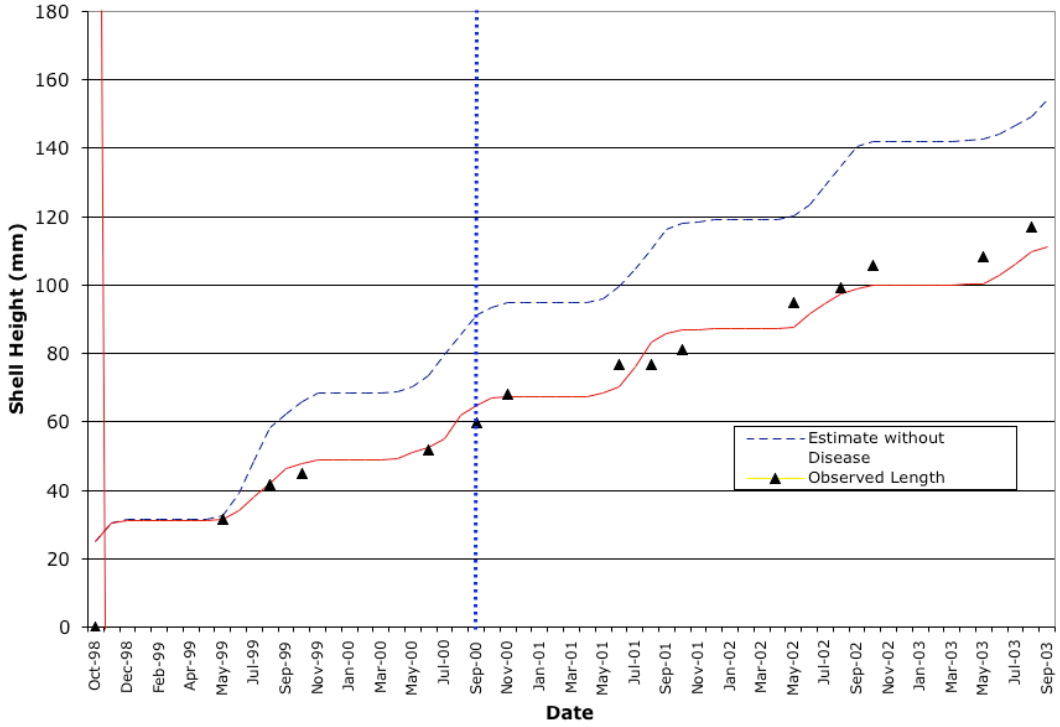
**Figure 9: Model Validation: Model predictions using data from Chesapeake Bay Program monitoring station LE1.1 to estimate growth at Kitts Marsh (Patuxent River) compared to observed mean lengths at Kitts Marsh**




The vertical solid line represents the time dermo infection is predicted in the model, the dotted vertical line represents the first observed incidence of dermo at the site.

The RMSE for the estimate is 5.75 mm.

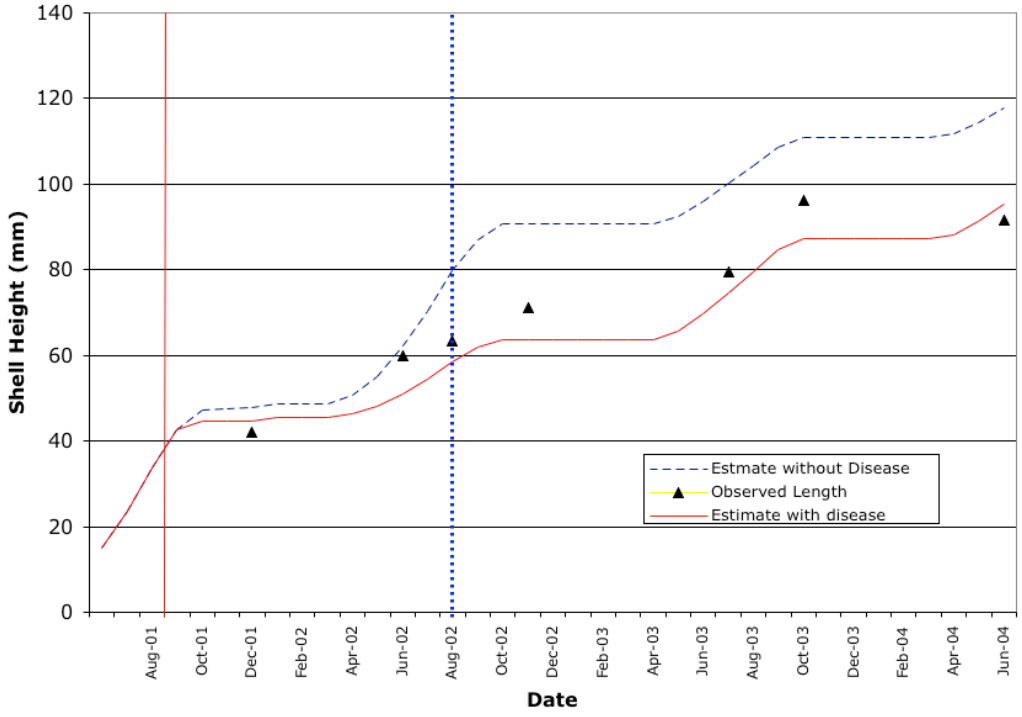
**Figure 10: Model Validation: Model predictions using data from Chesapeake Bay Program monitoring station ET4.2 to estimate growth at Shippen Creek (Chester River) compared to observed mean lengths at Shippen Creek**




The vertical solid line represents the time dermo infection is predicted in the model, the dotted vertical line represents the first observed incidence of dermo at the site.

The RMSE for the estimate is 7.53 mm.

**Figure 11: Model Validation: Model predictions using data from Chesapeake Bay Program monitoring station ET5.3 to estimate growth at Bolingbroke Sands (Choptank River) compared to observed mean lengths at Bolingbroke Sands**




The vertical solid line represents the time dermo infection is predicted in the model, the dotted vertical line represents the first observed incidence of dermo at the site.

The RMSE for the estimate is 6.07 mm.

**Figure 12: Model growth estimates for an extreme low salinity site: ET 4.1 in the upper Chester River**

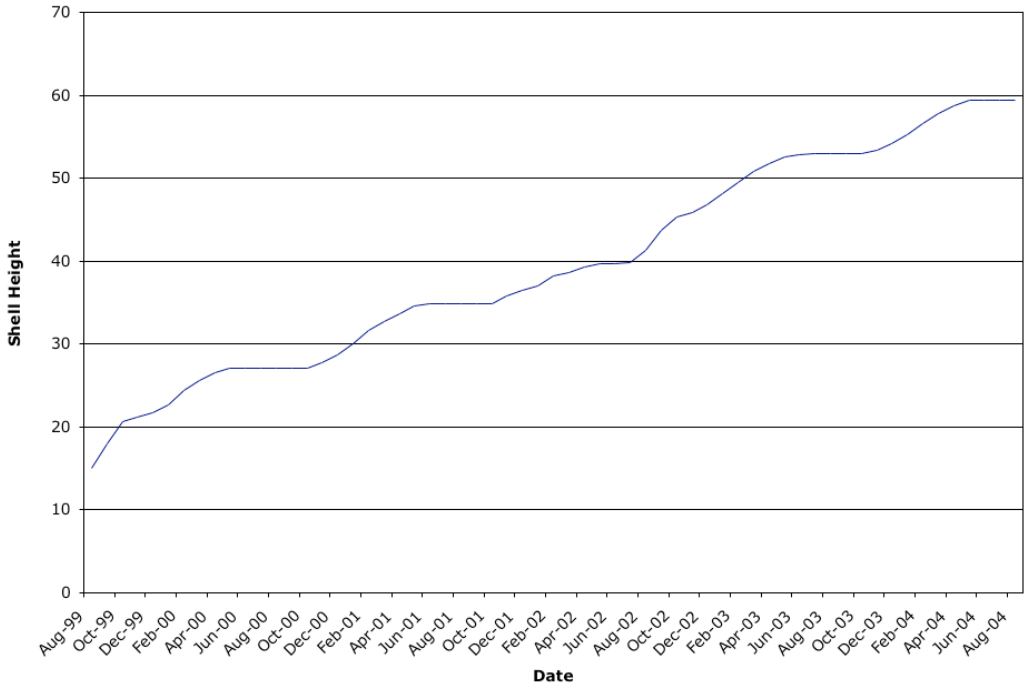
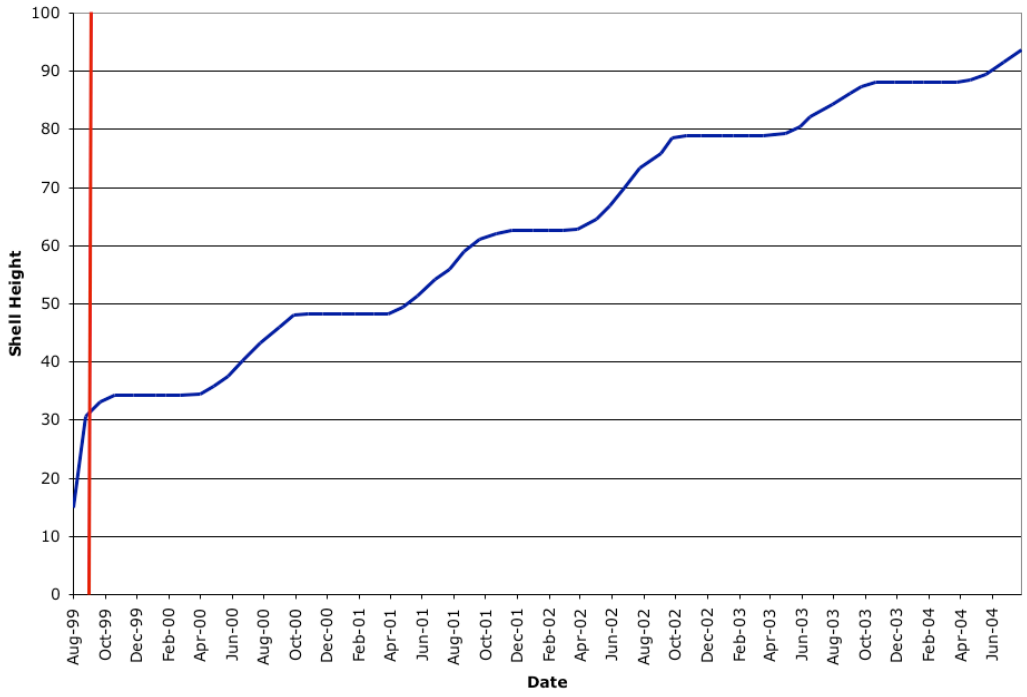


