

ABSTRACT

Title of Thesis: ECOLOGICAL ROLE OF ATLANTIC MENHADEN
(*BREVOORTIA TYRRANUS*) IN CHESAPEAKE BAY AND
IMPLICATIONS FOR MANAGEMENT OF THE FISHERY

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A simulation model was developed to characterize a range of solutions to the hypothesis that Atlantic menhaden are a significant consumer of primary productivity in Chesapeake Bay and that ecologically integrated management of the fishery could reduce eutrophication in the estuary. The model consisted of two components, one for pre-juvenile menhaden (age-0) and another for juvenile and adult menhaden (age 1-3). The parameters used in the models were drawn from the literature and through parameter estimation based on growth data provided by the National Marine Fisheries Service.

The simulation of age-0 menhaden indicated they could remove 1.5 - 39.1% of primary productivity. The value of the consumption of nitrogen in phytoplankton by age-0 menhaden ranged from \$1.17 to 15.0 million, while the commercial value of the

fishery ranged from \$0.41 to 5.03 million. Management adjustments in the simulation indicated that an unfished population could remove 3-4% more phytoplankton than a fished one in any given year.

The age 1-3 simulated population could consume 13.3 - 193% of primary productivity. The value of the consumption of nitrogen by this population ranged from \$10.3 to 74.3 million, while the commercial value of the fishery ranged from \$20 - 128 million. Management adjustments in the simulation indicated that an unfished population could remove 11% more phytoplankton than a fished one.

A fish migration term was estimated for use in nutrient budgets, indicating that this factor represents 0.84 - 25.9% of the total export of nitrogen from Chesapeake Bay annually. Various management analyses and strategies were considered.

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(*BREVOORTIA TYRRANUS*) IN CHESAPEAKE BAY AND
IMPLICATIONS FOR MANAGEMENT OF THE FISHERY

by

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DEDICATION

For my parents, Drs. Joan and Milton Gottlieb,

My brother Dr. Erik Gottlieb,

And especially, my husband, Dr. David Bader.

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The path to completing this work was longer and more circuitous than most, but I believe that every step was necessary. That said, I must acknowledge that I could not have completed the journey without the support and guidance of many individuals, some of whom I will mention here.

First and foremost is my adviser, Dr. Joseph A. Mihursky. He set me on the path to studying menhaden's importance as a component of the Chesapeake Bay ecosystem. More importantly, his confidence in my intellect and abilities has been unwavering, which in turn bolstered my confidence in myself as a researcher, scholar, and advocate. He, along with my committee members, Drs. Walter Boynton and Robert Ulanowicz have provided me with much food for thought and direction in my research.

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I learned about the cutting-edge tools and ideas in ecological science from Dr. Robert Costanza. Had he not introduced me to the use of STELLA for ecological modeling this work would have been much more cumbersome.

Graduate study is a massive financial as well as intellectual undertaking, and I cannot overlook the support that the Maryland Sea Grant College provided throughout this process. My interest in marine research was sparked by an Undergraduate Research Experience in 1993 sponsored by MDSG and the National Science Foundation. A year later, when I became a full-fledged graduate student at the University of Maryland, MDSG was there once again, supporting my work on two projects as a Trainee. During most of the time that I worked on this thesis, I was supported on National Oceanic and Atmospheric Administration Award Number NA46RG0091. Finally, I was awarded one of the highest honors available to graduate students in marine policy, the 1997 National Sea Grant Knauss Fellowship. The opportunity to work in the highest levels of Federal Government was priceless, and was an experience that influenced many other parts of my life, not the least of which was my education.

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Dr. Doug Lipton gave me the opportunity to extend my involvement in work begun during my Fellowship to quantify the economic valuation of environmental benefits in coastal areas.

I would not be here at all were it not for my parents who raised me in such a way that I could fully realize my natural abilities. They always stressed to me the importance of education and maintaining high standards for myself. Furthermore, they taught me through example that it is possible to overcome obstacles in life, as they earned their college and graduate degrees under much more difficult circumstances than I could imagine today. My debt to them is infinite, yet the only repayment they have ever asked was that I always do my best at whatever I attempt, and I have tried to do that with this work.

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Chapter I: Introduction

1.0 Eutrophication in Chesapeake Bay

In the mid 1970's, scientists recognized that Chesapeake Bay was suffering from an imbalance in its nutrient budget. The amounts of nitrogen (N) and phosphorous (P) being input to the Bay from point and non-point sources resulted in eutrophication, and a positive net ecosystem metabolism (Kemp et al., 1997) Massive algal blooms had begun to occur during the spring and summer months, in quantities far in excess of what higher trophic levels could consume. As a result, much of this plant matter was dying and sinking to the bottom, where it decayed, consuming most of the oxygen in the benthic regions of the Bay (Jonas and Tuttle, 1990). This created large areas of anoxia which most organisms found uninhabitable (Officer et al., 1984; Seliger et al., 1985; Tuttle et al., 1987). The benthic region of the Bay provides important nursery areas for the larvae of many kinds of fish, and forage area for crabs and other adult fish (Heck and Orth, 1980). In addition, the vast underwater beds of grass, or submerged aquatic vegetation (SAV), were destroyed as the dying algae coated the leaves, cutting off light to the plants (Hurley, 1992; Orth and Moore, 1983). Furthermore, the already stressed American oyster (*Crassostrea virginica*) population suffered from the anoxic conditions (Seliger et al. 1985; Kemp and Boynton, 1992), and has since declined to extremely low levels (Newell, 1988).

In response to these conditions, the Federal government and states in the Chesapeake Bay drainage basin agreed upon a coordinated effort to reduce the inputs of N and P to the Bay. In 1987, the second Chesapeake Bay Agreement mandated a 40% reduction from the controllable 1985 nutrient input level by the year 2000 (Chesapeake Executive Council, 1988). This reduction was to be achieved through a variety of means, including construction of waste water processing facilities, a phosphate detergent ban, agricultural land management practices, and reforestation of riparian buffer zones (Chesapeake Executive Council, 1988). As the deadline for achieving the reduction goal approaches, scientists and resource managers have questioned the ability of the Chesapeake Bay states to realize the 40% reduction goal, and once it is realized, if it will be enough to restore the Bay and its living resources (Boicourt 1992; Malone, 1992).

Recent “score cards” (Blankenship, 1997b) on the progress being made toward the nutrient input reduction goal have indicated that it is unlikely that the goal will be realized in time. As of 1996, 12.6 of the targeted 22.6 million pounds of N had been reduced from point sources; 16 million of the targeted 34 million pounds of N had been reduced from non-point sources. Progress in reducing P inputs has been better, largely due to the construction of waste water treatment plants, which by 1996 removed 51% of point source P, while the reduction target for this source is 58%. Non-point sources of P had been reduced by 1 million pounds of the targeted 3 million pounds (Blankenship, 1997b).

Some biologists have suggested that the restoration of parts of the biological component of the ecosystem that directly process primary productivity (i.e., oysters and other filter-feeders) could play an important role in the overall restoration of the Chesapeake Bay (Newell, 1988). Newell (1988) calculated that the pre-harvest population of oysters in the Bay could have filtered the entire water column in 3.3 d, while in 1988, with the population at about 1% its historical level, the turnover time would have been 325 d. Moreover, Newell (1988) estimated that the pre-harvest population may have been capable of removing 23-41% of the 1982 phytoplankton carbon production but by 1988, removal of only 0.4% would have been possible. The potential restoration of the native oyster or introduction of exotic oysters to fill this role has been explored (Mann 1979; Gottlieb and Schweighofer, 1996; Kennedy, 1996).

Another important filter-feeding species in Chesapeake Bay is the Atlantic menhaden, *Brevoortia tyrannus* Latrobe (Pisces: Clupeidae) which, as adults, filter-feed at an estimated rate of 15.2 L of water per minute and thus about 3.9×10^6 L in 180 d (Lippson, 1991). Nevertheless, the importance of planktivorous fish in affecting nutrient budgets in large marine or estuarine systems is often overlooked or assumed to be negligible, while trophic experiments with fish in small, freshwater systems are common (Carpenter and Kitchell, 1993). However, effects of fish grazing on phytoplankton in marine and estuarine systems may be significant (Boynton et al., 1995).

In their nitrogen (TN) and phosphorous (TP) budget for Chesapeake Bay, Boynton et al. (1995) account for TN and TP losses via commercial and recreational

catches but not for losses associated with growth and migration out of the Bay by certain abundant species of fish. They state that, “The fisheries yield term [does not] account for the [TN and TP] losses associated with growth and subsequent migration from the bay of very abundant fish species such as menhaden and anchovies. The migration term could represent a substantial loss because these species grow rapidly while in the bay during the warm seasons” (Boynton et al., 1995, p. 311). Yet they determined that the estimation of a migration term would be difficult due to lack of knowledge about stock size, age structure, growth, and natural mortality.

The purpose of this thesis is to estimate the relative importance of Atlantic menhaden as a consumer of the products of eutrophication in Chesapeake Bay in relation to managing the fishery, taking account of this important ecological service.

2.0 Menhaden life history and fishery

Adult Atlantic menhaden live during the summer on the Atlantic coast from northern Florida to Maine, latitudinally stratified by age and size, with older and larger fish in the northern region of the species’ range (Nicholson, 1978; Ahrenholz, 1991). In September, the northern population migrates south to the coastal waters off North Carolina. Almost the entire northern population remains in the North Carolina coastal area from December through March or April. While adult fish spawn throughout the year, spawning intensity is greatest during the winter months in the waters off North

Carolina. Adults migrate north again in spring, and are fully redistributed by June from Florida to Maine (Ahrenholz, 1991).

Within two months of the spawn, larvae are transported shoreward into estuarine bays, sounds, and streams to metamorphose into juveniles. The young-of-the-year reside in these nursery areas (including Chesapeake Bay) from spring until fall or early winter, feeding first on zooplankton, but increasingly filtering phytoplankton from the water column as their gill rakers develop (June and Carlson, 1971). Adult menhaden are filter-feeding planktivores, passively ingesting a mixture of phytoplankton, zooplankton and detritus in proportion to the ambient concentrations of these components of the plankton (Jeffries, 1975).

A portion of the adult fish stock also reside in the areas of high primary productivity in estuaries during the summer. It is during this period that heavy commercial fishing of Atlantic menhaden occurs. In Chesapeake Bay a pound net fishery for menhaden in Maryland and Virginia supplies bait for recreational fishing and purse seining for menhaden in Virginia supplies reduction plants that produce fish meal and oil (Jones et al., 1988). There is no closed season for Atlantic menhaden in Maryland, though in the Chesapeake Bay portion of the Virginia fishery purse seining is prohibited between the day following the third Friday of November and the day preceding the first Monday in May (Jones et al., 1988).

Information about the Chesapeake Bay Atlantic menhaden fishery has been incomplete since 1973 when commercial catch data became proprietary to the industry. The National Marine Fisheries Service (NMFS) reports the total Atlantic coast fishery

for Atlantic menhaden averaged about 270,000 metric tons (t) from 1964 to 1972 at an annual ex-vessel value of \$8.8 million (Personal Communication, National Marine Fisheries Service, Fisheries Statistics and Economics Division) In contrast, NMFS reported an average landing rate of 57,000 t from 1984 to 1994 at an annual ex-vessel value of about \$4.5 million (Personal Communication, National Marine Fisheries Service, Fisheries Statistics and Economics Division), though there is no indication that activity in the fishery was actually scaled back to this degree between the two time periods. In fact, menhaden landings reportedly increased during the 1970's to a peak of 418,000 t in 1983, and fell somewhat to 322,000 t in 1989 (Lippson, 1991)

The Chesapeake Bay comprised an average of 66% of the Atlantic fishery for menhaden from 1964 to 1972 (Vaughan et al., 1986) and reportedly still dominates the landings (Street et al., 1996). The Atlantic menhaden stock was recently determined to be healthy and fishing effort is declining (Street et al., 1996), however the fishery has come to rely increasingly on younger age classes of fish (pre-spawners, age-2 and younger) (Vaughan and Smith, 1988). The age structure of the Atlantic menhaden stock has been essentially truncated so that very few fish above the age of 6 exist in the stock (Ahrenholz et al., 1987); menhaden can live for 10-12 years and grow to a maximum total length of 500 mm (Ahrenholz, 1991) at an average weight (achieved after age 6) of about 454 g (Lippson, 1991).

In the past several years, the stock of menhaden has taken some serious blows, in particular from the hazardous algal bloom, *Pfiesteria piscicida*, which in 1991 claimed 1 billion menhaden in coastal North Carolina (Anonymous, 1998). The

National Marine Fisheries Service has reported a record decline in the menhaden stock based on its 1997 survey (Personal Communication, National Marine Fisheries Service, Fisheries Statistics and Economics Division). In 1997, there was an 11.5% decrease in the number of fish landed compared to 1996, and a 14.8% decrease over the previous five year period. These statistics have concerned fisheries scientists not only because of the effect on the commercial fishery and viability of the menhaden stock, but because menhaden provide an important food source for many other species of fish, including striped bass (*Morone saxatilis*), bluefish (*Pomatomus salatrix*) and weakfish (*Cynoscion regalis*) (Hartman, 1993; Rippeto, 1993). As the striped bass population recovers from its near demise in the 1980s and early 1990s, these piscivores are already placing increased pressure on the menhaden stock. Recent surveys of striped bass in Chesapeake Bay show that the fish may be suffering from starvation and malnutrition as the stock of their main food sources, menhaden and bay anchovy, have declined in recent years (Blankenship, 1997a).

3.0 Simulation modeling where whole-system experiments are not feasible

Ecological problems often can be approached with small and meso-scale experiments in controlled systems. In particular, trophic-level effects in freshwater systems have been studied a great deal in this manner (Carpenter et al., 1992; Carpenter and Kitchell, 1993). These types of studies provide insight into the potential effects of changes in the management regime for an ecosystem, such as fish stocking, fishing

moratoria, and nutrient load reductions. However, while such experiments are useful in relatively simple systems, they provide limited insight for managing a system as complex and large as Chesapeake Bay, which has freshwater and saltwater inputs and outputs, a complex food web that includes transient, highly migratory species, nutrient inputs, and large-scale commercial and recreational fishing. Moreover, whole-system experiments, such as fishing moratoria, are often economically and politically infeasible. However, with the development of high performance computers and simulation software, important questions about how best to manage the Chesapeake Bay system can be explored through simulation modeling (e.g. Cerco and Cole, 1993; Kemp et al., 1994; Cerco, 1995).

A number of new tools have recently become available that enable scientists and managers to envision ecological systems and to simulate various scenarios for their management. I have utilized these tools in my study of the ecological role of Atlantic menhaden and various fishery management strategies to maximize their ecological services while maintaining the integrity of the fishery. What follows is a brief discussion of the modeling approach I have taken using these tools.

3.1 Fish Bioenergetics Model - Evaluating Fish Growth and Consumption

The bioenergetics modeling approach is based on physiological processes at the individual level. The total of growth, excretion, and respiration by an organism must

be supported by an equivalent amount of consumption. The basic mass balance equation involved in fish bioenergetics is:

$$\text{Energy Consumed} = \text{Respiration} + \text{Waste} + \text{Growth}$$

For an herbivorous fish such as Atlantic menhaden, a normalized mass balance where energy consumed = 100 yields the following budget for a “typical” individual (Brett and Groves, 1979):

$$100 = 37 + 43 + 20$$

Details of how this model simulates fish growth and consumption can be found in Kitchell et al. (1977), and are outlined in Chapter 1 of this thesis.

Fish bioenergetics modeling is a useful tool for estimating growth or consumption of a particular population of fish. Since information about fish growth is often readily available, while direct information about fish consumption can be difficult to obtain, this modeling approach is indispensable for ecological studies involving fish populations. Because growth is a function of consumption, bioenergetics modeling can be used to estimate consumption over time given a series of observations on growth (Hewett and Johnson, 1992). Moreover, estimates of consumption from growth observations have proven more reliable than estimating growth from consumption observations (Bartell et al., 1986).

Fish bioenergetics research in the 1970's led to the development of software to automate the task of solving the equation and to allow users to explore a multitude of scenarios. Hewett and Johnson's (1992) “Wisconsin Model” allows users to scope fish bioenergetics problems with a minimum of field data or to build highly detailed models

when field and laboratory data are available. Uses for these models include determination of feeding requirements for aquaculture facilities, effects of stocking on native populations, bioaccumulation of persistent contaminants, and predator-prey interactions.

I have based this study on a fish bioenergetics model of age-0 Atlantic menhaden developed in a master's thesis by Rippetoe (1993). Rippetoe (1993) performed laboratory feeding experiments and collected wild fish from Chesapeake Bay to determine the needed model parameters. Specifically, Rippetoe determined the effects of temperature and prey type (*Artemia* sp. nauplii or *Ditylum brightwelli*) on absorption efficiencies and gastric evacuation rates, growth rates, daily ration, feeding periodicity, and energy density of age-0 menhaden. Thus, Rippetoe was able to validate the bioenergetics model he created for age-0 menhaden. I have extended Rippetoe's model to include adult menhaden up to age-3. Although some work on the bioenergetics of adult menhaden has been conducted (Durbin and Durbin, 1981; 1983), specific parameters for the Hewett and Johnson (1992) model have not been determined. Thus, the adult model extension provides only an estimate of consumption based on observed growth patterns.