**Figure 13: Model growth estimates for a high salinity site: LE 4.3 at the mouth of the York River.**




The vertical solid line represents the time dermo infection is predicted in the model.

**Figure 14: Model growth estimates for a high salinity site: LE 4.3 at the mouth of the York River, without disease enabled in the model**

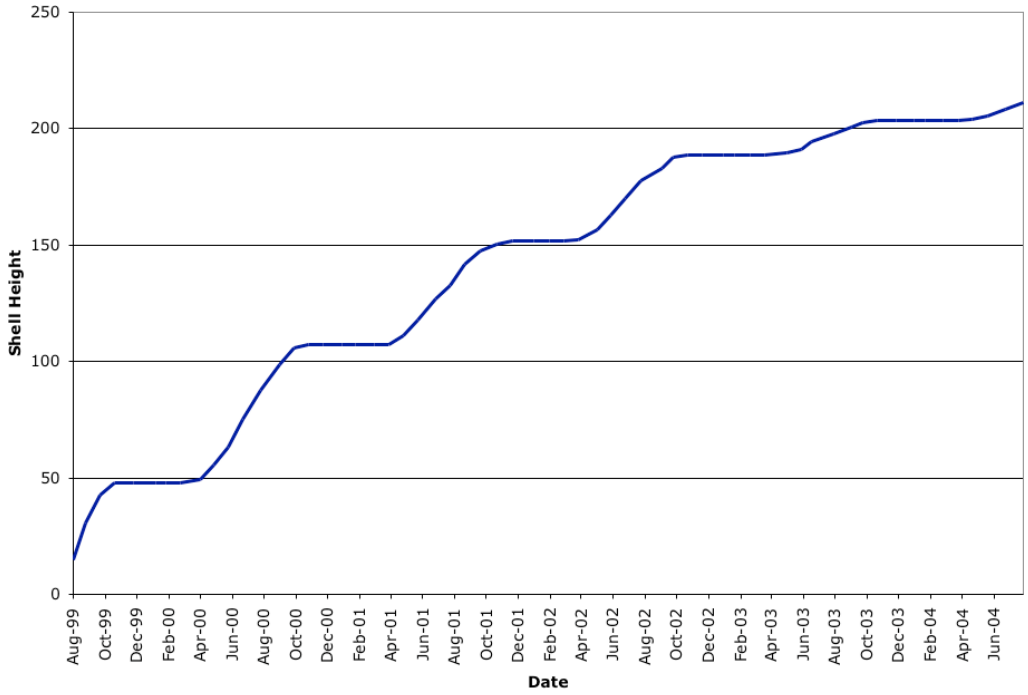


**Figure 15: Estimated mortality at ET 4.2 near Shippen Creek (Chester River)**

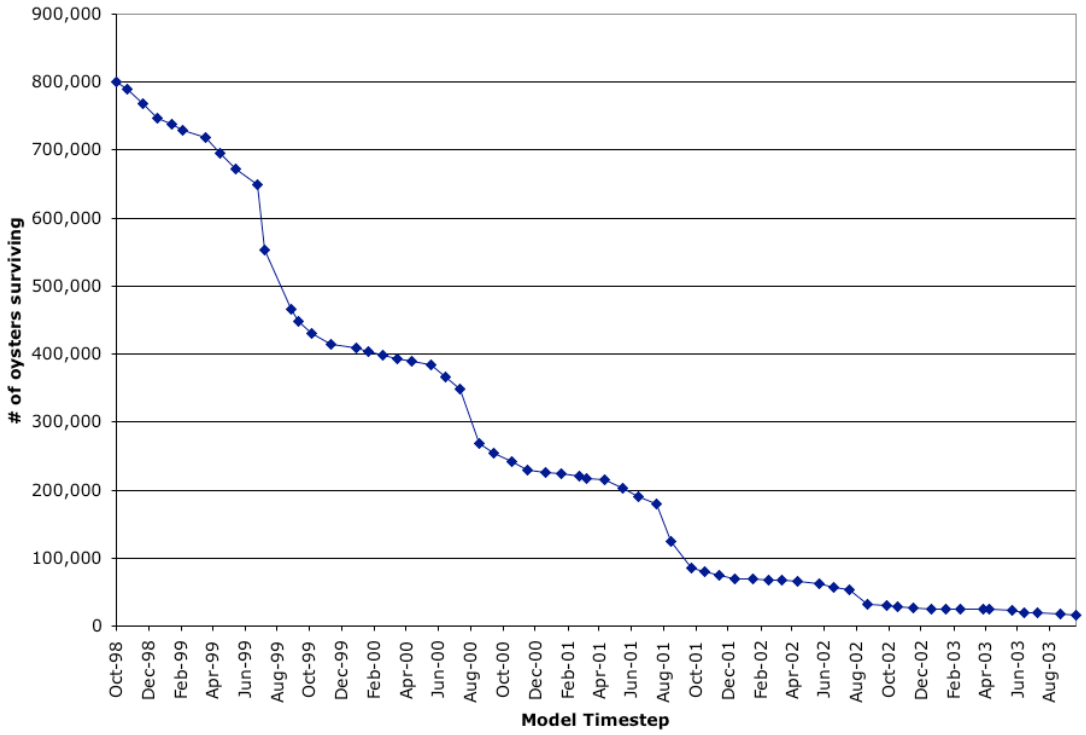


**Figure 16: Estimated mortality at a high salinity site LE 4.3 at the mouth of the York River.**

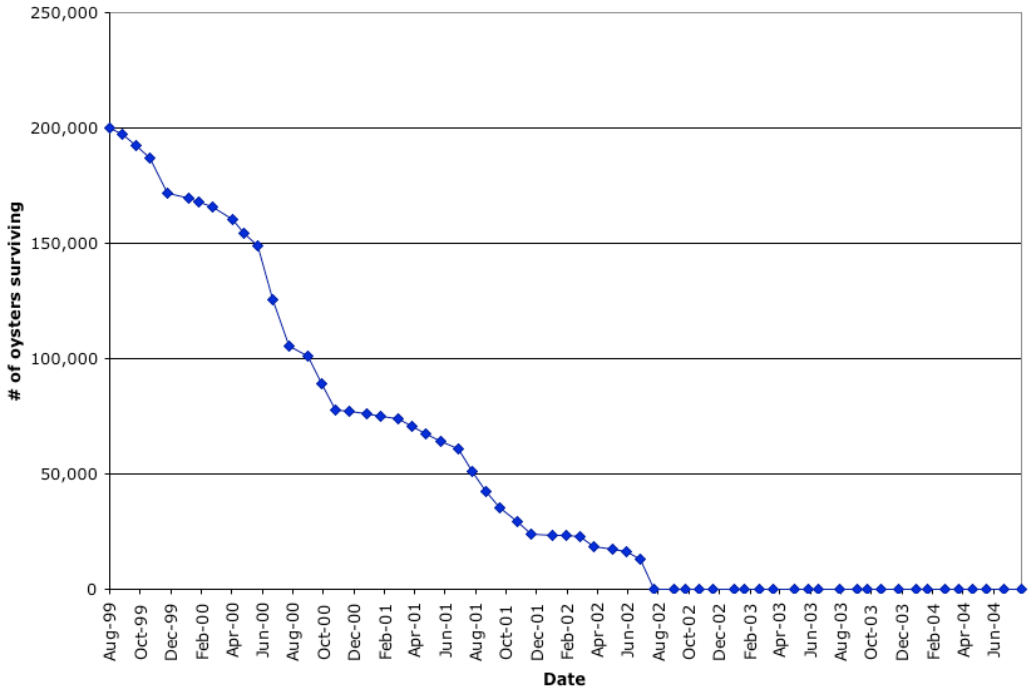


**Figure 17: Regression of oyster shell height against oyster biomass for oysters collected throughout the Maryland portion of Chesapeake Bay from 1997 to 2004.**

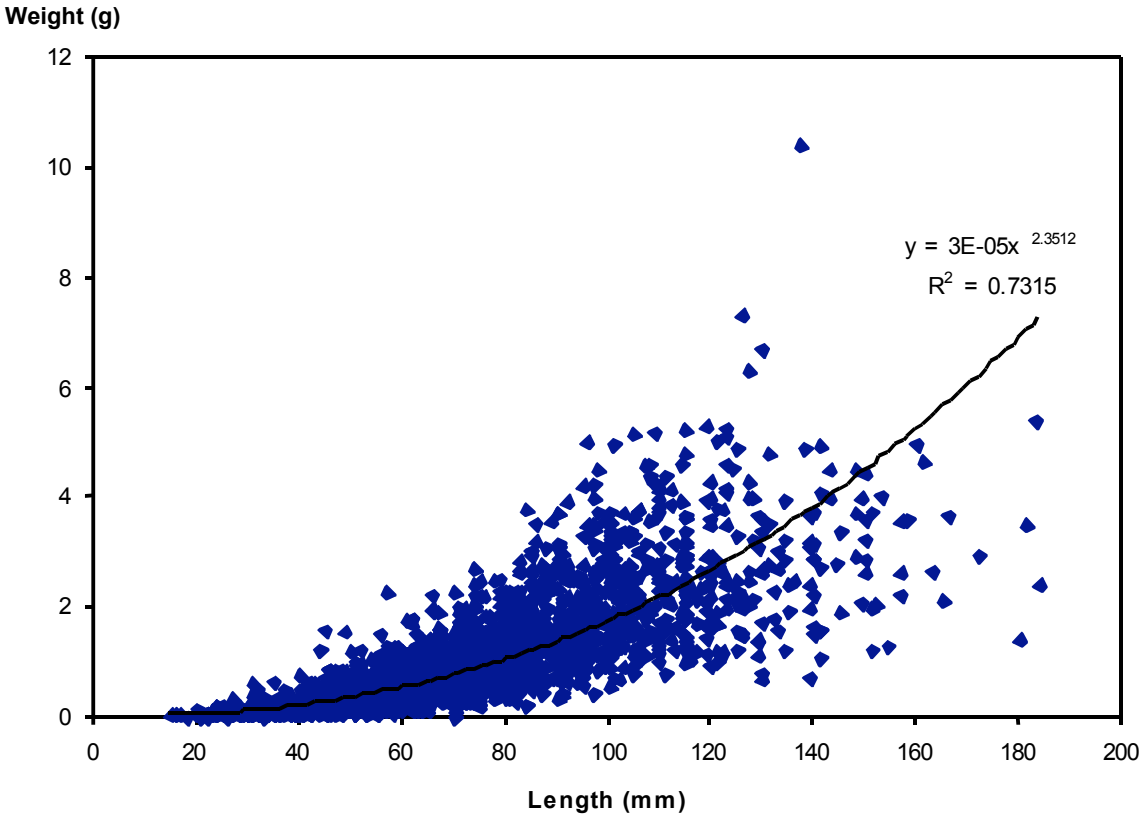


**Figure 18: Estimated oyster biomass per square meter at ET 4.2 near Shippen Creek (Chester River)**

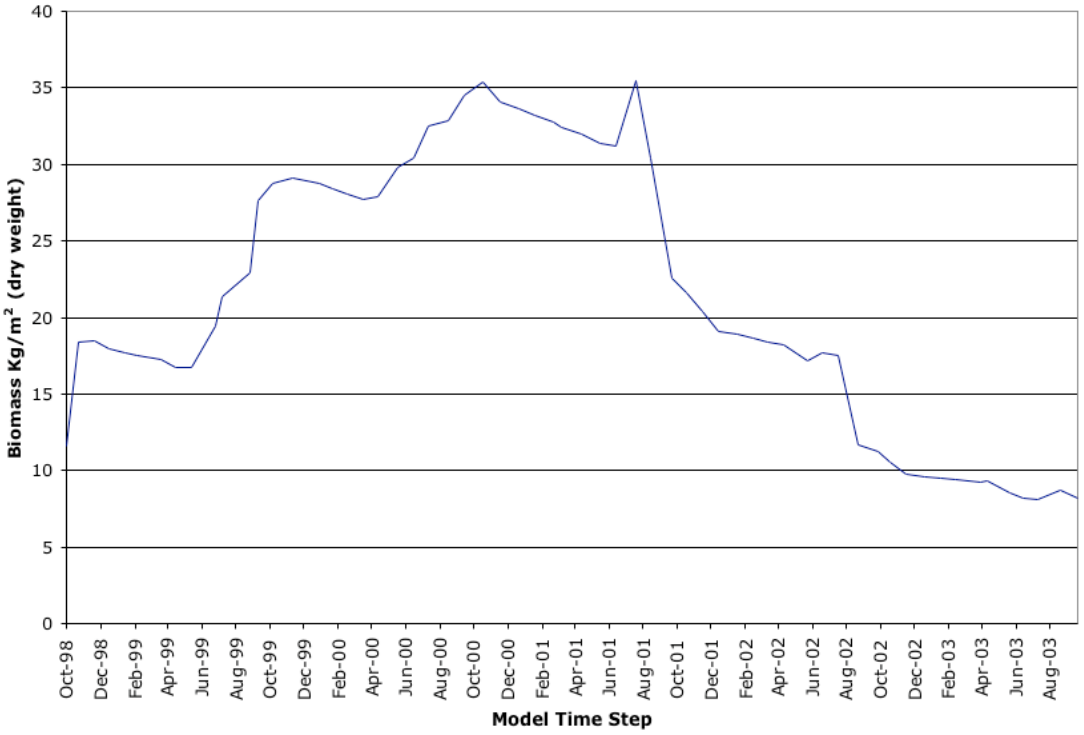


**Figure 19: Estimated Oyster Biomass per square meter at ET 5.3 near Bolingbroke Sands (Choptank River)**

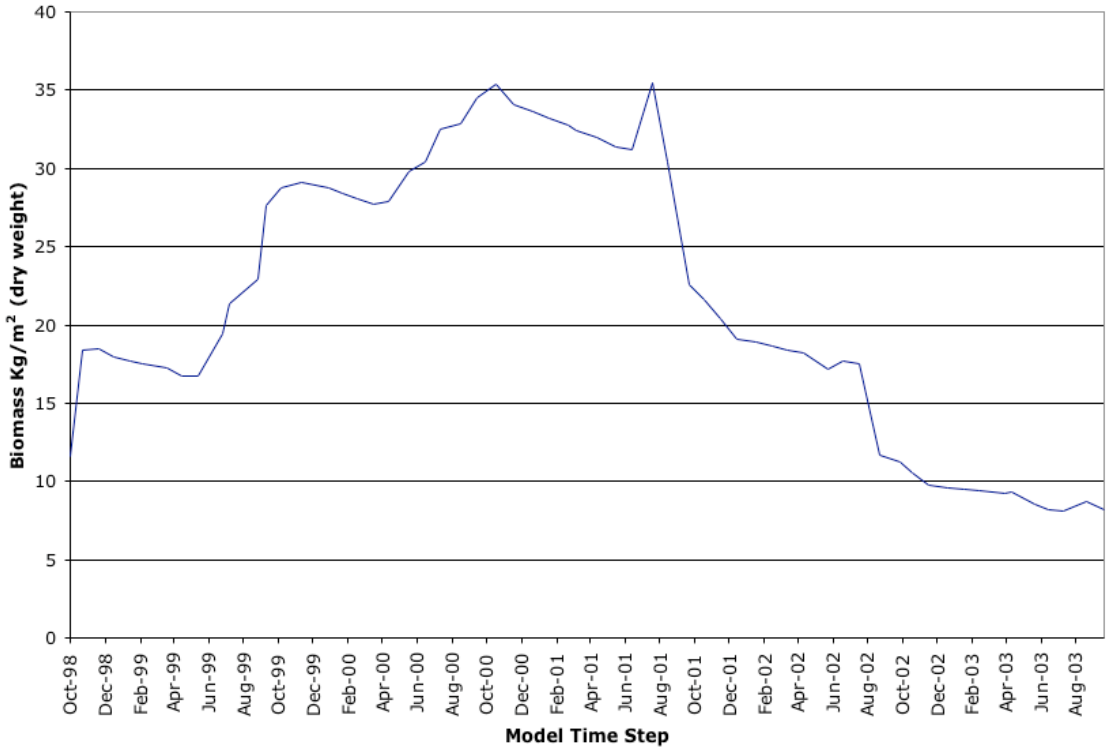


**Figure 20: Estimated monthly clearance rate (liters/month/ $m^2$) at ET 4.2 near Shippen Creek (Chester River)**

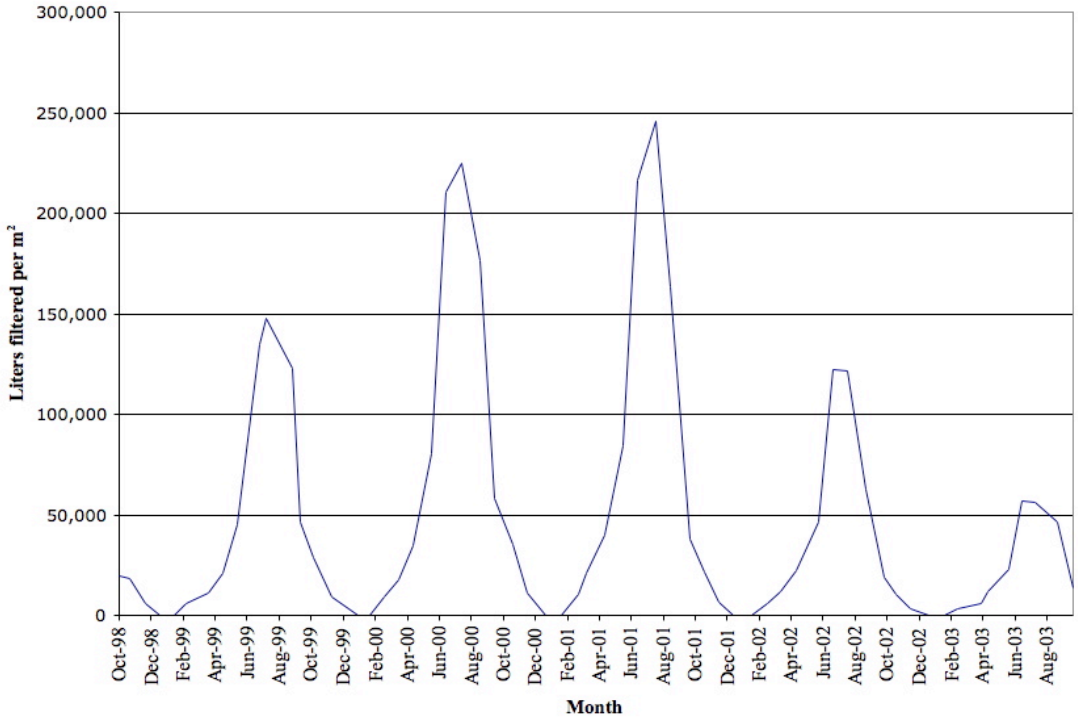