While the Fish Bioenergetics software (Hewett and Johnson, 1992) is a useful tool, it is limited to performing specified functions, including calculation of the desired physiological parameters, population production and consumption, and fish catch (if any). The purpose of this study is to estimate the relative ecological importance of Atlantic menhaden in Chesapeake Bay and to determine the economic impact of

changes to its management regime. In order to examine the complex interactions of Atlantic menhaden with the Chesapeake Bay ecosystem and economy, I embedded the basic individual bioenergetics model into an ecological-economic model using the software Stella, which is described in the next section.

3.2 Stella II - Dynamic Systems Modeling

Development of an ecological-economic model which included all the components necessary for evaluating the role of Atlantic menhaden in Chesapeake Bay and the effects of various management strategies on this role and on the fishing industry was greatly simplified by using the graphical programming language Stella (High Performance Systems, 1996). The Stella software “is a multi-level, hierarchical environment for constructing and interacting with models” (High Performance Systems, 1996, p. 1 - 3). The model construction level allows the basic structure of the model to be laid out in terms of stocks (state variables), flows, and information input. The second step in constructing a model in Stella is to define the interactions of model variables in terms of equations, graphs, or functions. Once the model has been constructed, Stella allows the user to interact easily with the model by changing parameter values and viewing the output in graphical or tabular form. Thus, the user can perform “experiments” to better understand the behavior of the system and its reaction to various management regimes.

This type of modeling is an interesting tool for examining potential solutions to environmental problems in that it allows relatively inexperienced users to develop models that simulate complex systems. Rather than being buried in lines of computer code unreadable to the average environmental manager, the structure of the model and relationships between variables in Stella models are transparently available and are easily changed by the user. Models developed in Stella are useful for scoping environmental problems when information about the system can only be estimated and can be used in the consensus-building process. Once a consensus has been reached about the parameters affecting the system, the model can be developed into highly detailed, realistic simulation with the collection of data, calibration and testing for uncertainty in the model (Costanza and Ruth, 1998).

The model presented in this thesis is a second-stage research model described by Costanza and Ruth (1998) as a detailed and realistic attempt to replicate the dynamics of a system of interest, in this case, the Atlantic menhaden fishery in Chesapeake Bay. In developing this model, I was concerned with using as much historical data as possible and evaluating model performance in terms of its ability to simulate the growth of individual Atlantic menhaden and behavior of the fishery. There are two main problems whose potential range of solutions I was able to explore:

1. How important is the Atlantic menhaden population as a consumer of phytoplankton in Chesapeake Bay, and what is the value of this service?

2. What would be the effect of changing the fishing regime for Atlantic menhaden to take advantage of its ecological service, and what optimal strategies exist for the management of the fishery?

Many data gaps, including lack of physiological parameters for older fish, no reliable information about fishery landings since the 1970's, and highly variable primary productivity in Chesapeake Bay prevented statistical verification of most of the model. Nevertheless, the model is useful in that it can simulate a potential range of outputs and it points to future research needs in the proper management of this important fishery. It is a “living” model, and can be amended and improved in the future when better information becomes available.

4.0 Philosophy of ecological economics and valuation of species and ecosystems

Traditionally, the field of natural resources economics has focused on the extractive value of resource-based commodities, such as minerals, fisheries, forestry and agricultural products. Analyses of optimal harvest and pricing for these goods included labor and capital costs, supply and demand curve estimation, and evaluation of profit margin. Often left out of these studies were issues of scarcity (in the case of non-renewables such as minerals and oil), biodiversity loss (for example, transforming a functioning forest ecosystem into a monocultured tree farm), and externalities (such

as nutrient runoff and topsoil loss due to certain agricultural practices). Long-term issues such as sustainability were not considered.

Recently, the new field of ecological economics had brought economists, ecologists, and policy makers together, combining their perspectives on the place of man in nature, and meshing their tools to create a more complete picture of natural resource use and costs versus benefits. Some recent work in this field has, on a grand scale, attempted to put a dollar value on the services that ecosystems, and even the entire biosphere provide to man (Costanza et al., 1997; Daily, 1997). These studies have taken a variety of approaches to the estimation of value, including the cost to replicate the service via an engineered solution to direct market values derived from tourism and real estate prices. Critics of these studies point out that determining the value of ecosystem services estimated by substitution costs or inferred from the value of the commodity the service supports is fatally flawed, and merely supports utilitarian precepts of traditional economic methods which consider only human welfare in their analyses (Sagoff, 1998). Indeed, the proposition that a price tag could be placed on ecosystems and organisms that have evolved over millions of years and existed long before market theory, is an ambitious one at the very least. Nevertheless, it is likely that traditional economics methods will continue to be used for policy decision making, and the effort to determine values and benefits derived from functioning ecosystems may be the best way to make sure these factors are considered.

Moreover, it seems clear that traditional stock assessment and fishery management analyses have been inadequate as evidenced by recent collapses in major

fisheries such as the George's Bank (Safina, 1995). Until recently, fisheries have been considered as independent units, unaffected by and not themselves affecting the ecosystem in which they reside. Stock assessments, based on species reproduction, recruitment, and mortality, are performed in part to determine the "maximum sustainable yield," or MSY that the fishery can support. It has become clear, however, that many external factors such as climate change and El Niño events, stock status of other species, and coastal pollution can affect the sustainability of a given level of harvest. Furthermore, annual variability in all of these factors can mean that a given harvest level is acceptable one year, but much too high (or low) the next. A "ratchet" effect, in which a series of good harvest years encourage additional investment in capital is followed by a period of lower productivity during which the government provides subsidies to the fishing industry leads to a heavily subsidized industry that over harvests the resource (Ludwig et al., 1993). Recent multi-species assessments have showed promise in considering the place of a species in its ecosystem, but still do not consider the whole picture.

The role or value of a given species of fish in an ecosystem can be evaluated from many points of view, including commercial and recreational fishing, as a food source for other fish, birds, and marine mammals, and as a consumer of other species. To fully account for a species' role in an ecosystem, all of these functions should be considered. Atlantic menhaden is an interesting case study for this type of assessment because it has been thoroughly studied as a commercially important species (e.g. Smith, 1991; Garrity-Blake, 1994; Vaughan and Merriner, 1991), and as a food source for

recreationally important species (Hartman, 1993; Hartman and Brandt, 1995), but less so in the latter consumer aspect (with the exception of Rippetoe's (1993) study and continuing work by Luo et al. (1998)). The ultimate significance of this study is not to assign a price tag to the Atlantic menhaden in Chesapeake Bay. Indeed, the gross revenues to the fishery industry from this species indicate that it is a highly valuable species, and one worth conserving as a natural resource. The take-home message from this analysis is that species, commercially important ones in particular, have a value beyond the market's ability to bear a given price for the products derived from them. Furthermore, the value of a species in terms of its place in ecosystem function extends to species that otherwise are considered to have no value to society at all because they are not harvested. This type of analysis can help to resolve the conflict between the goals of environmental conservation and economic development and provide guidance to policy makers whose decisions otherwise would be based on the ability of either ecologists or economists to argue more convincingly.

Chapter II: Consumption of Primary Productivity by Age-0 Atlantic menhaden in Chesapeake Bay

1.0 Introduction

In this chapter, I describe a simulation model developed to predict the relative magnitude of phytoplankton consumption by age-0 Atlantic menhaden under various fishery management regimes in Chesapeake Bay. I have focused on the zero age class because detailed physiological data on this stage in the menhaden's life history was readily available from the literature (June and Carlson, 1971; Jeffries, 1975; Durbin and Durbin, 1981; Rippetoe, 1993). Age-0 menhaden also make up a large proportion of the overall population of menhaden in Chesapeake Bay, with one estimate of the number of recruits to the fishery ranging from 1.5 to 18.6 billion (Jones et al., 1988). While it is unlikely that the larvae and pre-juveniles (known as "peanuts" in the fishery) make up a significant proportion of the landings (Personal Communication, J. Smith, National Marine Fisheries Service, Southeast Fisheries Science Center, Beaufort, NC), the fishery has come to rely increasingly on pre-spawn-aged (age-2) fish (Vaughan and Smith, 1988).

The approach that I have taken to estimate the relative importance of phytoplankton consumption by age-0 menhaden is as follows. Based on the physiological research and preliminary bioenergetics model of age-0 menhaden

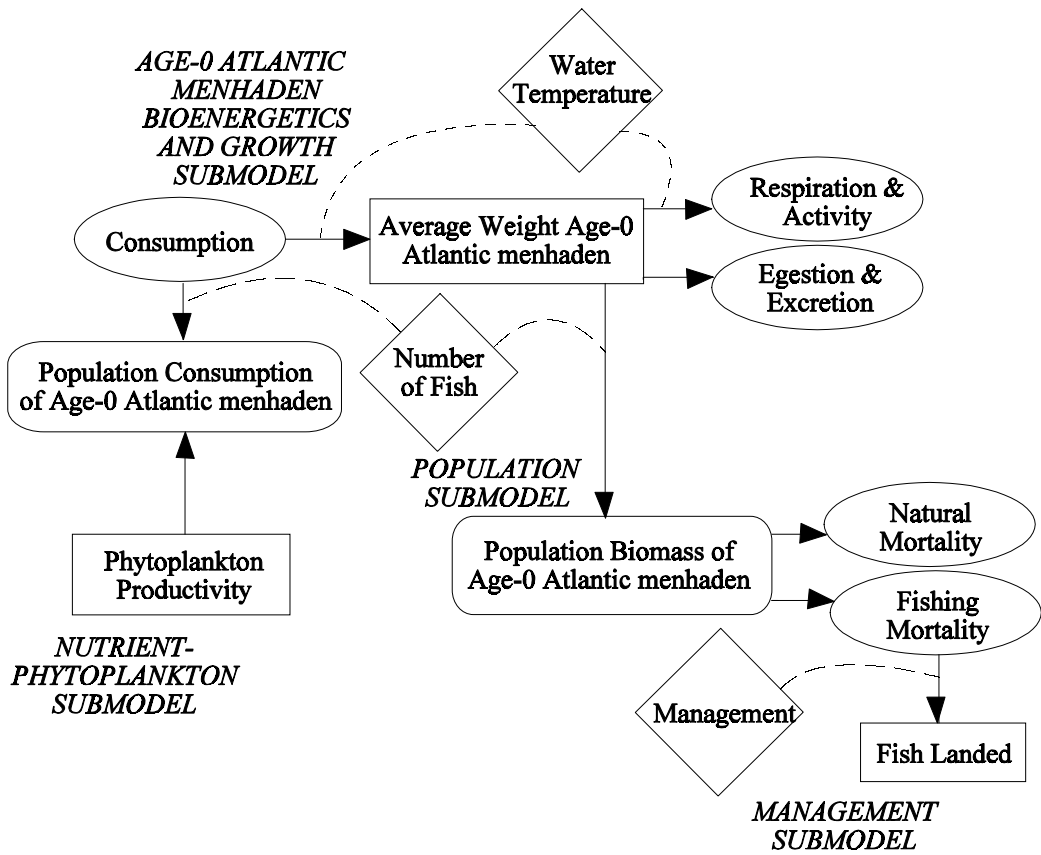
reported by Rippetoe (1993) and the fish bioenergetics equations (Kitchell et al., 1977) and software (Hewett and Johnson, 1992), I have created a dynamic simulation model of the bioenergetics of age-0 Atlantic menhaden using the software Stella (High Performance Systems, 1996). This approach enabled me to embed the basic physiology of the average individual fish into a population model affected by environmental factors and the fishery. I was also able to test various assumptions about the population size of age-0 menhaden and the magnitude of primary productivity in Chesapeake Bay to determine if the fish are a significant consumer of phytoplankton produced in the Bay.

The model also allows the user to act as a fishery manager, changing aspects of the fishery such as the length of the season and the degree of fishing mortality. While traditional fishery models focus on the determination of Maximum Sustainable Yield as a guide for management, the ultimate use of this model, which integrates the fishery into the function of the Chesapeake Bay ecosystem, is to assist in determining the optimal fishing strategy to maximize menhaden's role as a consumer of phytoplankton while maintaining its value as a traditional commodity. In this chapter, in order to gain some insight into the relative affect of fishing on age-0 menhaden's role as a consumer, the main management option considered is a fishing moratorium.

2.0 Model Overview

The model consists of four submodels representing (1) age-0 Atlantic menhaden bioenergetics and growth, (2) menhaden population dynamics, (3) fishery management operations, and (4) nitrogen-phytoplankton dynamics (Fig. 1). The menhaden growth submodel simulates weight changes of the average fish (g wet weight d^{-1}) as the net result of consumption (herbivory), respiration, activity, egestion, and excretion, which are functions of temperature and fish weight. Menhaden population dynamics are affected by initial number of fish, biomass increases of the average individual fish, and mortality due to fishing and natural causes. Fishery management operations allow the model user to change either the dates of the open fishing season for menhaden, or the fishing mortality of age-0 fish, and also calculates the gross value of the landed fish. The nitrogen-phytoplankton dynamics submodel calculates primary productivity over the model simulation and determines how much of this production is consumed by age-0 menhaden. Consumption of primary productivity is converted to units of nitrogen (N), carbon (C), and phosphorous (P) and to a dollar value of the consumption of N in terms of the effort to reduce N levels in Chesapeake Bay.

Fig. 1. Conceptual model representing the dynamics of nutrient consumption by age-0 Atlantic menhaden in the Chesapeake Bay ecosystem.



3.0 The Data Base

The model was parameterized and its performance evaluated based on information available from the literature. Most of the metabolic data on Atlantic menhaden are from a master's thesis by Rippetoe (1993). This work consisted of laboratory experiments to examine the effects of temperature and prey type on maximum consumption, absorption efficiency and gastric evacuation rates of age-0 Atlantic menhaden. Field measurements included stomach content analyses and fish weight. Details about the methods used to acquire the data may be found in Rippetoe (1993). Finally, Rippetoe (1993) developed a bioenergetics model to estimate consumption and production of age-0 Atlantic menhaden in mid-Chesapeake Bay using Fish Bioenergetics software (Hewett and Johnson, 1992). Many of the parameters Rippetoe (1993) used in his bioenergetics model were applied directly to the model described in this chapter (see Table 1). Output from the present Stella model using optimized parameters was compared to output from the Fish Bioenergetics Model using all of the parameters from Rippetoe (1993).

4.0 Model Description

The model runs for 183 days, with day one corresponding with May 31 (calendar day 150) and day 183 corresponding with November 31. This is

Table 1. Symbols and parameter values used to implement the bioenergetics submodel equations applied to age-0 Atlantic menhaden.

Equation in text	Symbol	Parameter description	Present value	Rippetoe (1993) value
(3) C	ac	Intercept for Cmax	1.294	1.294
	bc	Slope for Cmax	-0.42 [†]	-0.312
	CTO	Optimum temperature for consumption	28.0°C	28.0°C
	CK1	Proportion of Cmax at CTO, CTM	0.1 [★]	0.525
	CTM	Maximum temperature for consumption	29.0°C	29.0°C
	CTL	Temperature at which dependence is CK4	30.1°C	30.1
	CK4	Proportion of Cmax at CTL	0.01 [★]	0.81
	Qc	Slope for temperature dependence of consumption	6 [†]	18.2
(4) R	ar	Intercept for maximum standard respiration	0.003 [†]	0.0033
	br	Slope for maximum standard respiration	-0.003 [†]	-0.2246
	RTO	Optimum temperature for standard respiration	33.0°C	33.0°C
	RTM	Maximum temperature for standard respiration	36.0°C	36.0°C

Equation in text	Symbol	Parameter description	Present value	Rippetoe (1993) value
	Qr	Slope for temperature dependence of standard respiration	2.5 [†]	2.07
(5) S	SDA	Specific dynamic action coefficient	0.10	0.10
	ACT	Activity multiplier	1.5	1.5
(6) F	FA	Proportion of food consumed egested	0.14	0.14
(7) U	UA	Proportion of food assimilated excreted	0.10 [†]	0.01

*Hewett and Johnson (1992)

[†]Estimated in calibration

approximately the period during which the Atlantic menhaden fishery is open in Chesapeake Bay each year (Ahrenholz et al., 1987).

4.1 Environmental variables

Fish growth and consumption are strongly dependent on environmental temperature. The function:

$$T = 11 - 0.417d + 0.00624d^2 - 0.0000245d^3 + 0.0000000285d^4 \quad (1)$$

plus a random variation of $\pm 0.5^\circ\text{C}$ where d is the calendar day (Ritchie and Genys, 1975) is used to describe temperature over the model run. This function was determined for surface (1.22 m) water temperature of the Patuxent River Estuary at Solomons, Maryland. Postmetamorphic juvenile Atlantic menhaden are sampled in surface tows in the estuary (Friedland et al., 1996) and presumably spend a significant portion of the time feeding at the water surface.

4.2 Fish bioenergetics submodel

This portion of the model is a modification of the model developed by Kitchell et al. (1977) and expanded in Fish Bioenergetics Model software developed by Hewett and Johnson (1992). Specific fish growth is calculated as weight increment per unit of weight per time increment as follows:

$$\frac{d B}{B dt} = C - [(R + S) + (F + U)] \quad (2)$$

where C is consumption, R is respiration, S is specific dynamic action, F is egestion, U is excretion, and B is fish weight. Empirical observations of fish growth and metabolism are fit to weight-, temperature- and species-specific models to estimate consumption by the fish. All computations are made on a daily basis.

Consumption is an allometric function of weight based on the maximum specific feeding rate ($\text{g prey g predator}^{-1} \text{ day}^{-1}$) modified by water temperature and the P-Value, a factor representing the proportion of maximum consumption rate needed for the fish to attain an observed final weight within a given time period¹:

$$C = C_{\max} * P\text{-Value} * f(T) \quad (3)$$

where:

C_{\max} = $ac * W^{bc}$, maximum specific feeding rate ($\text{g g}^{-1} \text{ d}^{-1}$)

W = fish weight (g)

$f(T)$ = $Ka * Kb$, water temperature dependence function for consumption

P-Value = proportion of maximum consumption actually exhibited by the fish

Respiration and specific dynamic action (SDA) represent the total metabolic rate of the fish. Respiration is modeled as an allometric function of weight, modulated

¹Consumption Equation 3 in Hewett and Johnson (1992), see Table 1 for parameter values and descriptions and Appendix A for more detail.

by water temperature and a factor representing activity (ACT). Energy accounted for by the physical activity of the fish is a proportion of the assimilated energy lost to specific dynamic action. The basic equations are³:

$$R = R_{\max} * f(T) * ACT \quad (4)$$

$$S = SDA * C - F \quad (5)$$

where:

$$R_{\max} = r_a * W^{rb}, \text{ maximum specific respiration rate (g g}^{-1} \text{ d}^{-1}\text{)}$$

$$f(T) = V^X * e^{(X * (1-V))}, \text{ water temperature dependence function for respiration}$$

Egestion (fecal waste) and excretion (nitrogenous waste) are modeled as constant proportions of consumption. The basic equations are⁴:

$$F = FA * C \quad (6)$$

$$U = UA * C - F \quad (7)$$

³Respiration Equation Set 2 in Hewett and Johnson (1992), see Table 1 for parameter descriptions and values and Appendix A for more detail.

⁴Egestion/Excretion Equation Set 1 in Hewett and Johnson (1992), see Table 1 for parameter descriptions and values.

4.3 Fish population submodel

The fish bioenergetics submodel is applied to the total fish population by multiplying fish growth and consumption by the number of fish present on each day of the model run. The number of fish does not remain constant through the model run, but decreases due to fishing mortality (after the fishing season opens) and natural mortality (mostly due to predation). Mortality rates in the literature are often reported as annual instantaneous rates (M_{ann}). This value is converted in the model to daily instantaneous rates via the relation:

$$M_{day} = [-1 * \ln(1 - M_{ann})]/d \quad (8)$$

where M_{ann} is the proportion of fish dying over a given period of length d . The relation also applies to fishing mortality (F_{ann}). The number of fish removed from the population each day are then calculated as follows:

$$\text{fish removed} = F_{day} * (\text{fish population}) + M_{day} * (\text{fish population}) \quad (9)$$

This is subtracted from the previous day's population to arrive at the population on each model day.

4.4 Fishing submodel

Once the biomass of fish landed is calculated in the fish population sector, the value of the landings is calculated. A gross value of \$116 per metric ton of Atlantic menhaden is assumed. This value is derived from the Atlantic coast industry gross

revenue (\$46.4 million) in a high abundance year (7.2×10^9 recruits) in which the total catch is 398,100 t (Blomo, 1987).

4.5 Nutrient-phytoplankton submodel

I assumed for simplicity that phytoplankton productivity in Chesapeake Bay was constant in the model over space and time. I used various average levels of primary productivity obtained from the literature to calculate total primary production over the model run. Marshall and Nesius (1996) reported that primary productivity in the Bay ranged from a low of $82 \text{ gC m}^{-2} \text{ yr}^{-1}$ at the Bay entrance to $538 \text{ gC m}^{-2} \text{ yr}^{-1}$ at the York River entrance. The mean productivity reported ranged from $152 \text{ gC m}^{-2} \text{ yr}^{-1}$ at the Bay entrance to $335 \text{ gC m}^{-2} \text{ yr}^{-1}$ at the York River entrance. These values were averaged over four years, including months during which menhaden are not in residence in the Bay and primary productivity is lower. Sellner and Kachur (1987) estimated that daily productivity during the summer in the middle-reach of Chesapeake Bay at Calvert Cliffs, Maryland ranged from $1.37 \text{ gC m}^{-2} \text{ d}^{-1}$ to $2.75 \text{ gC m}^{-2} \text{ d}^{-1}$ (or $501 \text{ g C m}^{-2} \text{ yr}^{-1}$ to $1014 \text{ g C m}^{-2} \text{ yr}^{-1}$).

It is important to point out that this assumption is highly simplified and does not reflect a number of important aspects about primary productivity. First, primary productivity represents a *rate* and not a total amount that is available as food. Menhaden and other planktivores consume a portion of the standing stock that is available at a given time. The turnover time for phytoplankton standing stock can be

very fast, and therefore, only a portion of what is produced is available for consumption by menhaden. Second, primary productivity is highly variable in Chesapeake Bay, both spatially and temporally. Menhaden schools, particularly postmetamorphic juveniles tend to congregate in areas with the highest levels of phytoplankton biomass (Friedland et al., 1996). Gradients of chlorophyll *a* (chl *a*) are associated with surface salinity, with the chl *a* maxima occurring at 4-6‰. Finally, menhaden of different ages have different particle size thresholds that limit the types of plankton they consume. Larvae consume mainly zooplankton with lengths of 0.65 - 2.00 mm (June and Carlson, 1971). On the other hand, postmetamorphic juveniles are able to utilize smaller phytoplankters, as small as 5 µm, though filtering efficiency of particles this size is low. Friedland et al. (1984) identify four feeding stages for Atlantic menhaden, each characterized by a range of swimming speeds triggered by different concentrations of phytoplankton or zooplankton. Thus, it should be clear that modeling a constant, homogeneous rate of phytoplankton production is a mere abstraction of a more complex reality.

The economic value of the consumption of phytoplankton by age-0 Atlantic menhaden was determined as follows. Phytoplankton cells were assumed to consist of

1.85% C, 0.3% N, and 0.02% P by wet weight⁵. Shulyer (1995) reported on the cost of controlling the input of N to Chesapeake Bay towards a mandated 40% reduction from 1985 levels by the year 2000 (Chesapeake Executive Council, 1988). The overall cost is estimated at \$925,144,000 yr⁻¹. However, this total can be broken down by control strategy, from urban management practices (4,509,000 lb N reduced at \$142.64 lb⁻¹) to nutrient management practices in agricultural settings (16,096,000 lb N reduced at \$0.61 lb⁻¹). The weighted average over all management practices is \$6.00 kg N⁻¹.

5.0 Model Evaluation

5.1 Calibration

The ability of the model to simulate the effect of age-0 menhaden grazing on phytoplankton in Chesapeake Bay was evaluated in light of empirical data and output from a similar model created using Hewett and Johnson's (1992) Fish Bioenergetics Model 2 software (hereafter referred to as FB). All evaluation was performed using baseline conditions with parameters listed in Table 1 and Appendix A unless otherwise

⁵Durbin and Durbin (1981) report phytoplankton (*Dytilum brightwelli*) to be composed of 18.52% C and 3.04% N by dry weight and dry weight is 10% of wet weight. Proportion of P in phytoplankton was determined using the Redfield ratio of 108C : 16N : 1P and assuming 3.0% N.

noted. The bioenergetics component of the model was calibrated with empirical data on growth of individual menhaden. Figure 2 is a plot of fish growth over the first 133 days of the model simulation and the von Bertalanffy curve fit to Rippetoe's (1993) data⁶.

Baseline parameters minimized the average squared error between the von Bertalanffy predicted growth (W_i) and the model output, given by:

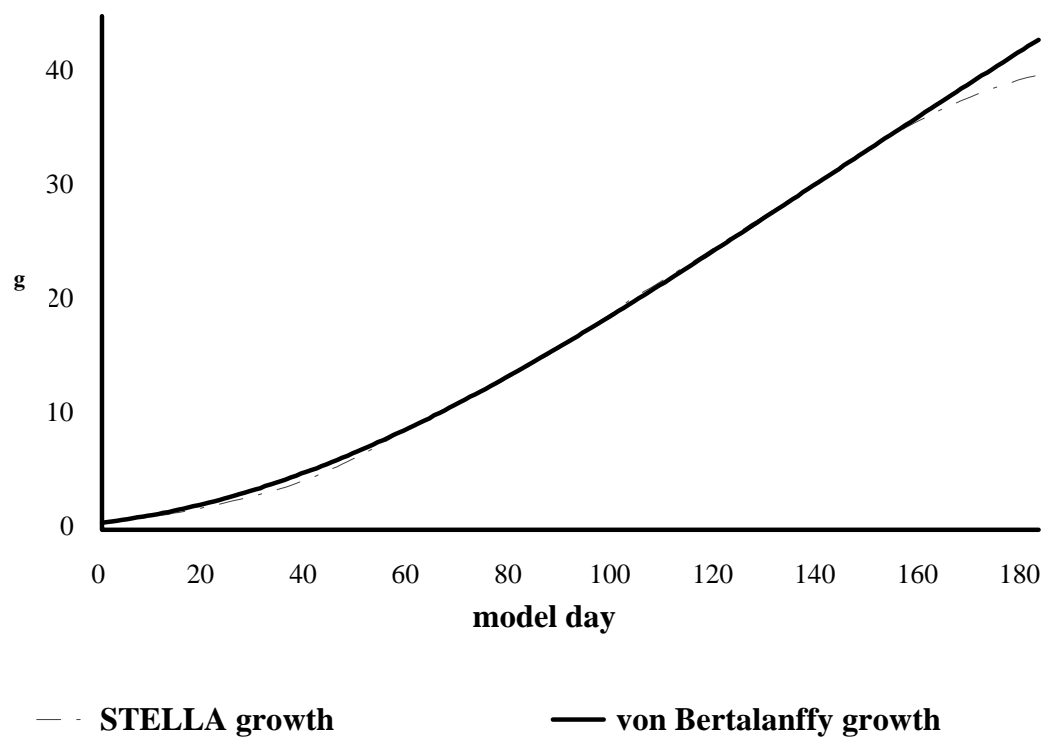
$$\left(\frac{\sum_{i=1}^{133} (W_{ii} - \text{model output}_i)^2}{133} \right) \quad (10)$$

This error is 0.071 over the 133 d for which data are available, and 0.41 over a full 183 d simulation. Individuals grew to a weight of 28.5 g by day 133 in the model as compared to a final average weight of 28.8 ± 0.028 g reported by Rippetoe (1993) on 11 October, 1992.

This calibration process resulted in the use of some parameters that are dissimilar from those used by Rippetoe (1993), because calibration was made to the von Bertalanffy growth curve and not to the growth output of Rippetoe (1993). Bartell

⁶ For age-0 Atlantic menhaden: $L_{\infty} = 215.96$, $K = 0.0064$, and $T_0 = -33.21$; Length is related to weight by $W = a * L^b$, where $a = 7.1 * 10^{-6}$ and $b = 3.07$ (Rippetoe, 1993).

Fig. 2. Simulated (STELLA) and observed growth of age-0 Atlantic menhaden. The von Bertalanffy growth curve is fit to Rippetoe's (1993) data. The von Bertalanffy growth curve coefficients are $L_{\infty} = 215.96$, $K = 0.0064$, and $T_0 = -33.21$; Length is related to weight by $W = a \cdot L^b$, where $a = 7.1 \cdot 10^{-6}$ and $b = 3.07$ (Rippetoe, 1993).

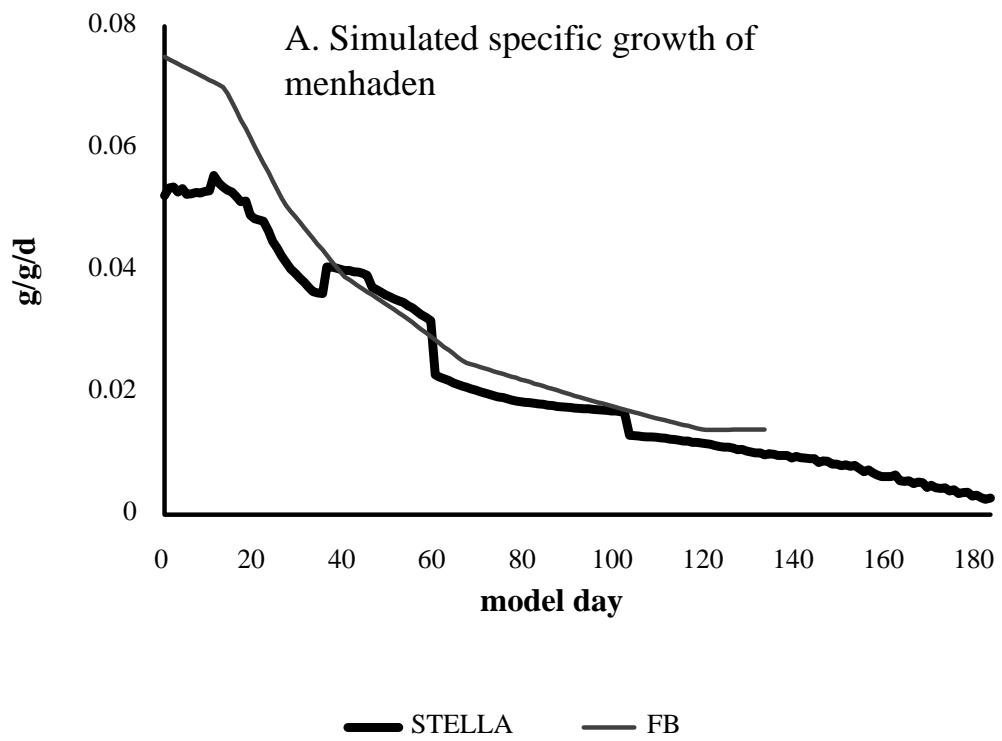


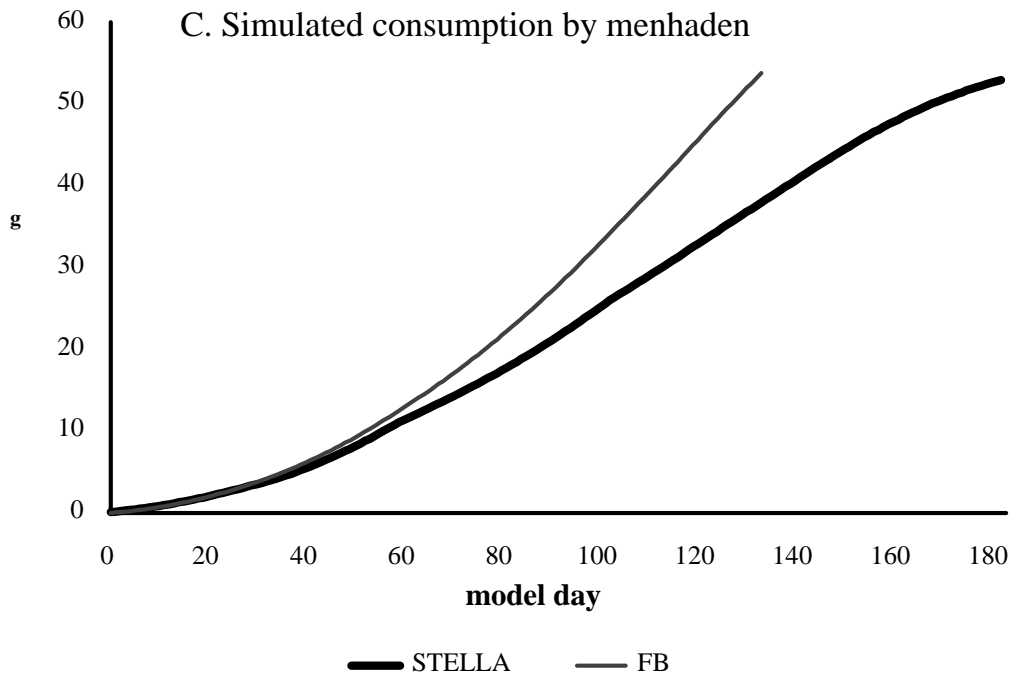
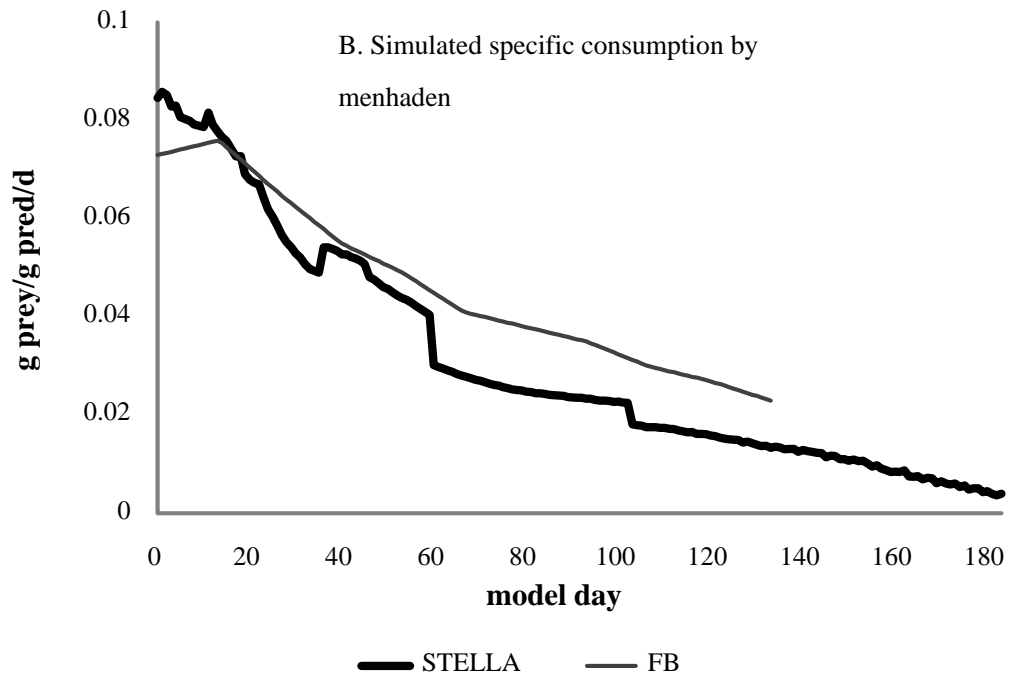
et al. (1986) determined that the bioenergetics model is most sensitive to a few parameters, especially the P-value, a_r , and b_r . Furthermore, they surmise that the P-value will likely vary over time; indeed, they reference a study in which three seasonal adjustments of the P-value were necessary to simulate the growth of largemouth bass in Lake Rebecca, Minnesota. I found that six minor adjustments in the P-value (see Appendix A) minimized the error between the model output and the von Bertalanffy growth curve. Because the parameters I used were in some cases adjusted in the calibration process, they should not be considered measurements of the actual physiology of age-0 Atlantic menhaden.