**Figure 21: Estimated monthly clearance rate (liters/month/ $m^2$) at ET 5.3 near Bolingbroke Sands (Choptank River)**

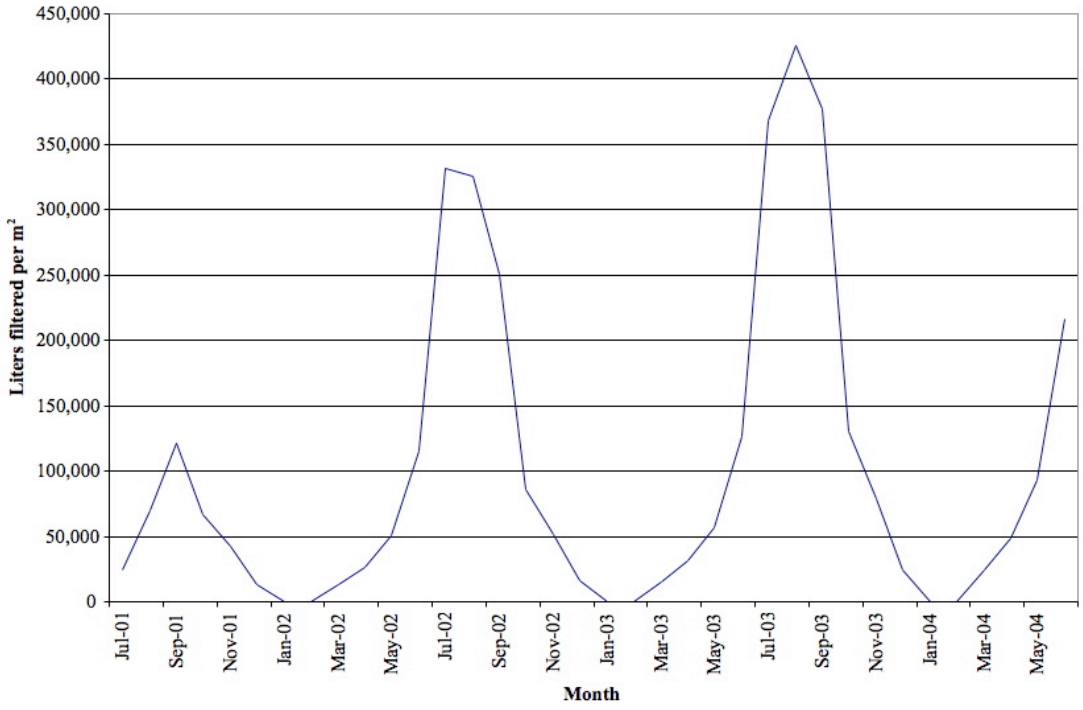


**Figure 22: Estimated total monthly nitrogen removal (g N/m$^2$) at ET 4.2 near Shippen Creek (Chester River)**

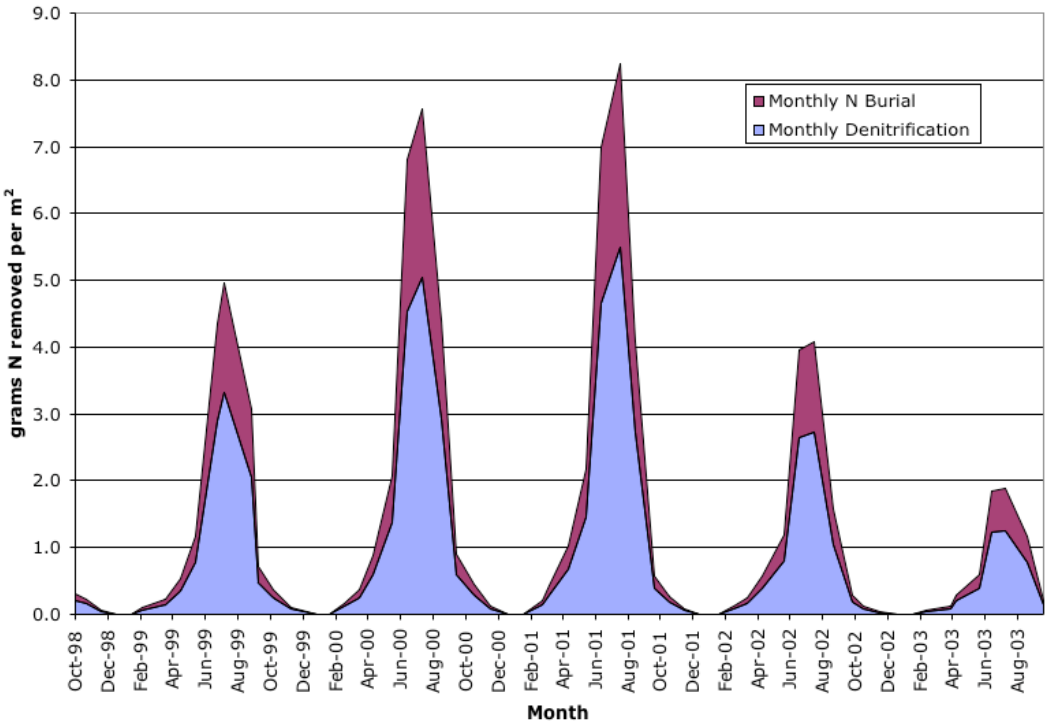


**Figure 23:Estimated total monthly nitrogen removal (g N/m$^2$) at ET 5.3 near Bolingbroke Sands (Choptank River)**

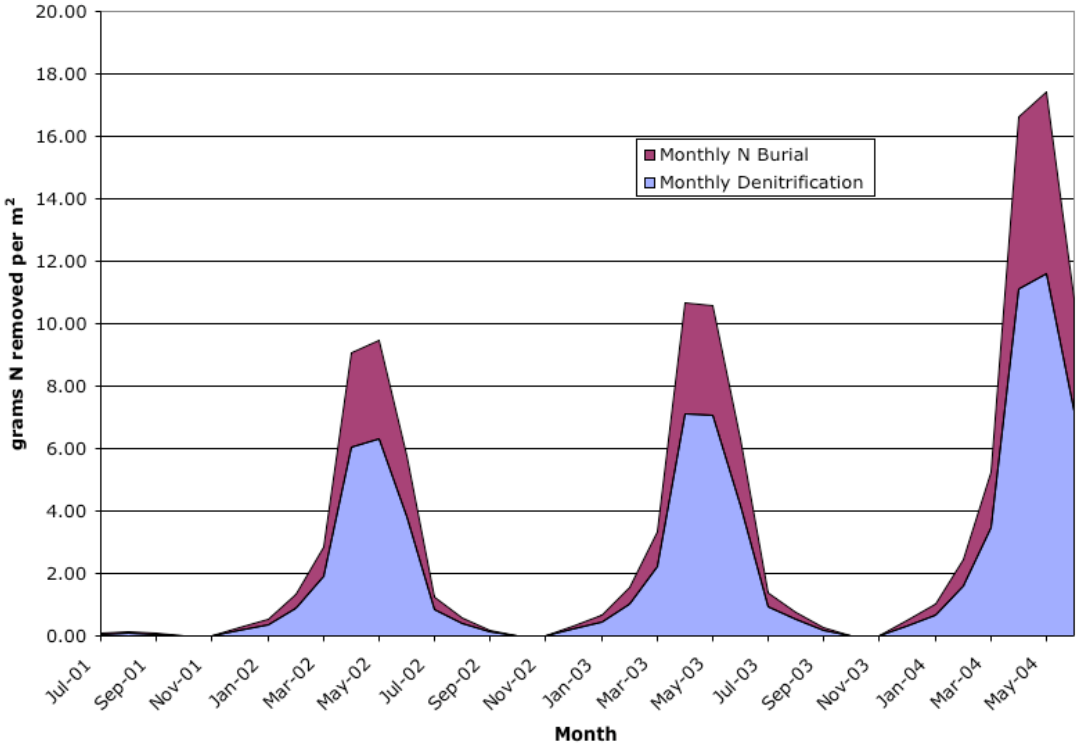