5.2 Verification

Performance of the bioenergetics component of the model was further evaluated in terms of specific rates of growth ($g\ g^{-1}\ d^{-1}$) and consumption ($g\ g^{-1}\ d^{-1}$). Both the Stella model and FB simulate how specific growth of the fish asymptotically approaches zero as the fish grows over time and as ambient temperature decreases (Fig. 3A). Similarly, the models simulate how specific consumption of phytoplankton by the fish asymptotically approaches zero (Fig 3B). In both of these plots the Stella output appears to be discontinuous because the P-Value is not constant over the model run (see Appendix A), but was adjusted over shorter periods for calibration with the von Bertalanffy growth curve.

Fig. 3. Comparisons of simulated specific growth (A), specific consumption (B) and total individual consumption © of age-0 Atlantic menhaden using Fish Bioenergetics (FB) Model 2 (Hewett and Johnson, 1992) and the STELLA model described in this paper with parameters given in Table 1.





Output of consumption from the model is plotted in Figure 3C with output from FB using parameters reported in Rippeto (1993) (see Table 1). Menhaden diet was assumed to consist of 100% phytoplankton, and under the baseline parameters each individual consumed 37.6 g as compared with 43.0 g reported in Rippeto (1993) for menhaden assumed to consume a diet of 99% phytoplankton. Output from FB using Rippeto's (1993) parameters indicates a much faster rise in consumption by the fish after model day 60 than the Stella output.

Rippeto (1993) analyzed the proportion of annual phytoplankton production that could theoretically be consumed by the total Chesapeake Bay population of menhaden during their residence in the Bay. Using different assumptions about initial fish abundance (100% of fish biomass in Chesapeake Bay) and mortality (41.7% annually), he estimated that 5% of primary productivity could have been consumed. I evaluated the potential relative importance of age-0 Atlantic menhaden as consumers of primary productivity in the Bay over the reported possible ranges of recruits to the fishery (Jones et al. 1988) and primary productivity (Sellner and Kachur, 1987; Marshall and Nesius, 1996). I also ran these simulations for an initial number of fish that would result in a landed biomass approximately equal to the average estimated

landings of age-0 Atlantic menhaden, 5346 t⁷. For calibration and verification, I assumed that natural mortality was $M_{\text{ann}} = 0.45$ (Ahrenholz et al., 1987) and fishing mortality was $F_{\text{ann}} = 0.13$ (Jones et al., 1988) and that the fishing season opened on day 1 of the simulation. The results are summarized in Table 2.

6.0 Management Simulations

The main fishery management operations that can be exerted in the Chesapeake Bay Atlantic menhaden fishery to reduce the catch of age-0 fish are by increasing purse seine net mesh size or delaying the opening date for the fishery. To examine the extreme case in which no age-0 fish are caught, a management simulation in which the fishery never opens (or equivalently in which fishing mortality for the zero age class is zero) was performed. The results of this simulation are given in Table 3 with output from a baseline simulation with normal fishing mortality ($F_{\text{ann}} = 0.13$) and an open season from day 1 in the model run.

⁷The National Marine Fisheries Service (Personal Communication, Fisheries Statistics and Economics Division) reports average landings of 4.5×10^4 t (1×10^8 lb) in the Atlantic fishery for the period 1984-94. The assumptions are that the catch consists of 18% age-0 fish (Street, 1993), and that the Chesapeake Bay fishery comprises 66% of the total Atlantic coast catch of menhaden (estimated from Vaughan et al. (1986) over the period 1964-72).

Table 2. Output values over a 183 d baseline simulation run of the Stella model of age-0 Atlantic menhaden in Chesapeake Bay.

Initial Number of Fish (10⁹)^a	1.5	3.0	18.6
Fishery Output (10 ³ t)	3.5	5.4	43
Population Consumption (10 ⁷ kg)	6.5	9.9	80
Primary Production yr⁻¹^b	% Annual Primary Production Consumed		
82 gC m ⁻² yr ⁻¹	9.3	14	110
152 gC m ⁻² yr ⁻¹	5.0	7.7	62
335 gC m ⁻² yr ⁻¹	2.3	3.5	28
538 gC m ⁻² yr ⁻¹	1.4	2.2	18
Primary Production d⁻¹^c	% Model Run Primary Production Consumed		
1.37 gC m ⁻² d ⁻¹ (501 gC m ⁻² yr ⁻¹)	3.0	4.7	38
2.75 gC m ⁻² d ⁻¹ (1014 gC m ⁻² yr ⁻¹)	1.5	2.3	19

^a Vaughan et al. (1986); Jones et al. (1988), Street et al. (1996); Personal Communication, National Marine Fisheries Service, Fisheries Statistics and Economics Division.

^b Marshall and Nesius (1996).

^c Sellner and Kachur (1987). Productivity values are integrated over the area of the Bay (8.52 * 10⁶ m²).

Table 3. Output values over a 183 d management simulation run of the Stella model of age-0 Atlantic menhaden in Chesapeake Bay.

Initial Number of Fish (10⁹)^a	1.5		2.3		18.6	
Annual Fishing Mortality	0.13	0	0.13	0	0.13	0
Fishery Output (10 ³ t)	3.5	0	5.4	0	43	0
Gross Fishery Value (10 ⁶ \$)	0.41	0	0.62	0	5.0	0
Population Consumption (10 ⁶ kg)	65	67	99	100	800	830
Primary Production yr⁻¹^b	% Annual Primary Production Consumed					
82 gC m ⁻² yr ⁻¹	9.3	9.6	14	15	110	120
538 gC m ⁻² yr ⁻¹	1.4	1.5	2.2	2.3	17	18
Primary Production d⁻¹ (yr⁻¹)^c	% Model Run Primary Production Consumed					
1.37 gC m ⁻² d ⁻¹ (501 gC m ⁻² yr ⁻¹)	3.0	3.2	4.7	4.8	38	39
2.75 gC m ⁻² d ⁻¹ (1014 gC m ⁻² yr ⁻¹)	1.5	1.6	2.3	2.4	19	20
N Consumed (10 ⁶ kg)	0.19	0.20	0.30	0.31	2.4	2.5
Value of N Consumption (10 ⁶ \$)	1.2	1.2	1.8	1.9	14	15
C Consumed (10 ⁶ kg)	1.2	1.3	1.8	1.9	15	15
P Consumed (10 ⁶ kg)	0.01	0.01	0.02	0.02	0.16	0.17

^a Vaughan et al. (1986); Jones et al. (1988); Street et al. (1996); Personal Communication, National Marine Fisheries Service, Fisheries Statistics and Economics Division.

^b Marshall and Nesius (1996).

^c Sellner and Kachur (1987). Productivity values are integrated over the area of the Bay (8.52 * 10⁶ m²).

This output indicates that age-0 menhaden could consume a significant amount of phytoplankton in Chesapeake Bay, in the range of $65 * 10^6$ kg to $830 * 10^6$ kg, with the actual value most likely around $99.5 * 10^6$ kg (because this was the median amount consumed by the moderately-sized population). Along with this consumption of phytoplankton, age-0 menhaden could remove a significant amount of C, N, and P. The range for consumption of C was $1.2 * 10^6$ kg to $15 * 10^6$ kg, with the most likely value around $1.85 * 10^6$ kg; N was consumed in the range of $0.2 * 10^6$ kg to $2.5 * 10^6$ kg, with the most likely value around $0.3 * 10^6$ kg; finally, P was consumed in the range of $0.01 * 10^6$ kg to $0.17 * 10^6$ kg, with the most likely value around $0.02 * 10^6$ kg. Using cost of preventing N from entering the Bay as a proxy for the value of nutrient consumption by menhaden, the total value of nutrient consumption by age-0 menhaden ranged from \$1.17 million to \$15.0 million, with the most realistic value around \$1.82 million. In comparison, the value of the fishery for age-0 menhaden ranged from \$0.41 million to \$5.03 million, with the most realistic value around \$0.62 million.

The output of the model indicated that the fishery has a moderate effect on the level of consumption exhibited by the age-0 menhaden population. The population of menhaden, regardless of the initial size, consumes about 3-4% more phytoplankton when it experiences no fishing mortality. Nonetheless, the most significant factor affecting the relative importance of age-0 Atlantic menhaden as a consumer of primary productivity is the initial number of recruits to the fishery. A sensitivity analysis on these factors (exerting a 10% change in the level of mortality and on the initial number of recruits separately, holding all other factors equal) shows why this is so. A 10%

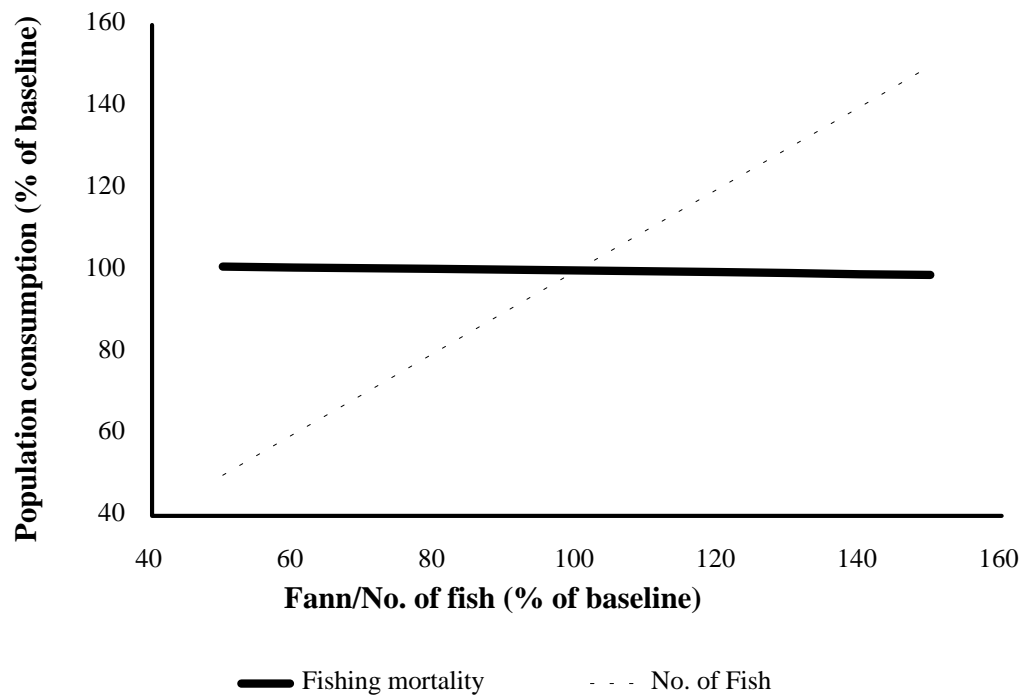
reduction or increase in the level of fishing mortality (i.e. from 0.130 to 0.117 or 0.143) yielded a less than 1% change in the level of population consumption of phytoplankton. A 10% reduction or increase in the initial number of fish (i.e. from 2.30×10^9 to 2.07×10^9 or 2.53×10^9) yielded a proportional 10% change in the population consumption of phytoplankton (Fig. 4).

Removing the zero age class of menhaden from the fishery without increasing the exploitation of older age classes would deprive the industry of \$0.41M to \$5.03M gross revenues. This strategy would have the ecological effect of allowing the fish to remove an additional 8000 to 90,000 kg of N at an economic value of \$44,530 to \$552,182. Here again, the initial number of fish is the largest population-level factor controlling the amount of N consumed by the fish and hence the economic value of this service.

7.0 Discussion

This study has shown that age-0 Atlantic menhaden could be an important consumer of primary productivity in Chesapeake Bay. Potentially, these young-of-the-year could be responsible for the consumption of 1.5 - 120% of the total annual primary productivity in Chesapeake Bay. Based on information about the menhaden biomass in the Bay from catch statistics, the actual value is most likely under 10%. Moreover, this level of consumption by age-0 menhaden would result in the consumption of a

Fig. 4. Relative sensitivity of population consumption of age-0 Atlantic menhaden to changing the initial number of fish or annual fishing mortality (F_{ann}).



significant amount of the nutrients implicated in the eutrophication of the Bay. The consumption of phytoplankton should have a moderating effect on anoxic conditions caused by unconsumed phytoplankton dying and decaying below the thermocline during summer months. Further analysis is necessary and will be performed in a later chapter to determine the optimal fishing level to derive the maximal ecological benefit from their consumption of primary productivity without compromising the value of the fishery.

Considering that older age classes of menhaden reside and continue to grow in Chesapeake Bay during summer the role of this fishery in the ecosystem as processors and transporters of organic materials should be a part of nutrient analyses. Deegan (1993) estimated the magnitude of nutrient and energy transport between Forleague Bay, Louisiana and the Gulf of Mexico by the gulf menhaden (*Brevoortia patronus*). She determined that average annual export of C, N and P by the fish amounted to approximately 5-10% of the total annual primary productivity in gulf estuarine systems, about the same magnitude as passive waterborne export. Furthermore, because of the lower C:N ratio in the fish than in detritus passively transported, the fish export greater quantities of N and P relative to C, an important point for a eutrophicated system.

The simulation presented here is intended to give an estimate of the potential magnitude of the ecological role of age-0 Atlantic menhaden in consuming phytoplankton in Chesapeake Bay. Another important use for the modeling exercise is to point out areas in need of further study and better quantification. This study has revealed that the estimation of the initial number of fish recruited to Chesapeake Bay in

spring is the largest population-level factor controlling the output of the simulations. It is not possible to estimate the number of menhaden in Chesapeake Bay in a given year from catch statistics since this information became proprietary to the industry in the 1970's. Efforts to enumerate fish of various species of fish in Chesapeake Bay using acoustic techniques are on the horizon (e.g. Luo and Brandt, 1993), and these data will be useful in perfecting analyses such as this one.

Chapter III: Consumption of Primary Productivity by Age 1-3 Atlantic menhaden in Chesapeake Bay

1.0 Introduction

In this chapter, I expand the bioenergetics model and discussion of the ecological role of Atlantic menhaden to older age-classes. I considered only the age-0 menhaden in the previous chapter, because the strong database of bioenergetics parameters available for this cohort aided in the development of a verifiable ecological model. However, the Atlantic menhaden is a long-lived species; the population historically consisted of 10 - 11 cohorts, though fishing has effectively truncated the population age structure, eliminating age-6-and-older fish (Powell, 1994). Adult menhaden, particularly ages 1-3 make up a significant proportion of the spring and summer population in Chesapeake Bay (Nicholson, 1978; Ahrenholz et al., 1987), and continue to filter-feed on phytoplankton, and can grow to a wet weight of more than 600 g (Durbin et al., 1983).

Lippson (1991) speculated that adult menhaden have an important ecological role in the Chesapeake Bay. Given an adult menhaden's filtering capacity of 15.2 L/min or $3.9 * 10^6$ L in 180 d (Lippson, 1991), the impact of these planktivores could be significant. A back-of-the-envelope calculation of the filtering capacity of the entire population of adult menhaden during their residence in Chesapeake Bay yields a minimum of about 2 days to a maximum of about 3.5 hours for the population to filter

a volume equal to the entire Bay⁸. This said, it is important to point out that because of the tight schooling pattern and spatial heterogeneity in the distribution of Atlantic menhaden in Chesapeake Bay that there is a high rate of recirculation of water filtered within a school. Thus, the filtering capacity just calculated does not imply that menhaden actually filter the entire physical volume of the Bay in any time period.

Extensive research into the physiology and bioenergetics of adult menhaden has been conducted (e.g., Durbin and Durbin, 1981,1983; Durbin et al., 1983). However, this research focused on menhaden's feeding response to varying food particle sizes and concentrations rather than on the effects of temperature and allometric functions of feeding and growth which are required by the Hewett and Johnson (1992) computer model. Because of the lack of applicable information about the bioenergetics of adult menhaden, I have parameterized the model of menhaden in the age 1-3 cohorts based on simulations of the growth of wild menhaden from data provided by the National Marine Fisheries Service (Personal Communication, J. Smith, National Marine Fisheries Service, Southeast Fisheries Science Center, Beaufort NC).

Bioenergetics studies often suffer from a similar lack of laboratory and field data. The bioenergetics software (Hewett and Johnson, 1992) is commonly used as a tool to estimate population consumption over a season when little data, other than

⁸For the minimum estimate, assume $3.6 * 10^9$ adult menhaden, filtering for 12 h/d. For the maximum estimate, assume $23.8 * 10^9$ adult menhaden, filtering for 24 h/d. The volume of the Bay is assumed to be $74 * 10^{12}$ L (Schubel and Pritchard, 1987).

information about growth, are available. Kitchell et al. (1977) predicted that the bioenergetics model would be a more precise estimator of fish consumption rate, given growth data, than an estimator of growth, given consumption data. This hypothesis was tested and supported in work by Bartell et al. (1986).

For the past several decades, Chesapeake Bay landings of menhaden have constituted the largest proportion of the Atlantic fishery in terms of total landings and yield-per-recruit (Nicholson, 1978; Vaughan and Smith, 1991). Although the fishery has come to rely more heavily on age-0 menhaden, adult menhaden make up the most significant proportion of the spring and summer population in Chesapeake Bay up to the age-3 cohort (Vaughan and Smith, 1991). Most of the landings of age-0 fish, or “peanuts,” occur in the North Carolina fall fishing season, as they migrate out of the Chesapeake Bay nursery area (Vaughan and Smith, 1991). Researchers have considered the effectiveness in terms of increasing yield-per-recruit of various strategies aimed at reducing the catches of age 0-3 menhaden (Vaughan and Smith, 1991). The impact of these management regimes on the ecological role of menhaden was not considered. I consider the magnitude of the ecological role of age-classes 1-3 in this chapter.

2.0 Model Overview

The basic model structure is unchanged from Chapter 1. I have utilized Stella’s array feature (High Performance Systems, 1996) to run parallel simulations of all three

age-classes. Each age class has its own bioenergetics and fishery parameters, but the environmental conditions experienced by each cohort is identical. Each arrayed parameter (see Appendix B) is one-dimensional, that is, the dimension (Cohorts) is broken into 3 separate population elements, age-1, age-2, and age-3.

3.0 The Data Base

Data on growth of Atlantic menhaden in Chesapeake Bay were provided by the National Marine Fisheries Service (Personal Communication, J. Smith, National Marine Fisheries Service, Southeast Fisheries Science Center, Beaufort, NC). Raw port data on length, weight, and age of landed menhaden was collected monthly from May to November during 1990 - 1996. All samples were collected within the Chesapeake Bay (inside the Bay Bridge Tunnel). I assumed, for simplicity, that the monthly data were simultaneously collected on the first day of each month. I then averaged the data from each month for each year over all seven years. This resulted in the following growth pattern (weight values are in g, standard deviation given in parentheses):

	Model Day	1	31	62	93	123	154
Cohort							
Age 1		85.6 (16.1)	117.2 (22.2)	143.6 (29.7)	121.4 (32.4)	126.4 (50.2)	162.1 (51.0)
Age 2		167.1 (34.1)	184.2 (31.9)	230.9 (41.4)	265.3 (46.4)	302.0 (58.2)	301.7 (74.9)
Age 3		284.8 (51.6)	277.8 (68.5)	320.3 (56.7)	365.7 (39.2)	387.5 (51.9)	332.2 (148.5)

Model Day 1 corresponds to May 31. These are the values used as the “Growth Data” input to the bioenergetics portion of the model to calculate C_{\max} (see Appendix B). Because of the irregularity of the growth pattern that resulted from averaging the data (Fig. 5), I performed an exponential fit using Quattro’s Exponential Fit Tool (Novell, Inc. 1994) to obtain a smoother estimate of growth for model calibration. In addition, a value for the weight of a fish in each cohort was needed for d 183 in the model so that the simulation could be run for the entire residence time of menhaden in Chesapeake Bay. Since data were available only to d 154, the values for d 183 were estimated using Quattro’s Forecast Tool (Novell, Inc., 1994) based on the linear trend of growth for each cohort. The results of the exponential fit are presented in Fig. 6 and as follows (weight values in g):

	Model Day	1	31	62	93	123	154	183
Cohort								
Age 1		98.1	107.6	118.0	129.6	142.2	156.0	165.2
Age 2		170.0	193.8	220.8	251.7	286.9	327.0	349.6
Age 3		284.3	300.2	316.9	334.6	353.3	373.1	388.3

These values were used as input for the “Fit Data” parameter (see Appendix B) to test the performance of the model in simulating growth of menhaden ages 1-3.

The size and seasonal structure of the Atlantic menhaden population is a subject of speculation, but there is little direct information available. While the total landings for Atlantic menhaden are known, data on a finer scale (by boat, reduction plant, or even by state) became proprietary to the industry in the early 1970's after a precipitous

Fig. 5. Growth of age 1-3 Atlantic menhaden averaged from data collected by the National Marine Fisheries Service (Personal Communication, J. Smith, National Marine Fisheries Service, Southeast Fisheries Science Center, Beaufort, NC)

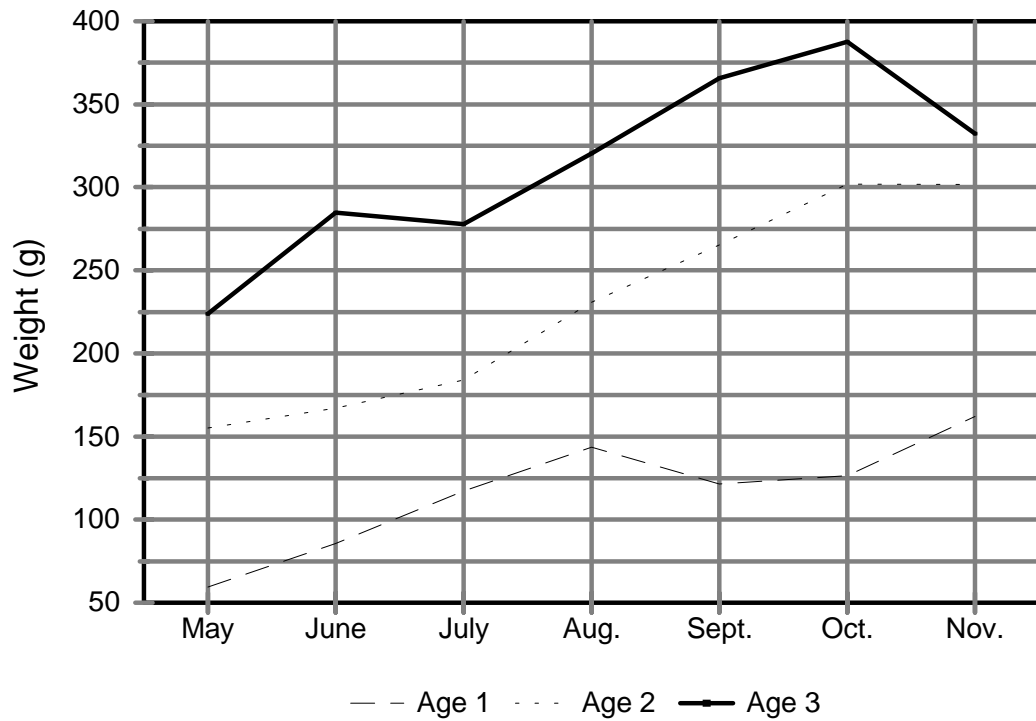
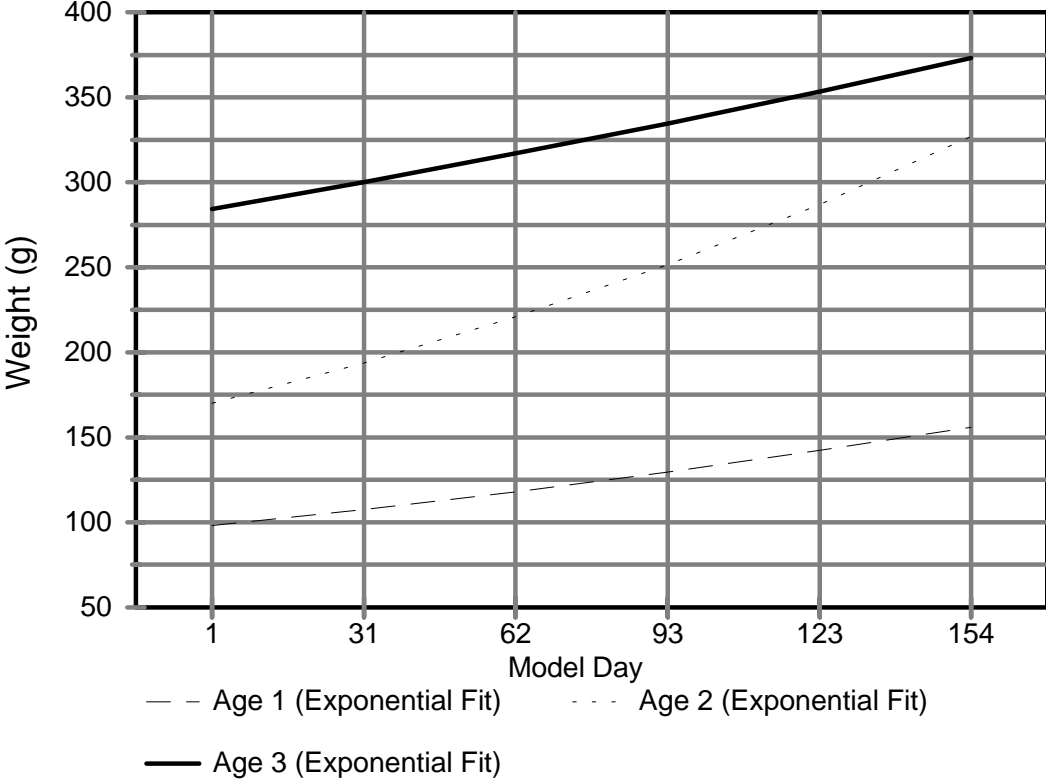


Fig. 6. Exponential fit of averaged growth data for age 1-3 Atlantic menhaden collected by the National Marine Fisheries Service (Personal Communication, J. Smith, National Marine Fisheries Service, Southeast Fisheries Science Center, Beaufort, NC).



decline in the stock north of Chesapeake Bay forced the closure of many plants on the east coast. The total number of reduction plants fell from 15 in 1955 to four in 1989 (Smith, 1991) and only two remain as of this writing. As a result, I have had to use estimates of the boundary limits of the population from a Virtual Population Analysis in Ahrenholz et al. (1987). Using conservative values for fishing mortality ($F = 0.25$ for age-1 and 0.50 for age-2+), Ahrenholz et al. (1987) back-calculated the population of the age 1-3 classes during 1950 - 1959 in the following ranges:

Age Class	Low Estimate (Year)	High Estimate (Year)
1	$2.2 * 10^9$ (1959)	$14.8 * 10^9$ (1958)
2	$1.2 * 10^9$ (1959)	$6.6 * 10^9$ (1958)
3	$0.24 * 10^9$ (1954)	$2.0 * 10^9$ (1951)

I used these estimates of population structure and as input for the “Initial Number” parameter (see Appendix B) in simulations with low and high populations, respectively. These populations are overestimates of the actual population in Chesapeake Bay.

For a moderate estimate of the initial number of menhaden in each age-class, I performed a back-calculation based on recent fishery statistics. Street and others (1993, 1996) reported landings of about 325,000 t in 1992 and 295,000 t in 1994. Both years were reported to have had unusually low landings (15 - 25% lower than the five previous years), although the stock was considered to be healthy. In addition, Chesapeake Bay landings were reported to dominate the landings for the Atlantic

fishery. Thus, I assumed a conservative annual landing rate of 300,000 t in Chesapeake Bay.

Street and others (1993, 1996) also reported the proportion of each age class represented in the landings. In 1992, ages 1-3 made up 78% of the total landings, with 49% age-1, 46% age-2, and 3% age-3 in the mid-Atlantic and Chesapeake Bay (Street, 1993). In 1994, ages 1-3 made up 95% of the total landings, with age-2 comprising 71% of landings in Chesapeake Bay (Street et al., 1996). Although the proportions of each age-class in the landings appear to be quite variable on a yearly basis, I assumed for simplicity that the landings consist of 19% age-1, 72% age-2, and 9% age-3 for all simulations with the moderate initial population estimate. With these landings proportions, a total landing estimate of 300,000 t, and $F_{\text{ann}} = 0.25$ for age-1, $F_{\text{ann}} = 0.50$ for age-2+ (Ahrenholz et al., 1987), I back-calculated the initial population to consist of $3.00 * 10^9$ age-1, $2.45 * 10^9$ age-2, and $2.80 * 10^8$ age-3. This initial population structure was used for all simulations with a moderate population.

4.0 Model Evaluation and Calibration

Model performance in terms of simulating the growth of menhaden in the age 1-3 classes was evaluated using the exponential fit of growth data provided by the National Marine Fisheries Service (Personal Communication, J. Smith, National Marine Fisheries Service, Southeast Fisheries Science Center, Beaufort, NC). All evaluation was performed using baseline conditions with parameters listed in Table 4

and Appendix B unless otherwise noted. Figs. 7a-c are plots of fish growth simulated by the model compared with the exponential fit. Baseline parameters minimized the average squared error between the exponential fit and the model output over a 154 d simulation, given by:

$$\left(\frac{\sum_{i=1}^{154} (\text{fit } data_i - \text{model output}_i)^2}{154} \right)$$

The final weights (g) and error are:

	Final Wt. (Sim.)	Final Wt. (Fit)	Avg. Squared Error
Age - 1	154.9	156.0	1.31
Age - 2	327.6	327.0	1.32
Age - 3	373.5	373.1	1.95

Bartell et al. (1986) determined that consumption estimates based on fitting the bioenergetics model to growth are most sensitive to a small number of parameters, including the P-value, a_r and b_r (see Table 4). Using Rippetoe's (1993) parameters as a baseline, I varied the P-value, a_r , b_r , b_c , and Q_c to achieve the best possible fit to the averaged and forecast growth data. The P-value (proportion of maximum ration consumed by the fish over the run interval) is a strong factor in affecting the overall growth rate, and there is little reason to suspect that it would remain constant through time for fish (Bartell et al., 1986). I found that at least one adjustment to the P-value

Fig. 7a. Growth of age-1 menhaden simulated by a Stella model and exponential fit of averaged growth data.

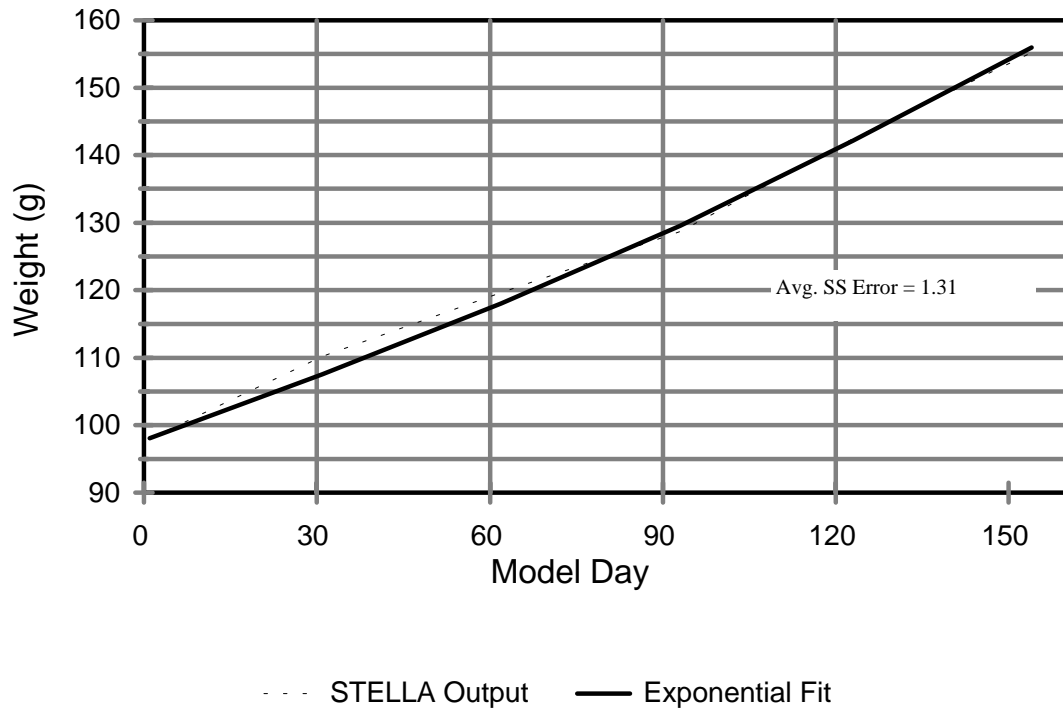


Fig. 7b. Growth of age-2 menhaden simulated by a Stella model and exponential fit of averaged growth data.