**Figure 24: Estimated monthly phosphorus burial at ET 4.2 near Shippen Creek (g P/m$^2$)**

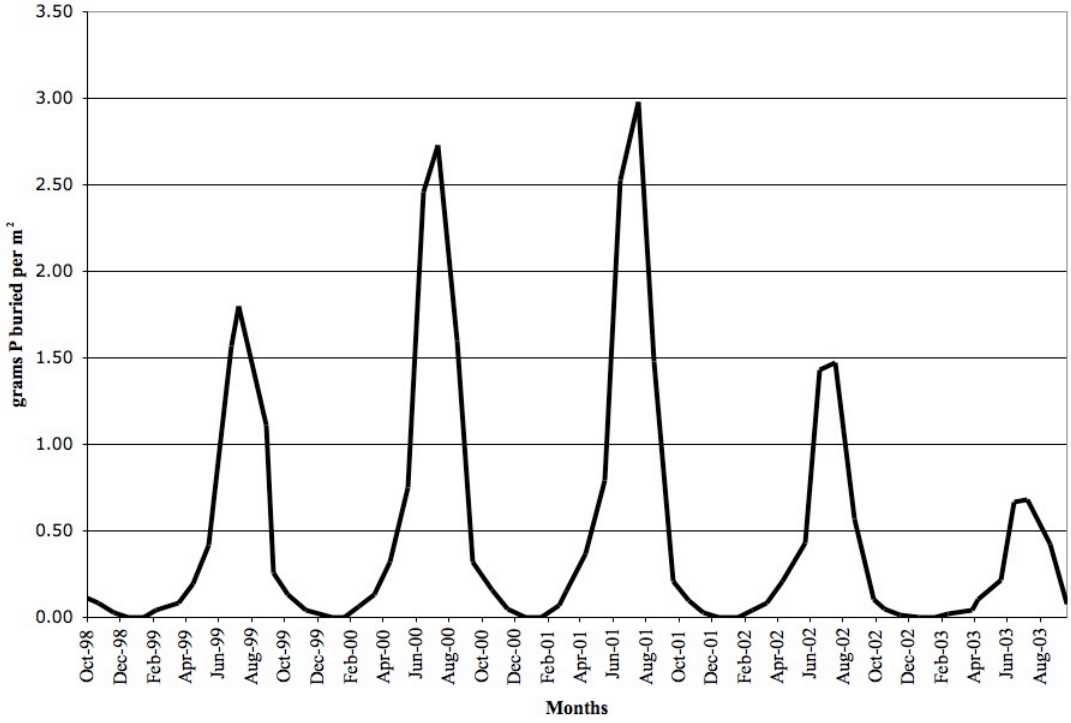


**Figure 25: Estimated monthly phosphorus burial at ET 5.3 near Bolingbroke Sands ($g/m^2$)**

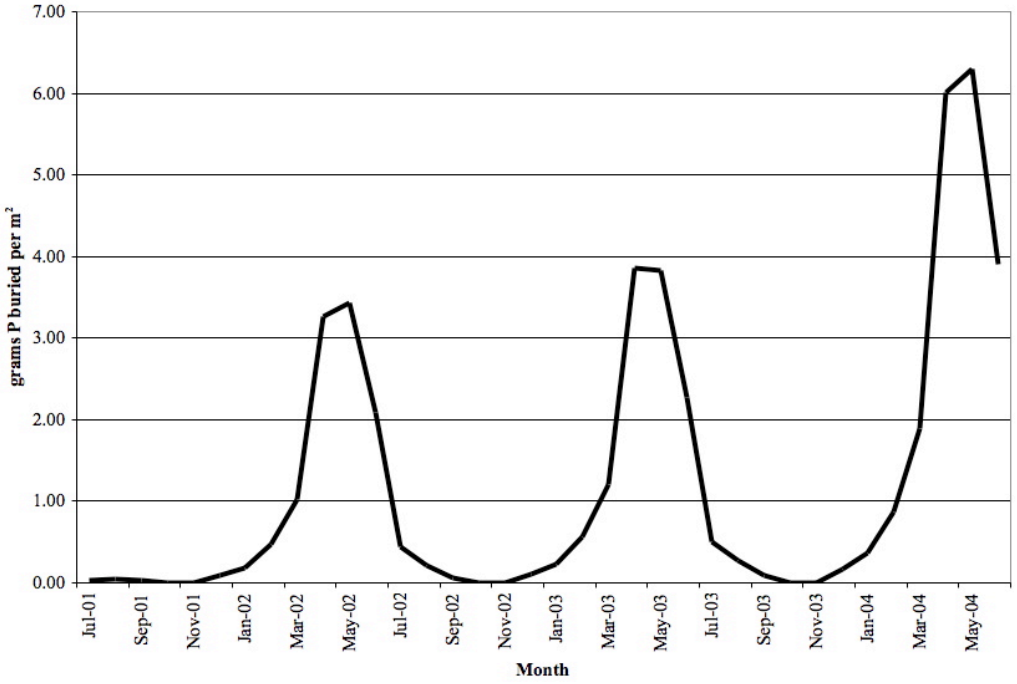


**Figure 26: Estimated annual nutrient removal at ET 4.2 near Shippen Creek compared to Boynton et al. (1995) Estimates**

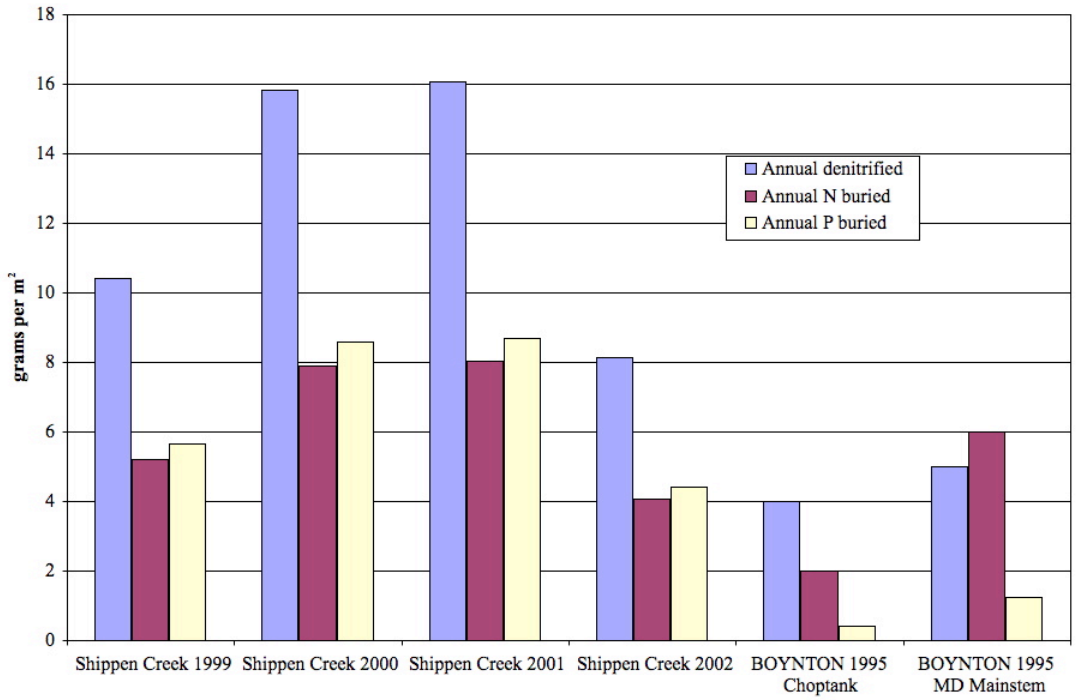


**Figure 27: Estimated annual nutrient removal at ET 5.3 near Bolingbroke Sands compared to Boynton et al. (1995) estimates.**

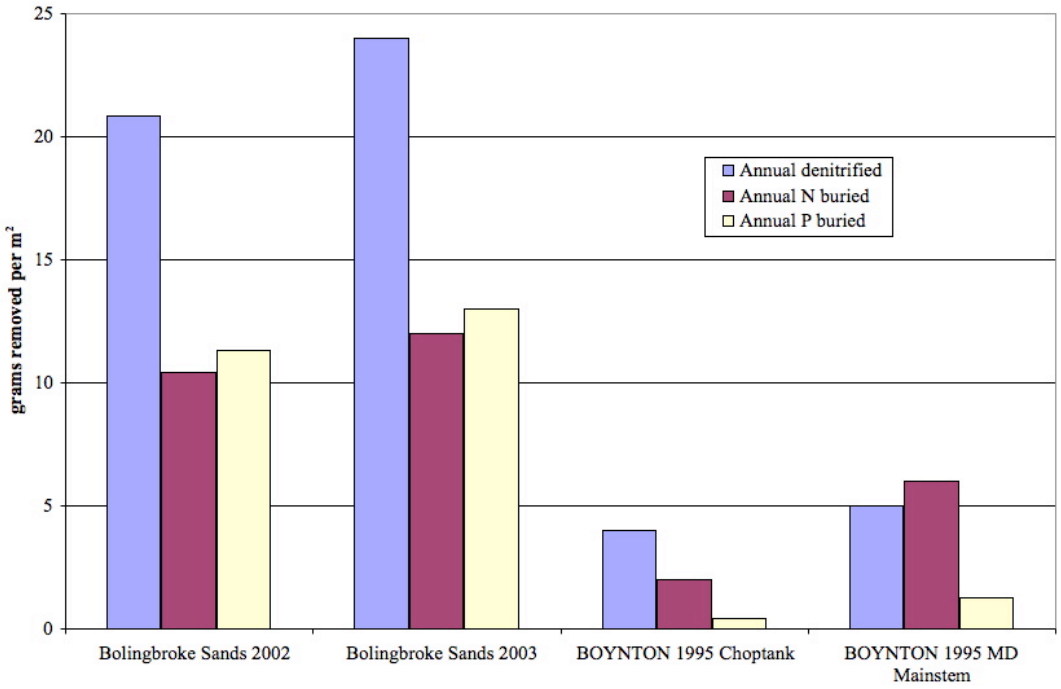
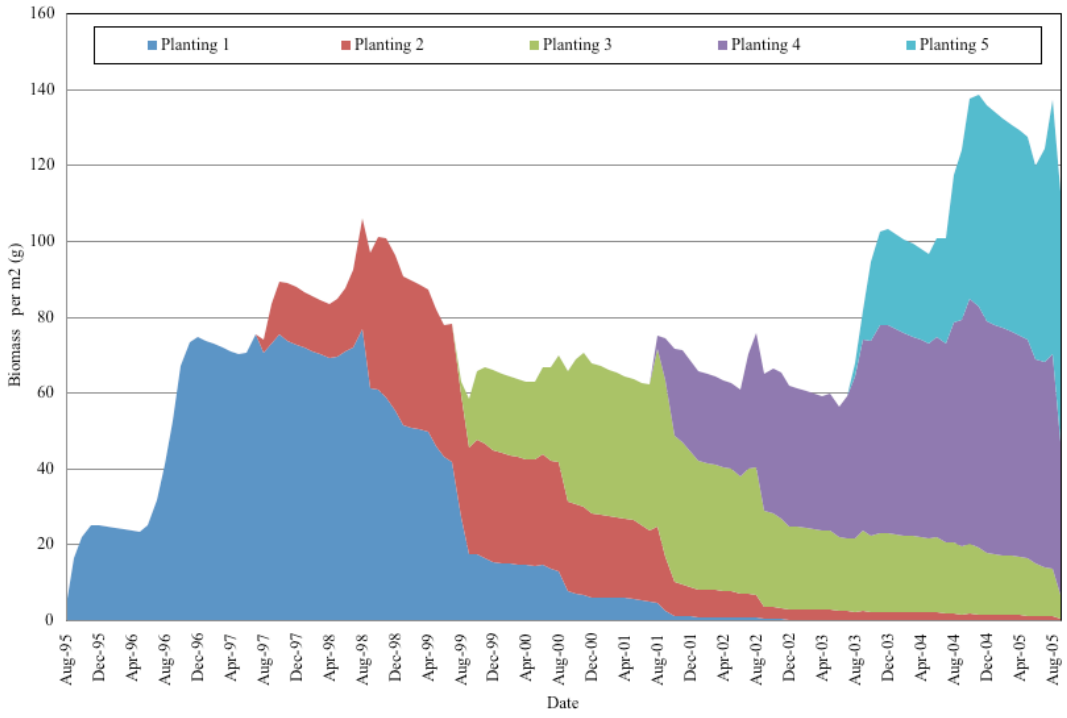


**Figure 28: Estimated biomass per meter square for a 10 year restoration program with replanting every 2 years at ET 4.2 (Chester River)**