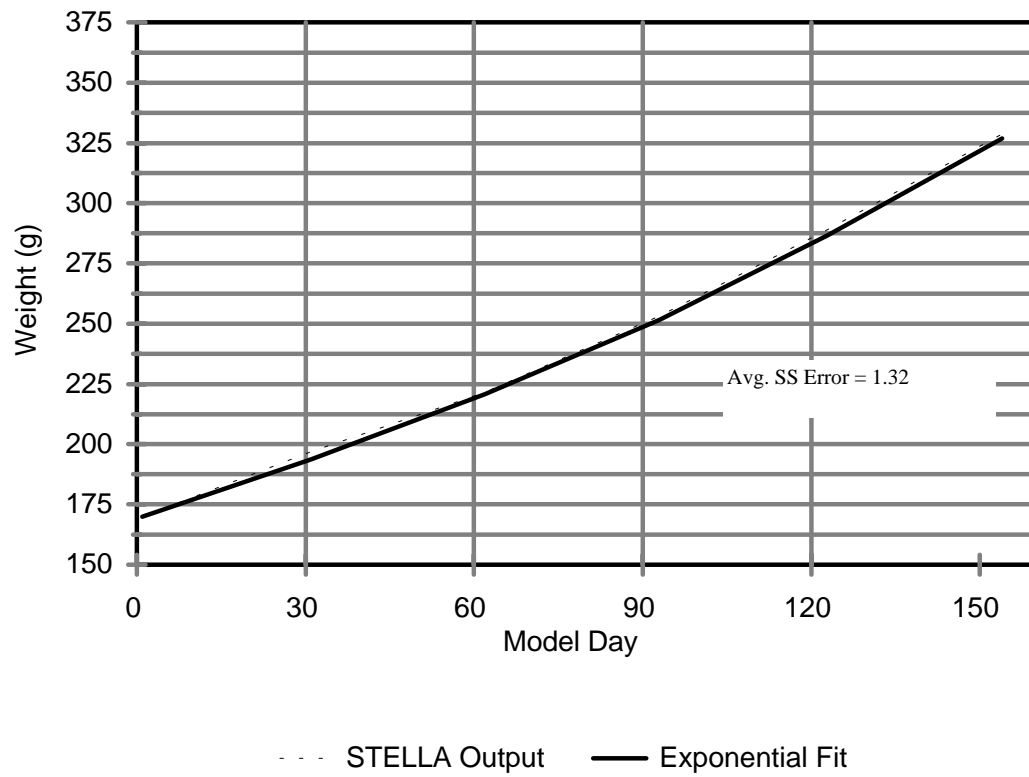


Fig. 7c. Growth of age-3 menhaden simulated by a Stella model and exponential fit of averaged growth data.

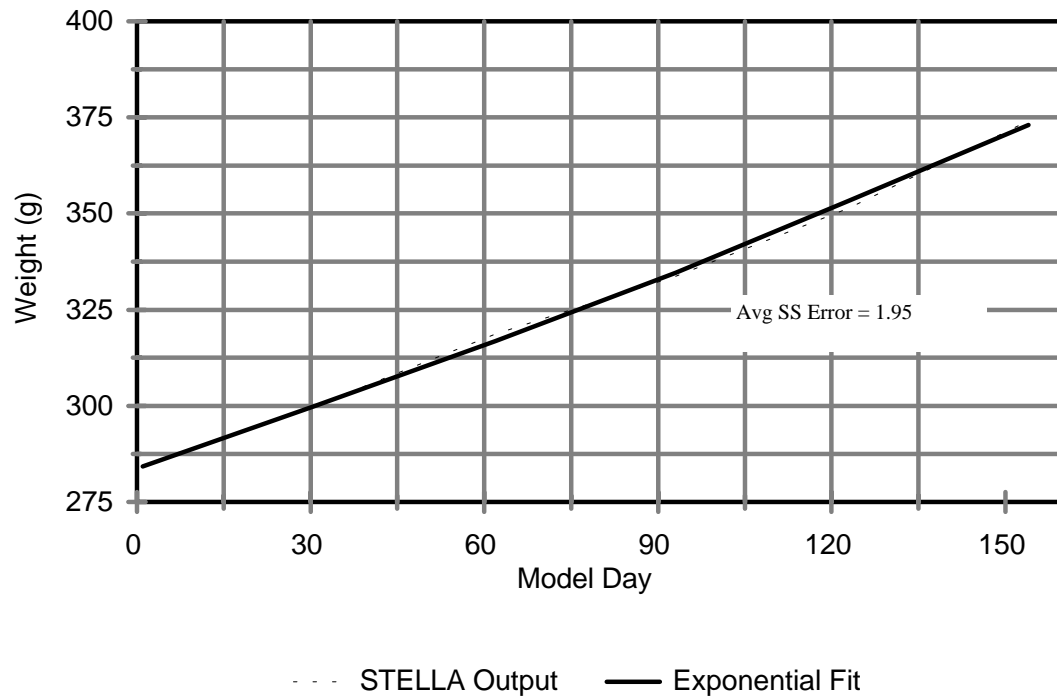


Table 4. Symbols and parameter values used to implement the bioenergetics submodel equations applied to age 1-3 Atlantic menhaden.

Equation in chapter 2	Symbol	Parameter description	Age 1	Age 2	Age 3
(3) C	ac	Intercept for Cmax	1.294	1.294	1.294
	bc	Slope for Cmax	-0.421	-0.425	-0.42 before d 68; -0.425 from d 68 to end
	CTO	Optimum temperature for consumption	28.0°C	28.0°C	28.0°C
	CK1	Proportion of Cmax at CTO, CTM	0.1	0.1	0.1
	CTM	Maximum temperature for consumption	29.0°C	29.0°C	29.0°C
	CTL	Temperature at which dependence is CK4	30.1°C	30.1°C	30.1°C
	CK4	Proportion of Cmax at CTL	0.01	0.01	0.01
	Qc	Slope for temperature dependence of consumption	6.5	5.2	6.0
(4) R	ar	Intercept for maximum standard respiration	0.00294	0.0027	0.003

Equation in chapter 2	Symbol	Parameter description	Age 1	Age 2	Age 3
	br	Slope for maximum standard respiration	-0.0085	-0.01	-0.01
	RTO	Optimum temperature for standard respiration	33.0°C	33.0°C	33.0°C
	RTM	Maximum temperature for standard respiration	36.0°C	36.0°C	36.0°C
	Qr	Slope for temperature dependence of standard respiration	2.5	2.5	2.5
(5) S	SDA	Specific dynamic action coefficient	0.1	0.1	0.1
	ACT	Activity multiplier	1.5	1.5	1.5
(6) F	FA	Proportion of food consumed egested	0.14	0.14	0.14
(7) U	UA	Proportion of food assimilated excreted	0.1	0.1	0.1

for ages-2 and -3 were required for the best fit to growth. The parameters estimated from this calibration process should not be considered to be the bioenergetic properties of age 1-3 Atlantic menhaden as they were the result of minimizing error and not from physiological research.

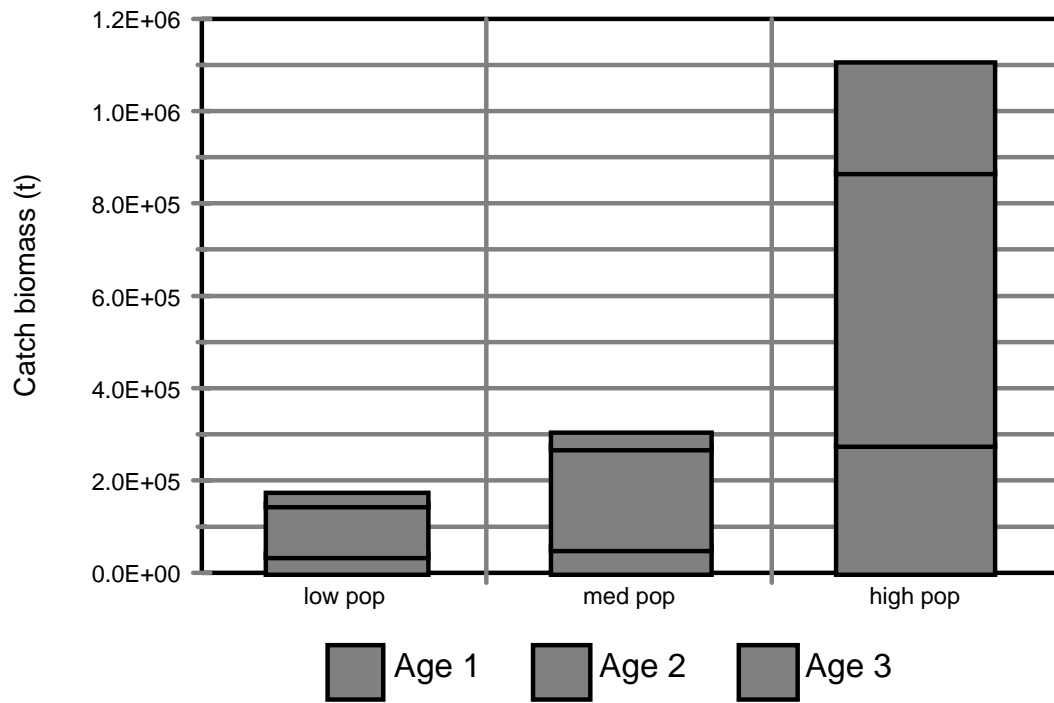
5.0 Management simulations

To examine the extremes of the management spectrum, I performed two initial simulations in which: 1) normal fishing of Atlantic menhaden (age-1 $F_{ann} = 0.25$, age-2+ $F_{ann} = 0.50$) occurs over the entire 183 d simulation; and 2) no fishing occurs. The results of these simulations are presented in Table 5.

The proportion of each cohort represented in simulated landings is represented in Fig. 8. Ages-1 and -2 dominated the landings, with age-2 dominating in terms of biomass, consistent with fishery analyses (Nicholson, 1978; Ahrenholz et al., 1987; Smith, 1991). These proportions in terms of fish biomass are as follows:

	Low population	Medium population	High population
Age 1	24%	19%	25%
Age 2	63%	72%	54%
Age 3	14%	9%	21%

Fig. 8. Proportion of each cohort represented in simulated landings under various population size assumptions.



Eliminating fishing mortality nominally alters the proportion of primary production consumed by each cohort. These proportions are represented in Fig. 9. The simulated proportions phytoplankton of biomass consumed are as follows:

	Low population		Medium population		High population	
	fished	not fished	fished	not fished	fished	not fished
Age 1	42%	40%	34%	32%	44%	42%
Age 2	49%	51%	60%	62%	42%	44%
Age 3	9%	8%	6%	6%	14%	14%

Eliminating fishing mortality increases the total amount of nutrients (C, N, and P) consumed by the population. These amounts are presented in Table 5 and Fig. 10. The unexploited moderate population consumes 390,000 t of N more than the exploited moderate population. Eliminating fishing mortality at this population level also results in the consumption of an additional 2.5 million t of C and 26,000 t of P compared to the exploited population. Overall, an unfished population (of any initial size) of age 1-3 menhaden consumes about 11% more phytoplankton than a fished one.

Fig. 9. Proportion of total primary production consumed by each cohort under various population size assumptions and fishing regimes ('nf' signifies that no fishing mortality occurred in the simulation.)

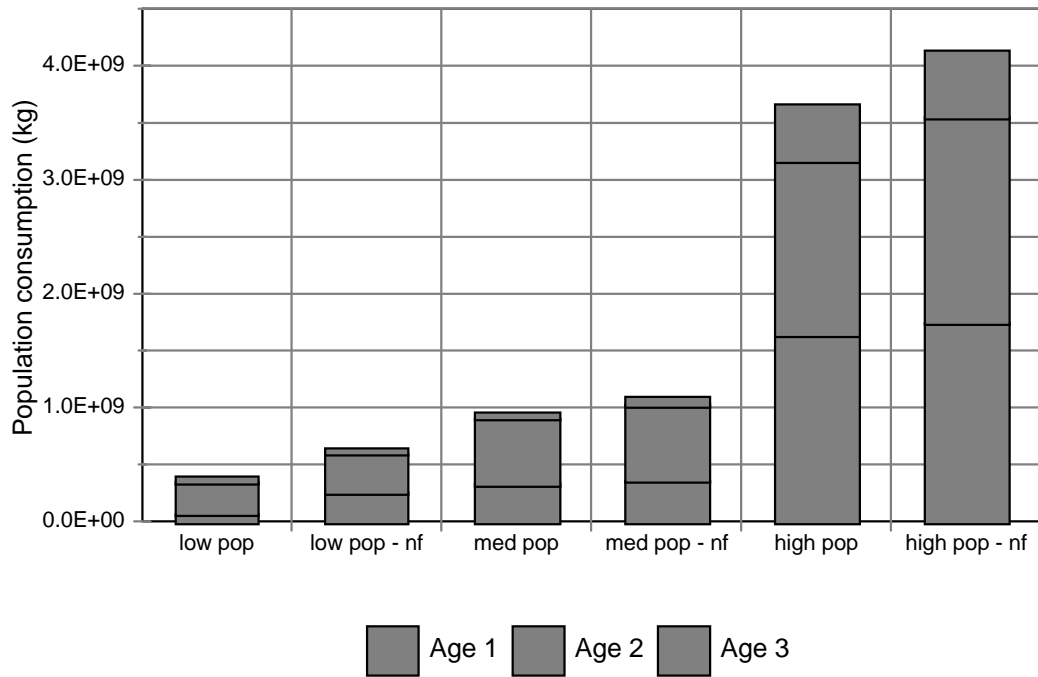


Table 5. Output values over a 183 d management simulation run of the Stella model of age 1-3 Atlantic menhaden in Chesapeake Bay. (Y= Fishing occurred; N = No fishing occurred).

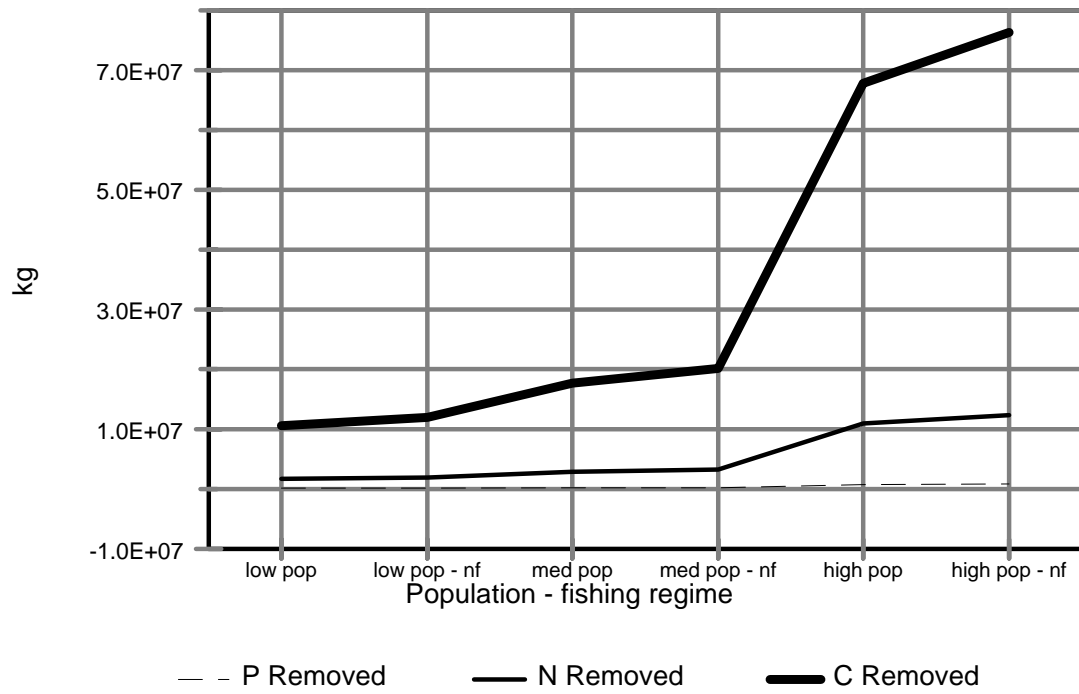
Initial Number of Fish (10⁹)^a	3.64		5.73		23.8	
Fishing	Y	N	Y	N	Y	N
Fishery Output (10 ⁶ t)	0.17	0	0.30	0	1.1	0
Gross Fishery Value (10 ⁶ \$)	20	0	32	0	130	0
Population Consumption (10 ⁶ kg)	570	640	950	1100	3700	4100
Primary Production yr⁻¹^b	% of Total Annual Primary Production					
82 gC m ⁻² yr ⁻¹	82	92	140	160	520	590
538 gC m ⁻² yr ⁻¹	12	14	21	24	80	90
Primary Production d⁻¹ (yr⁻¹)^c	% of Model Run Primary Production					
1.37 gC m ⁻² d ⁻¹ (501 gC m ⁻² yr ⁻¹)	28	30	45	51	170	190
2.75 gC m ⁻² d ⁻¹ (1014 gC m ⁻² yr ⁻¹)	13	15	22	25	85	96
N Consumed (10 ⁶ kg)	1.7	1.9	3.0	3.3	11.0	12
Value of N Consumption (10 ⁶ \$)	10	12	17	20	66	74
C Consumed (10 ⁶ kg)	11	12	18	20	68	76
P Consumed (10 ⁶ kg)	0.11	0.13	0.19	0.22	0.73	0.82

^a Vaughan et al. (1986); Jones et al. (1988); Street et al. (1996); Personal Communication, National Marine Fisheries Service, Fisheries Statistics and Economics Division.

^b Marshall and Nesius (1996).

^c Sellner and Kachur (1987). Productivity values are integrated over the area of the Bay (8.52 * 10⁶ m²).

Fig. 10. Total amounts of nutrients consumed in simulations under various population size assumptions and fishing regimes.



6.0 Discussion

This study has shown that the population of age 1-3 menhaden could be responsible for the consumption of a significant proportion of primary production during their residence in Chesapeake Bay. The simulations indicated a potential range of consumption of 13.3 - 193% of primary production over the model run and 12.5% - 591% of annual primary production. These values represent the absolute extreme estimates of menhaden population and primary productivity, and the actual proportion is not likely to be more than 50% of primary productivity over the model run.

The simulations also indicate that the value of the ecological service provided by menhaden as it removes nutrients (based on the cost of mitigating nitrogen input) is somewhat more than half the value of the fish as a traditional commodity. For example, a moderately sized population (5.73×10^9) of age 1-3 menhaden that is exploited at a conservative rate ($F_{\text{ann}} = 0.25$ for age-1; $F_{\text{ann}} = 0.5$ for age-2+) has a gross port value of \$32.3 million, while the value of its service in removing nitrogen is \$17.3 million. Eliminating fishing at this population level increases the value of nitrogen consumption by \$2.3 million, about 7% of the revenues that would be lost to the fishing industry under this management strategy.

These simulations, while they can only present a rough estimate of the relative importance of age 1-3 menhaden as a consumer of primary productivity, and thus as a mitigator of eutrophication in Chesapeake Bay, nevertheless point to the possibility that the fishery could be managed more efficiently. While the strict reduction or complete

elimination of the fishery is not called for, it is possible that certain regulations on gear (such as decreasing net mesh size to exclude age-0 menhaden) or season (such as restricting harvest to later in the season) could increase the ecological benefits provided by the menhaden population.

In the next chapter I will combine the results of the models of age-0 and age 1-3 menhaden and discuss approaches for analyzing the role of Atlantic menhaden in the trophic structure of Chesapeake Bay.

Chapter IV: Discussion and Conclusions

1.0 Introduction

The final aspect to consider is how to use results of the modeling exercise in making a policy recommendation on management of the Atlantic menhaden fishery. Unlike traditional fishery analyses, which result in the calculation of a Maximum Sustainable Yield or Yield Per Recruit, this analysis does not provide a metric that directly guides the decision of the fishery manager. Rather, information is provided about the magnitude of the ecological services provided by Atlantic menhaden and how the management of the fishery may affect the Chesapeake Bay ecosystem. Value of these services can be determined in a number of ways, for example in terms of cost avoidance in the nutrient management strategy, or in more indirect ways, such as contributory value to other fisheries. It would be a mistake to use only one metric to analyze the value of ecological services provided by Atlantic menhaden. In this chapter I will first compare the results of the model presented in the two previous chapters with similar work on Atlantic menhaden in Narragansett Bay and consider a number of ways in which the results of the model can be interpreted for use in making policy decisions regarding the Atlantic menhaden fishery in Chesapeake Bay.

2.0 Comparisons with Atlantic menhaden in Naragansett Bay

Recent work by Durbin and Durbin (1998) provides a good basis for comparison to this study. The researchers constructed a general bioenergetic model for Atlantic menhaden (applied to all age-classes) and used information about the population size and mean weight of menhaden in Naragansett Bay to determine the role of menhaden predation on plankton populations in that estuary. They make a rough estimate of the magnitude of the effect that menhaden have on plankton populations and the proportion of nutrients that menhaden remove from the system. This calculation is based on the net export by menhaden as determined by the following equation:

Net export of N = N in catch + N in out-migration - N in in-migration - N in dead fish

While their analysis is similar to the one presented in this thesis, there are some differences in the assumptions that the Durbins make from those that I have made. These similarities and differences are summarized in Table 6.

Naragansett Bay is a smaller system and the population of Atlantic menhaden is proportionally smaller than in Chesapeake Bay. Nevertheless, Durbin and Durbin (1998) conclude that menhaden cause significant effects in the trophic structure of Naragansett Bay. In summary, the results of their model indicated that medium and large population sizes of menhaden would cause negative growth rates for zooplankton >20 μ m and that phytoplankton growth actually is stimulated by menhaden's excretion of N, and only negatively affected by grazing at the highest population estimates. In

addition, menhaden compete with ctenophores for food, and could affect the population

Table 6. Similarities and major differences in the assumptions made in Durbin and Durbin (1998) and this study.

Similarities	Major Differences
Time period studied = May to November	Durbin and Durbin assume constant temperature of 20°C
Assume juveniles feed mainly on phytoplankton	Durbin and Durbin assume greater dependence on zooplankton for food by adults (70% of diet)
Population size and catch estimates from Ahrenholz et al. (1987)	Durbin and Durbin assume $F_{ann} = 0.527$ for all age-classes

of the comb jellies. In terms of nutrient transport, Durbin and Durbin (1998) conclude that menhaden could be responsible for 4.4% of the total input of N into the bay (through in-migration and natural mortality) and 3.3 - 6.2% of the export of nitrogen out of the bay (through out-migration and fishing mortality). They point out that export could be somewhat higher since some natural mortality is due to predation and predators leave the bay in the fall.

Thus, the results of the model I have presented, which indicate that Atlantic menhaden aged 0-3 most likely consume approximately 30-40% of the primary production in Chesapeake Bay should be viewed as a gross estimate. This figure must be moderated by the effect of N excretion and natural mortality.

3.0 Net Export of Nitrogen

Although the calculation of net export of nitrogen was not a component of my models of age-0 and age 1-3 menhaden, it is simple enough to calculate a rough estimate of this value. The calculation of the net export of nitrogen by a moderately-sized population of Atlantic menhaden ages 0-3 (total initial number of fish = 8.03×10^9) in Chesapeake Bay is as follows.

3.1 Nitrogen Export in Catch Biomass

The total nitrogen exported in the biomass of fish that are removed from the population by the fishing industry is calculated as follows:

$$\text{N in biomass landed} = \text{biomass landed} * \text{N content in menhaden}$$

The biomass landed was $5.36 * 10^6$ kg age-0 plus $3.00 * 10^8$ kg age 1-3 for a total of $3.05 * 10^8$ kg. Durbin and Durbin (1998) report that the N content in Atlantic menhaden is 0.0803 by dry weight with a wet weight to dry weight ratio of 0.334.

Thus,

$$\text{N in biomass landed} = 3.05 * 10^8 \text{ kg} * (0.334 * 0.0803) = \underline{8.2 * 10^6 \text{ kg}}$$

3.2 Nitrogen Export in Out-Migration

The total nitrogen exported in the biomass of fish that leave the estuary in the fall is calculated as follows:

$$\text{N in biomass out-migrating} = \text{biomass remaining} * \text{N content in menhaden}$$

The biomass remaining in the population at the end of the season was $8.26 * 10^7$ kg age-0 plus $8.14 * 10^8$ kg age 1-3 for a total of $8.97 * 10^8$ kg. Thus,

$$\text{N in biomass out-migrating} = 8.97 * 10^8 \text{ kg} * (0.334 * 0.0803) = \underline{2.48 * 10^7 \text{ kg}}$$

3.3 Nitrogen Import through In-Migration

The total nitrogen introduced to the system through in-migration of menhaden is calculated as follows:

$$\text{N in biomass in-migrating} = \text{initial biomass} * \text{N content of menhaden}$$

The initial biomass was $2.1 * 10^6$ kg age-0 plus $7.9 * 10^8$ kg age 1-3 for a total of $7.92 * 10^8$ kg. Thus,

$$\text{N imported in in-migration} = 7.92 * 10^8 \text{ kg} * (0.334 * 0.0803) = \underline{2.12 * 10^7 \text{ kg}}$$

3.4 Nitrogen Imported through Natural Fish Mortality

The total nitrogen introduced to the system through natural fish mortality is calculated as follows:

$$\text{N in dead fish} = \text{dead fish biomass} * \text{N content of menhaden}$$

The total biomass of dead fish was $3.0 * 10^7$ kg age-0 plus $3.3 * 10^8$ kg age 1-3 for a total of $3.6 * 10^8$ kg. Thus,

$$\text{N in dead fish} = 3.6 * 10^8 \text{ kg} * (0.334 * 0.0803) = \underline{9.7 * 10^6 \text{ kg}}$$

3.5 Net Nitrogen Export

The above analysis gives a rough idea of the magnitude of nutrient import and export via menhaden migration, metabolism, growth and capture. The total import term

is $3.03 * 10^7$ kg N. The total export term is $3.3 * 10^7$ kg. The sum of the above import and export calculations indicates that there is a net export of $2.7 * 10^6$ kg N.

The nutrient reduction goal in the Chesapeake Bay region is to lower the load of Point Source and controllable Nonpoint Source total to $112.793 * 10^6$ lbs yr⁻¹ ($5.12 * 10^7$ kg yr⁻¹) (Chesapeake Executive Council, 1988). The net export of N by a moderately sized menhaden population thus represents about 5.3% of the reduction goal. It is clear that menhaden are a significant player in the nutrient dynamics in Chesapeake Bay, though the trophic-level effects are spatially heterogeneous due to menhaden's schooling patterns, particularly the juveniles (Friedland et al., 1996).

4.0 Estimation of the Migration Term

Nutrient budgets of large systems like the Chesapeake Bay often exclude a term for the losses associated with out-migration of species such as menhaden and other species. It is possible to estimate a migration term for Atlantic menhaden in Chesapeake Bay from the results of my simulation models. The N lost due to migration of Atlantic menhaden is calculated according to the following equation:

$$\text{N lost to migration} = \text{N in biomass out-migrating} - \text{N in biomass in-migrating}$$

The calculation of the N lost to migration for a moderately-sized population of Atlantic menhaden ages 0-3 (total initial number of fish = $8.03 * 10^9$) in Chesapeake Bay is as follows.

4.1 Nitrogen in Biomass Out-Migrating

The total nitrogen exported from the system by out-migration is calculated as follows:

N in biomass out-migrating = biomass at end of simulation * N content of menhaden

The total biomass of fish at the end of the simulation was $8.26 * 10^7$ kg age-0 plus $8.14 * 10^8$ kg age 1-3 for a total of $8.97 * 10^8$ kg. Thus,

$$\text{N in biomass out-migrating} = 8.97 * 10^8 \text{ kg} * (0.334 * 0.0803) = \underline{2.41 * 10^7 \text{ kg}}$$

4.2 Nitrogen in Biomass In-Migrating

The total nitrogen introduced to the system through in-migration is calculated as follows:

N in biomass in-migrating = biomass at start of simulation * N content of menhaden

The total biomass of in-migrating fish was $2.1 * 10^6$ kg age-0 plus $7.90 * 10^8$ kg age 1-3 for a total of $7.92 * 10^8$ kg. Thus,

$$\text{N in biomass in-migrating} = 7.92 * 10^8 \text{ kg} * (0.334 * 0.0803) = \underline{2.12 * 10^7 \text{ kg}}$$

4.3 Estimated Migration Term

The sum of the above values indicates that the N lost due to migration of menhaden ages 0-3 in Chesapeake Bay is $2.8 * 10^6$ kg N yr⁻¹. Boynton et al. (1995)

estimated the total export of N from Chesapeake Bay to be $152 * 10^6$ kg N yr⁻¹. Thus, the migration term estimated here represents approximately 1.8% of the total input of N to Chesapeake Bay annually (with age-0 menhaden responsible for 77% of the migration export value) .

A similar analysis can be performed on a moderate population size that is not fished. If this is done, the result is an estimated export of N due to migration of menhaden age 0-3 is $9.82 * 10^6$ kg N yr⁻¹. This represents approximately 6.5% of the total input of N to Chesapeake Bay, with age-0 exporting 23.6% of the migration export value). Eliminating fishing mortality for just the age-0 fish would result in an N export of $3.0 * 10^6$ kg N yr⁻¹ (2.0% of the total input of N, with age-0 representing 77% of the total migration export term).

A similar analysis can be performed on a low population size ($5.14 * 10^9$) that is fished and a high population size ($42.4 * 10^9$) that is not fished to determine a range of possible migration export terms. A low population size that is fished yields a migration export of $1.28 * 10^6$ kg N (0.84% of the total input, with age-0 exporting 84% of the migration export value). A high population size that is not fished yields a migration export of $39.3 * 10^6$ kg N (25.9% of the total input, with age-0 exporting 37% of the migration export value).

These analyses of the estimated migration term are summarized below:

	Low Pop	Medium Population			High Pop
	fished	fished	age-0 not fished	not fished	not fished
Export of N (10⁶ kg)	1.3	2.8	3.0	9.8	39
% of Total Input	0.8	1.8	2.0	6.5	26

A final note about the relative impact of Atlantic menhaden on nutrient budgets in Chesapeake Bay. Schools of Atlantic menhaden have been found to have significant local effects on oxygen and chl *a* levels due to the nitrogen content in their excreta (Oviatt et al., 1972). The results of the model presented in this thesis indicated that a medium population that is fished would excrete $4.34 * 10^7$ kg ammonia-N. While this is not an introduction of nutrients into the system, it is a significant redistribution in N-containing compounds, and is highly concentrated within the schools.

5.0 Marginal Economic Output

The economic output results of the model were expressed in terms of totals for the whole Chesapeake Bay population of menhaden. However, it is important to distinguish between total value and marginal value if an economic analysis is to be performed. Prices can be thought of as an individual's willingness to pay for an additional, or marginal, unit of a good or service (Goulder and Kennedy, 1997). The marginal amount of fishery output and consumption by fish is presented in Table 7a-c

Table 7a. Calculation of marginal output for a low population of age 0-3 Atlantic menhaden in Chesapeake Bay (total initial number of fish = $5.14 * 10^9$)

Criterion	<i>Total fish output (kg)</i>	<i>Marginal fish output (kg fish⁻¹)</i>	<i>Total Consumption (kg)</i>	<i>Marginal Consumption (kg fish⁻¹)</i>
Option				
<i>Normal Fishing</i>	$1.7649 * 10^8$	0.034	$6.36 * 10^8$	0.124
<i>No Fishing</i>	0	0	$7.073 * 10^8$	0.138

Table 7b. Calculation of marginal output for a medium population of age 0-3 Atlantic menhaden in Chesapeake Bay (total initial number of fish = $8.03 * 10^9$)

Criterion	<i>Total fish output (kg)</i>	<i>Marginal fish output (kg fish⁻¹)</i>	<i>Total Consumption (kg)</i>	<i>Marginal Consumption (kg fish⁻¹)</i>
Option				
<i>Normal Fishing</i>	$3.0536 * 10^8$	0.038	$10.5 * 10^8$	0.13
<i>No Fishing</i>	0	0	$11.9 * 10^8$	0.15

Table 7c. Calculation of marginal output for a high population of age 0-3 Atlantic menhaden in Chesapeake Bay (total initial number of fish = $42.4 * 10^9$)

Criterion	<i>Total fish output (kg)</i>	<i>Marginal fish output (kg fish⁻¹)</i>	<i>Total Consumption (kg)</i>	<i>Marginal Consumption (kg fish⁻¹)</i>
Option				
<i>Normal Fishing</i>	$11.5 * 10^8$	0.0272	$44.6 * 10^8$	0.105
<i>No Fishing</i>	0	0	$49.7 * 10^8$	0.117

for various population sizes and fishery regimes. The marginal fish output and consumption are highest for the moderately sized population of menhaden, but because this population size was determined based on actual landings statistics, I will use these amounts for the purposes of this discussion.

The most straightforward method of estimating the value of the menhaden fishery in terms of its traditional commodity value and ecological service is to assign prices to these attributes. As discussed in Chapter 1, a good estimate of the gross value of menhaden landings is $\$116 \text{ t}^{-1}$, or about $\$0.12 \text{ kg}^{-1}$ (Blomo, 1987). The value of menhaden's service in the consumption of nutrients via consumption of phytoplankton is assigned based on what it would cost to prevent the same amount of N to enter the Bay. This value, also discussed in Chapter 1, is estimated at $\$6.00 \text{ kg}^{-1}$ (Shulyer, 1995), and can be considered a cost avoidance. That is, if society were not to be responsible for reducing the amount of N that the population of menhaden consumes, then the cost of that nutrient reduction is avoided, and the money can be spent on other things, like habitat restoration, recreational fishing licenses, or recreational boats.

Given these dollar values, the value of the menhaden fishery, assuming a moderately sized population ($8.03 * 10^9$ fish aged 0-3) can be computed as follows. At a commercial fishery production rate of $0.038 \text{ kg fish}^{-1}$ (see Table 7b), and a phytoplankton consumption rate of $0.13 \text{ kg fish}^{-1}$ (see Table 7b) the value of an additional fish would be approximately $\$0.004 [0.038 \text{ kg fish}^{-1} * \$0.12 \text{ kg}^{-1}]$ plus $\$0.78 [0.13 \text{ kg fish}^{-1} * \$6.00 \text{ kg}^{-1}]$, for a total of $\$0.784$. In an intact population (one with no fishing mortality), the only value is the consumption component, at a rate of 0.15 kg

fish⁻¹, and thus a value of \$0.90 on the margin. Thus, the additional marginal value provided by an intact population is \$0.116. This brief analysis would seem to indicate that the fishing rate for menhaden could be reduced significantly, while actually increasing the marginal value of the fishery to society.

This analysis on the margin seems to contradict the conclusion one would draw from the total values determined from the model output, presented in Chapters 1 and 2. For a moderately sized population ($8.03 * 10^9$ fish aged 0-3) the total fishery output of 305,360 t yields a gross value of approximately \$35.4 million, and consumes about $3.2 * 10^6$ kg of phytoplankton at a value of \$19 million, for a total value of \$54.4 million. On the other hand, an intact menhaden population consumes about $3.6 * 10^6$ kg of phytoplankton at a value of \$21.5 million. There is no revenue to the fishery so the total value is \$21.5 million, less than half the value of a population that is fished at current levels.

It is important to point out that a traditional economic analysis does not end with the calculation of either marginal or total value of a good or service. The next step is to construct supply and demand functions which intersect at the price the market will bear for that good or service. From these functions, the consumer and producer surplus can be determined. These surpluses arise because individuals would be willing to buy or sell the first few units of a good or service for a higher or lower price, respectively, but since all units carry the same price, consumers and producers derive an excess of utility from those first few units (Norton et al., 1983). In addition, an assessment of the economic impact of the fishing industry on other sectors could be

performed to gain a clearer picture of the commercial value of menhaden. This type of study would require a great deal of data gathering through surveys and unpublished data sources (Norton et al., 1983). A full economic analysis such as this is beyond the scope of this thesis.