**APPENDIX I: Matlab Model Code**

```
function varargout = oystermodel(varargin)
% OYSTERMODEL M-file for OysterModel.fig
%    OYSTERMODEL, by itself, creates a new OYSTERMODEL or raises
the existing
%    singleton*.
%
%    H = OYSTERMODEL returns the handle to a new OYSTERMODEL
or the handle to
%    the existing singleton*.
%
%    OYSTERMODEL('CALLBACK',hObject,eventData,handles,...) calls
the local
%    function named CALLBACK in OYSTERMODEL.M with the given
input arguments.
%
%    OYSTERMODEL('Property','Value',...) creates a new
OYSTERMODEL or raises the
%    existing singleton*.  Starting from the left, property value pairs are
%    applied to the GUI before OysterModel_OpeningFunction gets called.
An
%    unrecognized property name or invalid value makes property
application
%    stop.  All inputs are passed to OysterModel_OpeningFcn via varargin.
%
%    *See GUI Options on GUIDE's Tools menu.  Choose "GUI allows only
one
%    instance to run (singleton)".
%
% See also: GUIDE, GUIDATA, GUIHANDLES

% Edit the above text to modify the response to help OysterModel

% Last Modified by GUIDE v2.5 14-Sep-2005 13:59:22

% Begin initialization code - DO NOT EDIT
gui_Singleton = 1;
gui_State = struct('gui_Name',     mfilename, ...
                   'gui_Singleton',  gui_Singleton, ...
                     'gui_OpeningFcn', @OysterModel_OpeningFcn, ...
                     'gui_OutputFcn',  @OysterModel_OutputFcn, ...
                     'gui_LayoutFcn',  [] , ...
```

```
                'gui_Callback',   []);
if nargin && ischar(varargin{1})
   gui_State.gui_Callback = str2func(varargin{1});
end

if nargout
   [varargout{1:nargout}] = gui_mainfcn(gui_State, varargin{:});
else
   gui_mainfcn(gui_State, varargin{:});
end
% End initialization code - DO NOT EDIT


% --- Executes just before OysterModel is made visible.
function OysterModel_OpeningFcn(hObject, eventdata, handles, varargin)
% This function has no output args, see OutputFcn.
% hObject    handle to figure
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    structure with handles and user data (see GUIDATA)
% varargin   command line arguments to OysterModel (see VARARGIN)

% Choose default command line output for OysterModel
handles.output = hObject;

% Initialize variables
handles.file='temp_sal_series.csv';
handles.Lplant=15;
handles.AreaPlant=1000;
handles.DensityPlant=200;
handles.diseasefirst=0;
handles.fileout='oysterout.csv';
handles.natmortrate=0.15;




% Update handles structure
guidata(hObject, handles);

% UIWAIT makes OysterModel wait for user response (see UIRESUME)
% uiwait(handles.figure1);


% --- Outputs from this function are returned to the command line.
function varargout = OysterModel_OutputFcn(hObject, eventdata,
handles)
```

```
% varargout  cell array for returning output args (see VARARGOUT);
% hObject    handle to figure
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    structure with handles and user data (see GUIDATA)

% Get default command line output from handles structure
varargout{1} = handles.output;



function datafile_Callback(hObject, eventdata, handles)
% hObject    handle to datafile (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    structure with handles and user data (see GUIDATA)

% Hints: get(hObject,'String') returns contents of datafile as text
%        str2double(get(hObject,'String')) returns contents of datafile as a
double

handles.file=get(hObject,'String');

guidata(hObject, handles);


% --- Executes during object creation, after setting all properties.
function datafile_CreateFcn(hObject, eventdata, handles)
% hObject    handle to datafile (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    empty - handles not created until after all CreateFcns called

% Hint: edit controls usually have a white background on Windows.
%       See ISPC and COMPUTER.
if ispc && isequal(get(hObject,'BackgroundColor'),
get(0,'defaultUicontrolBackgroundColor'))
   set(hObject,'BackgroundColor','white');
end



function Lplant_Callback(hObject, eventdata, handles)
% hObject    handle to Lplant (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    structure with handles and user data (see GUIDATA)

% Hints: get(hObject,'String') returns contents of Lplant as text
%        str2double(get(hObject,'String')) returns contents of Lplant as a
```

```
double

handles.Lplant=str2double(get(hObject,'String'));

guidata(hObject, handles);

% --- Executes during object creation, after setting all properties.
function Lplant_CreateFcn(hObject, eventdata, handles)
% hObject    handle to Lplant (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    empty - handles not created until after all CreateFcns called

% Hint: edit controls usually have a white background on Windows.
%       See ISPC and COMPUTER.
if ispc && isequal(get(hObject,'BackgroundColor'),
get(0,'defaultUicontrolBackgroundColor'))
   set(hObject,'BackgroundColor','white');
end



function DensityPlant_Callback(hObject, eventdata, handles)
% hObject    handle to DensityPlant (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    structure with handles and user data (see GUIDATA)

% Hints: get(hObject,'String') returns contents of DensityPlant as text
%        str2double(get(hObject,'String')) returns contents of DensityPlant
as a double


handles.DensityPlant=str2double(get(hObject,'String'));

guidata(hObject, handles);

% --- Executes during object creation, after setting all properties.
function DensityPlant_CreateFcn(hObject, eventdata, handles)
% hObject    handle to DensityPlant (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    empty - handles not created until after all CreateFcns called

% Hint: edit controls usually have a white background on Windows.
%       See ISPC and COMPUTER.
if ispc && isequal(get(hObject,'BackgroundColor'),
get(0,'defaultUicontrolBackgroundColor'))
   set(hObject,'BackgroundColor','white');
```

```
end



function AreaPlant_Callback(hObject, eventdata, handles)
% hObject    handle to AreaPlant (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    structure with handles and user data (see GUIDATA)

% Hints: get(hObject,'String') returns contents of AreaPlant as text
%        str2double(get(hObject,'String')) returns contents of AreaPlant as a
double

handles.AreaPlant=str2double(get(hObject,'String'));

guidata(hObject, handles);


% --- Executes during object creation, after setting all properties.
function AreaPlant_CreateFcn(hObject, eventdata, handles)
% hObject    handle to AreaPlant (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    empty - handles not created until after all CreateFcns called

% Hint: edit controls usually have a white background on Windows.
%       See ISPC and COMPUTER.
if ispc && isequal(get(hObject,'BackgroundColor'),
get(0,'defaultUicontrolBackgroundColor'))
   set(hObject,'BackgroundColor','white');
end


% --- Executes on button press in RunModel.
function RunModel_Callback(hObject, eventdata, handles)
% hObject    handle to RunModel (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    structure with handles and user data (see GUIDATA)



        % Variable Definitions
        handles.Lmax=250;
        %handles.natmortrate=0.15;


        %Load Temp and Sal Data
```

```
        %Data needs to be in a comma separated variable file with evenly
spaced
        %montly mean temperatures
        data= csvread(handles.file,1,1);

        %extract temp time series
        handles.Temp = data(:,1);
        %extract salinity time series
        handles.Sal = data(:,2);

        %create timesteps array
        handles.timestep=1:(length(handles.Temp)+1);


        %TIME TO FIRST DISEASE
        %Determine time of first disease. This is a threshold value of 12
and 16C.  when
        %salinity is goes above this value the bar is considered diseased
henceforth

        handles.Diseasestate=zeros((length(handles.Temp(:)))+1,1);

        diseaseflag=0;

        for diseasecounter=1:(numel(handles.Temp))
           if (diseaseflag==1)
              diseaseflag=1;
           elseif ((handles.Sal(diseasecounter)>= 12) &
(handles.Temp(diseasecounter)>=16))
              diseaseflag=1;
              handles.diseasefirst=diseasecounter;
           else diseaseflag=0;
           end;

           if (diseaseflag==1)
             handles.Diseasestate(diseasecounter+1)=1;
           end;
        end;



        %table=[Sal, Diseasestate]

        %GROWTH
        %Create matrix for values of Growth Constant K
        %formula used is based on Partial Least Squares regression using
```

```
virginica
        %data from the ariakensis study
        %New version uses Least squares linear regression based and a
        %cross product based to account for temp and Sal covariance

        handles.K= -
0.43427+(0.02539*handles.Temp)+(0.01762*handles.Sal)+(0.00312*((han
dles.Temp-17.72692).*(handles.Sal-9.40128)));% new version

        %Create a matrix of growth values Length

        handles.meansize=ones(length(handles.Temp)+1,1); %defines
meanlenght as and array of zeros with the same length as the temp array

        handles.meansize(1)= handles.Lplant;  %first value is Lplant

        for counter=1:(numel(handles.Temp))
           inc=counter+1;
           grow=((handles.Lmax-handles.meansize(counter))*(1-(exp(-
handles.K(counter)*0.08333))));
           if grow<=0
              grow=0;
           end


             if (handles.Diseasestate(counter)==0)
              handles.meansize(inc)=((handles.meansize(counter))+grow);
              %von B function for incremental Growth (fabens 1965) time
interval
              %is one month (0.08333 years)  grow is growth increment
           else

              if handles.Sal(counter)>=16
                 groweffect=.8;
              elseif ((handles.Sal(counter)>=12) &
(handles.Sal(counter)<16))
                 groweffect=.6; % was .4
              elseif ((handles.Sal(counter)>=8) &
(handles.Sal(counter)<12))
                 groweffect=0; % was .1
              else
                 groweffect=0;
              end


handles.meansize(inc)=((handles.meansize(counter))+((grow)*(1-
```

```
groweffect)));
                %for oysters in a disease state growth increment is
                %reduced based on Paynter & Burreson 1991

            end


        end

        %NATURAL MORTALITY

        handles.population=zeros((length(handles.Temp(:)))+1,1);
        handles.population(1)=(handles.AreaPlant*handles.DensityPlant);
        monthmort=(handles.natmortrate/12);



        %Dermo Mortality  (this is based mostly on assumptions about
        %the effect of temp and sal on Dermo, most rates and effects on
        %rates are based on reports from the book: The Eastern Oyster:
        %Crassostrea Virginica (Kennnedy et al. 1996) and other sources
        %such as Paynter and Burresson 1991.  Most of the values are
        %theoretical inferences based on reported disease dynamics.
        %the model model for this remains unvalidated.



        BaseDermoMortRate=0.15; %assumed annual mortality rate when
infected with Dermo



        for mortcounter2=1:(numel(handles.Temp))
            inc5=mortcounter2+1;
            DermoMortRate=BaseDermoMortRate;

            if (handles.Diseasestate(mortcounter2)==0) %if not in disease
state there is no disease mortality
                DermoMortRate=0;
            end

            %time since infection effect

            monthsinfected=inc5-handles.diseasefirst;
            if monthsinfected <=0
```

```
            DermoMortRate=0;
        else
            timeeffect=((monthsinfected/12)+1);  %the longer the time
since infection the higher the mortality
            DermoMortRate=DermoMortRate*timeeffect;
        end


       %Temp and Sal effect
        if (handles.Sal(mortcounter2)<=9)
            DermoMortRate=0; %no Dermo mortality below 10
        end

        if (handles.Temp(mortcounter2)<=10)
            DermoMortRate=0;  %no winter mortality (paynter)
        end

        if (handles.Temp(mortcounter2)>=25)
            DermoMortRate= DermoMortRate*6; %Mackin 1951 Greatly
increased mortality above 25C
        end

        if (handles.Sal(mortcounter2)>=24) %estimated from Fisher
1992
            DermoMortRate= DermoMortRate*4;
        end


        %TOTAL MORTALITY
        MonthDermoMort=DermoMortRate/12;

        TotalMonthMort=MonthDermoMort+monthmort;

        if TotalMonthMort>1
            TotalMonthMort=1;
        end


      handles.population(inc5)=((1-
(TotalMonthMort))*(handles.population(mortcounter2)));

    end
```

```
        %Density Calculation

        handles.Density=zeros((length(handles.Temp(:)))+1,1);
        handles.Density(1)=(handles.DensityPlant);
        for densitycounter=1:(numel(handles.Temp))
           inc3=densitycounter+1;

handles.Density(inc3)=((handles.population(inc3))/(handles.AreaPlant));
        end


        %BIOMASS CALCULATION

        handles.Biomass=zeros((length(handles.Temp(:))+1),1);
        handles.TotalBiomass=zeros((length(handles.Temp(:))+1),1);

        for biomasscounter=1:(numel(handles.Temp)+1)

handles.Biomass(biomasscounter)=((((0.0001*((handles.meansize(biomas
scounter))^2))+(0.0045*handles.meansize(biomasscounter)))*(handles.De
nsity(biomasscounter)))/1000);

handles.TotalBiomass(biomasscounter)=(handles.Biomass(biomasscount
er)*handles.AreaPlant);
        end


        %OUTPUT


        %population Plot
        axes(handles.PopPlot)
        plot(handles.timestep,handles.population);

        hold on
        axis([1 (length(handles.timestep)) 0
(max(handles.population)*1.05)])

            disy=[0,(max(handles.population))];
            disx=handles.diseasefirst.*[1,1];

            axes(handles.PopPlot)
            plot(disx,disy,'r--');


        hold off
```

```
        xlabel('Month');
        ylabel('population')
        title('Oyster Population')

        %Lenght Plot
        axes(handles.LengthPlot)
        plot(handles.timestep,handles.meansize);

        hold on
        axis([1 (length(handles.timestep)) 0 (275)])

            disy=[0,(275)];
            disx=handles.diseasefirst.*[1,1];

            axes(handles.LengthPlot)
            plot(disx,disy,'r--');

        hold off

        xlabel('Month');
        ylabel('Mean Length (mm)')
        title('Mean Length')


         %Biomass Plot
        axes(handles.biomassplot)
        plot(handles.timestep,handles.TotalBiomass);

        hold on
        axis([1 (length(handles.timestep)) 0
(max(handles.TotalBiomass)*1.05)])

            disy=[0,(275)];
            disx=handles.diseasefirst.*[1,1];

            axes(handles.biomassplot)
            plot(disx,disy,'r--');

        hold off

        xlabel('Month');
        ylabel('Total Biomass (Kg)');
        title('Biomass');

        %handles.TotalBiomass
```

```
        %Month of first disease output
        set(handles.firstdis,'String', handles.diseasefirst);

        %Ending Density output

set(handles.EndDensity,'String',handles.Density(length(handles.Temp(:))+
1));

        %Ending Biomass output

set(handles.outputareabiomass,'String',handles.Biomass(length(handles.T
emp(:))+1));

set(handles.outputtotalbiomass,'String',handles.TotalBiomass(length(hand
les.Temp(:))+1));

        %write to file


writefile=[handles.timestep',handles.meansize,handles.population,handles
.Density,handles.TotalBiomass,handles.Diseasestate];
       csvwrite(handles.fileout,writefile);



function edit5_Callback(hObject, eventdata, handles)
% hObject    handle to edit5 (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    structure with handles and user data (see GUIDATA)

% Hints: get(hObject,'String') returns contents of edit5 as text
%        str2double(get(hObject,'String')) returns contents of edit5 as a
double


% --- Executes during object creation, after setting all properties.
function edit5_CreateFcn(hObject, eventdata, handles)
% hObject    handle to edit5 (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    empty - handles not created until after all CreateFcns called

% Hint: edit controls usually have a white background on Windows.
%       See ISPC and COMPUTER.
if ispc && isequal(get(hObject,'BackgroundColor'),
get(0,'defaultUicontrolBackgroundColor'))
```

```
    set(hObject,'BackgroundColor','white');
end



function firstdis_Callback(hObject, eventdata, handles)
% hObject    handle to firstdis (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    structure with handles and user data (see GUIDATA)

% Hints: get(hObject,'String') returns contents of firstdis as text
%        str2double(get(hObject,'String')) returns contents of firstdis as a
double


% --- Executes during object creation, after setting all properties.
function firstdis_CreateFcn(hObject, eventdata, handles)
% hObject    handle to firstdis (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    empty - handles not created until after all CreateFcns called

% Hint: edit controls usually have a white background on Windows.
%       See ISPC and COMPUTER.
if ispc && isequal(get(hObject,'BackgroundColor'),
get(0,'defaultUicontrolBackgroundColor'))
    set(hObject,'BackgroundColor','white');
end



function outfile_Callback(hObject, eventdata, handles)
% hObject    handle to outfile (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    structure with handles and user data (see GUIDATA)

% Hints: get(hObject,'String') returns contents of outfile as text
%        str2double(get(hObject,'String')) returns contents of outfile as a
double

handles.fileout=get(hObject,'String');

guidata(hObject, handles);


% --- Executes during object creation, after setting all properties.
function outfile_CreateFcn(hObject, eventdata, handles)
```

```
% hObject    handle to outfile (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    empty - handles not created until after all CreateFcns called

% Hint: edit controls usually have a white background on Windows.
%       See ISPC and COMPUTER.
if ispc && isequal(get(hObject,'BackgroundColor'),
get(0,'defaultUicontrolBackgroundColor'))
   set(hObject,'BackgroundColor','white');
end



function EndDensity_Callback(hObject, eventdata, handles)
% hObject    handle to EndDensity (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    structure with handles and user data (see GUIDATA)

% Hints: get(hObject,'String') returns contents of EndDensity as text
%        str2double(get(hObject,'String')) returns contents of EndDensity as
a double


% --- Executes during object creation, after setting all properties.
function EndDensity_CreateFcn(hObject, eventdata, handles)
% hObject    handle to EndDensity (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    empty - handles not created until after all CreateFcns called

% Hint: edit controls usually have a white background on Windows.
%       See ISPC and COMPUTER.
if ispc && isequal(get(hObject,'BackgroundColor'),
get(0,'defaultUicontrolBackgroundColor'))
   set(hObject,'BackgroundColor','white');
end



function inputmortrate_Callback(hObject, eventdata, handles)
% hObject    handle to inputmortrate (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    structure with handles and user data (see GUIDATA)

% Hints: get(hObject,'String') returns contents of inputmortrate as text
%        str2double(get(hObject,'String')) returns contents of inputmortrate
as a double
```

```
handles.natmortrate=str2double(get(hObject,'String'));

guidata(hObject, handles);



% --- Executes during object creation, after setting all properties.
function inputmortrate_CreateFcn(hObject, eventdata, handles)
% hObject    handle to inputmortrate (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    empty - handles not created until after all CreateFcns called

% Hint: edit controls usually have a white background on Windows.
%       See ISPC and COMPUTER.
if ispc && isequal(get(hObject,'BackgroundColor'),
get(0,'defaultUicontrolBackgroundColor'))
   set(hObject,'BackgroundColor','white');
end



function outputareabiomass_Callback(hObject, eventdata, handles)
% hObject    handle to outputareabiomass (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    structure with handles and user data (see GUIDATA)

% Hints: get(hObject,'String') returns contents of outputareabiomass as
text
%        str2double(get(hObject,'String')) returns contents of
outputareabiomass as a double


% --- Executes during object creation, after setting all properties.
function outputareabiomass_CreateFcn(hObject, eventdata, handles)
% hObject    handle to outputareabiomass (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    empty - handles not created until after all CreateFcns called

% Hint: edit controls usually have a white background on Windows.
%       See ISPC and COMPUTER.
if ispc && isequal(get(hObject,'BackgroundColor'),
get(0,'defaultUicontrolBackgroundColor'))
   set(hObject,'BackgroundColor','white');
end
```

```
function outputtotalbiomass_Callback(hObject, eventdata, handles)
% hObject    handle to outputtotalbiomass (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    structure with handles and user data (see GUIDATA)

% Hints: get(hObject,'String') returns contents of outputtotalbiomass as
text
%        str2double(get(hObject,'String')) returns contents of
outputtotalbiomass as a double


% --- Executes during object creation, after setting all properties.
function outputtotalbiomass_CreateFcn(hObject, eventdata, handles)
% hObject    handle to outputtotalbiomass (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    empty - handles not created until after all CreateFcns called

% Hint: edit controls usually have a white background on Windows.
%       See ISPC and COMPUTER.
if ispc && isequal(get(hObject,'BackgroundColor'),
get(0,'defaultUicontrolBackgroundColor'))
    set(hObject,'BackgroundColor','white');
end


% --- Executes during object creation, after setting all properties.
function biomassplot_CreateFcn(hObject, eventdata, handles)
% hObject    handle to biomassplot (see GCBO)
% eventdata  reserved - to be defined in a future version of MATLAB
% handles    empty - handles not created until after all CreateFcns called

% Hint: place code in OpeningFcn to populate biomassplot
```

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