6.0 Contributory Value

Menhaden also have a “contributory value” as food for sport fish in Chesapeake Bay such as striped bass, bluefish and weakfish. Ulanowicz (1991) defines this value as the relative contribution that one unit of a medium (for example, the C provided by a food source such as Atlantic menhaden) entering a compartment (for example, the C content of a predator, such as striped bass) makes towards creating final products (for example, the C content of total landings of striped bass made by recreational fishermen in a year). The contributory value may be accounted by a single “reference medium,” or currency, such as C or N, and other reference media that flow together through a system may be estimated via scaling with the currency (using the Redfield ratio, for example).

Stomach content analyses of striped bass in Chesapeake Bay during January 1990 through March 1992 revealed that Atlantic menhaden constitute a significant proportion of the diets of these fish age-1-3-and-older during the fall and winter (Hartman and Brandt, 1995). The percent biomass of menhaden in the stomachs of age-1 striped bass ranged from about 20% in July and August to about 60% in

November and December. For age-2 striped bass, the proportion ranged from about 20% in July and August to nearly 100% in November and December. Dependency on menhaden as a food source seemed to increase in proportion and duration over the year with age, as revealed by stomach contents of age-3-and-older striped bass, which consisted of 10% menhaden in May and June to 100% in November-December. Stomach contents of striped bass age-2-and-younger included little or no menhaden during May and June.

As Ulanowicz (1991) points out, not all contributory sources to an output are equal in terms of the reference medium they provide, though the reference medium retains the same value, regardless of its source. Hartman and Brandt's (1995) study revealed that Chesapeake Bay piscivores rely on two trophically distinct food sources, benthic and pelagic, depending on age and time of year. They determined that the pelagic food sources, particularly Atlantic menhaden, contributed most to the production of piscivores by providing energy that supported growth after mid-July. They conclude that, "Atlantic menhaden are likely of considerable importance to annual production of striped bass and bluefish because much of the annual growth of these predators occurs when menhaden dominate the diets" (Hartman and Brandt, 1995, p. 530). Furthermore, they speculate that pelagic food sources, such as Atlantic menhaden, may have become more important for piscivores since the collapse of the oyster (*Crassostrea virginica*) population and destruction of the submerged aquatic vegetation in Chesapeake Bay.

The striped bass fishery, which is supported by the existence of Atlantic menhaden as a food source, is of great value along the entire Atlantic coast. Although the most recent study of the economic value of this species was conducted during 1979-1980 (Norton et al., 1983), the recent political battle to institute a fishing moratorium and the research effort spent over the last decade to restore the fishery are testaments to its continued importance.

Preliminary analyses of the striped bass population in Chesapeake Bay during the summer of 1998 indicate that the predators have not been able to use Atlantic menhaden as a primary food source this year. As a result, many striped bass are in poor nutritional condition, and there is serious concern that the striped bass population may be threatened by this situation (Personal Communication, Jim Price, Chesapeake Bay Acid Rain Foundation, Easton, MD).

7.0 Conclusion and Future Work

If the above analyses do not lead to a definitive solution to the problem of managing the Atlantic menhaden fishery, they at least make clear the importance of the species in the trophic structure of the Chesapeake Bay. Developing a fishery management plan is never a simple task, but one which must balance the interests of commercial and recreational users with ecological factors. While it may seem simpler to use a traditional fishery population analysis as the sole biological factor, this

approach is flawed (as seen by recent crashes in major fisheries) and may work counter to other efforts to improve environmental quality in the species' habitat.

The uncertainty in my analyses result from two missing elements: an accepted index of ecological importance of a species in a system, and imperfect information about the menhaden population in Chesapeake Bay. Boynton et al. (1995) state that, "It is frustrating to find that one of the prime reasons for initiating the expensive and difficult task of rehabilitating eutrophicated systems is also the least certain in terms of these evaluations [of nutrient budgets]" (p. 302). It is vitally important that standard measures be developed to determine the status and role of a species in its environment. This will help to focus efforts in ecological restoration on the factors with the greatest impact. It is also essential that studies of fish populations be conducted on a finer scale than is currently done. Fishery management plans and ecological studies that assume a homogeneous distribution of a species are inaccurate and inadequate.

Fishery management in the Chesapeake Bay historically has been more crisis management than anything else. Managers waited too long in the oyster fishery, with the result that this once plentiful resource has dwindled to practically non-existent. The species had been economically, culturally and ecologically integral to the Chesapeake Bay, and warnings about mismanagement have been voiced for over a hundred years. Efforts to restore the native species have given way to discussion of introducing a new species entirely (Gottlieb and Schweighofer, 1996). It took a complete moratorium in the striped bass fishery to achieve recovery of this predatory

species. The Chesapeake Bay blue crab fishery is a gamble that now concerns fishermen every season.

There is no reason to believe that an economy based on natural resources is out of reach. Sustainable use of the resource base is the key, and this approach will require better information and more thorough analyses. I have attempted to move in this direction by considering Atlantic menhaden in a way that is often overlooked. It is my hope that this study will be used as a part of a sustainable fishery management plan for menhaden and as an example for other commercially and ecologically important species.

APPENDIX A: Stella model structure and equations for age-0 Atlantic menhaden as described in Chapter II.

Bioenergetics constants

ac = 1.294 {g/g/d Intercept of Cmax}
activity_const = 1.5 {activity multiplier}
ar = 0.003 {g O2/g/d, Intercept of maximum respiration}
bc = -0.42 {slope of C max}
br = -0.05 {slope of maximum respiration}
CK1 = 0.1 {proportion of Cmax at CTO, CTM}
CK4 = 0.01 {proportion of Cmax at CTL}
CTL = 30.1 {degrees Celsius, Temperature for CK4}
CTM = 29.0 {degrees Celsius, temp. for CK3}
CTO = 28.0 {degrees Celsius, Temperature for CK2}
FA = 0.14 {proportion of food consumed egested}
P_value = If TIME<11 then 0.074 else
if TIME<19 then 0.078 else
if TIME<36 then 0.076 else
if TIME<46 then 0.085 else
if TIME<60 then 0.082 else
if TIME<103 then 0.062 else
0.05
Qc = 6 {water temperature dependence coefficient}
Qr = 2.5 {slope of temperature dependence}
RTM = 36.0 {Degrees Celsius, maximum temperature for respiration}
RTO = 33.0 {Degrees Celsius, optimum temperature for respiration}
SDA = 0.10 {Specific Dynamic Action coefficient}
Temp_Function = 11 - (0.417*(TIME+150)) + (0.00624*(TIME+150)^2) -
(0.0000245*(TIME+150)^3) + (0.0000000285*(TIME+150)^4) +
RANDOM(-0.5,0.5,5)
UA = 0.10 {Proportion of food assimilated excreted}
FB_specific_cons = GRAPH(TIME)
(0.00, 0.073), (13.3, 0.076), (26.6, 0.065), (39.9, 0.055), (53.2, 0.049), (66.5, 0.041),
(79.8, 0.038), (93.1, 0.035), (106, 0.03), (120, 0.027), (133, 0.023)
FB_specific_growth = GRAPH(TIME)
(0.00, 0.075), (13.3, 0.07), (26.6, 0.051), (39.9, 0.039), (53.2, 0.0325), (66.5, 0.025),
(79.8, 0.022), (93.1, 0.019), (106, 0.0163), (120, 0.0139), (133, 0.014)
Growth_Data = GRAPH(TIME)
(0.00, 0.9), (11.1, 1.35), (22.2, 2.22), (33.3, 4.63), (44.3, 5.68), (55.4, 8.20), (66.5,
11.6), (77.6, 14.8), (88.7, 16.8), (99.7, 18.2), (111, 20.1), (122, 23.4), (133, 28.8)

Bioenergetics equations

$C_{max} = a_c * \text{EXP}(b_c * \text{LOGN}(\text{Growth_Data})) \text{ \{g/g/d\}}$
 $fT_{cons} = K_a * K_b$
 $fT_{resp} = \text{EXP}(X * \text{LOGN}(V)) * \text{EXP}(X * (1-V))$
 $G1 = (1/(CTO-Q_c)) * \text{LOGN}((0.98*(1-CK1)) / (CK1*0.02))$
 $G2 = (1/(CTL-CTM)) * \text{LOGN}((0.98*(1-CK4)) / (CK4*0.02))$
 $K_a = (CK1*L1) / (1+CK1 * (L1-1))$
 $K_b = (CK4*L2) / (1+CK4*(L2-1))$
 $L1 = \text{EXP}(G1 * (\text{Temp_Function}-Q_c))$
 $L2 = \text{EXP}(G2*(CTL-\text{Temp_Function}))$
 $V = (RTM-\text{Temp_Function}) / (RTM-RTO)$
 $W = Z*(RTM-RTO)$
 $X = (W^2 * (1+(1+(40/Y))^0.5)^2)/400$
 $Y = \text{LOGN}(Q_r) * (RTM-RTO + 2)$
 $Z = \text{LOGN}(Q_r)$

Fish Pop Sector

$\text{Fish_Catch_No}(t) = \text{Fish_Catch_No}(t - dt) + (\text{Fishing_Mortality_daily}) * dt$

INIT Fish_Catch_No = 0

Fishing_Mortality_daily = If TIME < open_season THEN (Number_of_Fish*0)
ELSE (Number_of_Fish*(-1*(LOGN(1-Fmort)/365)))

Number_of_Fish(t) = Number_of_Fish(t - dt) + (- Natural_Mortality -
Fishing_Mortality_daily) * dt

INIT Number_of_Fish = Initial_Number

Natural_Mortality = Number_of_Fish*(-1*(LOGN(1-Mmort)/365))

Fishing_Mortality_daily = If TIME < open_season THEN (Number_of_Fish*0)
ELSE (Number_of_Fish*(-1*(LOGN(1-Fmort)/365)))

Pop_consumption_kg(t) = Pop_consumption_kg(t - dt) + (Pop_cons_rate) * dt

INIT Pop_consumption_kg = 0

Pop_cons_rate = Number_of_Fish*individual_consumption/1000 {kg}

Catch_biomass_tons = (Fish_Catch_No*Growth_g)/1000000 {tons}

Fmort = 0.13

Gross_Value_of_Catch = (Price {\$/t} * Catch_biomass_tons) {\$}

Initial_Number = 1.5*10⁹

Mmort = 0.45

open_season = 0

Pop_biomass_kg = Number_of_Fish*Growth_g/1000 {kg}

Price = 116{\$/metric ton}

Menhaden Bioenergetics Sector

$$\text{Activity}(t) = \text{Activity}(t - dt) + (\text{activity_eq}) * dt$$

$$\text{INIT Activity} = \text{activity_eq}$$

$$\text{activity_eq} = \text{SDA} * (\text{C} - \text{F}) \text{ \{g/g/d\}}$$

$$\text{Consumption_g}(t) = \text{Consumption_g}(t - dt) + (\text{individual_consumption}) * dt$$

$$\text{INIT Consumption_g} = \text{individual_consumption}$$

$$\text{individual_consumption} = \text{consumption_eq}$$

$$\text{Egestion_g}(t) = \text{Egestion_g}(t - dt) + (\text{egest_eq}) * dt$$

$$\text{INIT Egestion_g} = \text{egest_eq}$$

$$\text{egest_eq} = \text{Growth_g} * (\text{FA} * \text{C}) \text{ \{g waste/d\}}$$

$$\text{Excretion_g}(t) = \text{Excretion_g}(t - dt) + (\text{excretion_eq}) * dt$$

$$\text{INIT Excretion_g} = \text{excretion_eq}$$

$$\text{excretion_eq} = \text{Growth_g} * (\text{UA} * (\text{C} - \text{F})) \text{ \{g waste/d\}}$$

$$\text{Growth_g}(t) = \text{Growth_g}(t - dt) + (\text{consumption_eq} - \text{resp_eq} - \text{activity_eq} - \text{egest_eq} - \text{excretion_eq}) * dt$$

$$\text{INIT Growth_g} = 0.7$$

$$\text{consumption_eq} = \text{Growth_g} * (\text{Cmax} * \text{P_value} * \text{fT_cons}) \text{ \{g/d\}}$$

$$\text{resp_eq} = \text{Growth_g} * ((\text{ar} * \text{Growth_g}^{\text{br}}) * \text{fT_resp} * \text{activity_const}) \text{ \{g/d\}}$$

$$\text{activity_eq} = \text{SDA} * (\text{C} - \text{F}) \text{ \{g/g/d\}}$$

$$\text{egest_eq} = \text{Growth_g} * (\text{FA} * \text{C}) \text{ \{g waste/d\}}$$

$$\text{excretion_eq} = \text{Growth_g} * (\text{UA} * (\text{C} - \text{F})) \text{ \{g waste/d\}}$$

$$\text{Respiration_g}(t) = \text{Respiration_g}(t - dt) + (\text{resp_eq}) * dt$$

$$\text{INIT Respiration_g} = \text{resp_eq}$$

$$\text{resp_eq} = \text{Growth_g} * ((\text{ar} * \text{Growth_g}^{\text{br}}) * \text{fT_resp} * \text{activity_const}) \text{ \{g/d\}}$$

$$\text{C} = \text{consumption_eq} / \text{Growth_g}$$

$$\text{F} = \text{egest_eq}$$

Miscellaneous Calculations

$$\text{Growth_SS_error}(t) = \text{Growth_SS_error}(t - dt) + (\text{Growth_Sq_error}) * dt$$

$$\text{INIT Growth_SS_error} = 0$$

$$\text{Growth_Sq_error} = (\text{Growth_g} - \text{Wt})^2$$

$$\text{Average_error} = \text{Growth_SS_error}/183$$

$$\text{specific_cons} = \text{consumption_eq}/\text{Growth_g}$$

$$\text{specific_growth} =$$

$$(\text{consumption_eq} - (\text{activity_eq} + \text{egest_eq} + \text{excretion_eq} + \text{resp_eq}))/\text{Growth_g}$$

N-Phytoplankton Sector

$$\$_{\text{Value of Removal of N by Menhaden}}(t) =$$

$$\$_{\text{Value of Removal of N by Menhaden}}(t - dt) + (\text{N_to_}\$) * dt$$

$$\text{INIT } \$_{\text{Value of Removal of N by Menhaden}} = 0 \{ \$ \}$$

$$\text{N_to_}\$ = \$_{\text{per Kg N}} * \text{phyto_to_N} \{ \text{kg N} \}$$

$$\text{C_Removed_by_Menhaden_kg}(t) = \text{C_Removed_by_Menhaden_kg}(t - dt) + (\text{phyto_to_C}) * dt$$

$$\text{INIT C_Removed_by_Menhaden_kg} = 0$$

$$\text{phyto_to_C} = \text{Pop_cons_rate} * \text{C_Conversion} \{ \text{kg C/d} \}$$

$$\text{N_Removed_by_Menhaden_kg}(t) = \text{N_Removed_by_Menhaden_kg}(t - dt) + (\text{phyto_to_N}) * dt$$

$$\text{INIT N_Removed_by_Menhaden_kg} = 0 \{ \text{kg N} \}$$

$$\text{phyto_to_N} = (\text{Pop_cons_rate} \{ \text{kg/d} \} * \text{N_Conversion} \{ \text{proportion N} \}) \{ \text{kg N} \}$$

$$\text{Phyto_Model_Run_Prod_Kg}(t) = \text{Phyto_Model_Run_Prod_Kg}(t - dt) + (\text{Phyto_Daily_Prod_Kg}) * dt$$

$$\text{INIT Phyto_Model_Run_Prod_Kg} = 1$$

$$\text{Phyto_Daily_Prod_Kg} = (\text{Prod_Rate_Daily} \{ \text{gC/m}^2/\text{d} \} * 8.52\text{e}+09 \{ \text{m}^2 \}) / 1000 \{ \text{kg C} \}$$

$$\text{Phyto_removal_kg}(t) = \text{Phyto_removal_kg}(t - dt) + (\text{Removal_rate}) * dt$$

$$\text{INIT Phyto_removal_kg} = 0$$

$$\text{Removal_rate} = \text{Pop_cons_rate} \{ \text{consumption kg} \}$$

$$\text{P_Removed_by_Menhaden_kg}(t) = \text{P_Removed_by_Menhaden_kg}(t - dt) + (\text{phyto_to_P}) * dt$$

$$\text{INIT P_Removed_by_Menhaden_kg} = 0$$

$$\text{phyto_to_P} = \text{Pop_cons_rate} \{ \text{kg/d} \} * \text{P_Conversion} \{ \text{kg P/d} \}$$

$\$_per_Kg_N = 6.00 \{ \$/kg \text{ N removed} \}$
 $annual_pp_kg = annual_pp_per_vol \{ gC/m^2/yr \} * bay_volume \{ m^2 \} / 1000 \{ g/kg \}$
 $annual_pp_per_vol = 82 \{ gC/m^2/yr \}$
 $bay_volume = 8.52e+09 \{ m^2 \text{ in Chesapeake Bay} \}$
 $C_Conversion = 0.0185 \{ \text{proportion of C in phytoplankton by (wet) wt} \}$
 $N_Conversion = 0.003 \{ \%N \text{ in phytoplankton by (wet) weight} \}$
 $percent_annual_phyto_removed = (Phyto_removal_kg/annual_pp_kg)*100$
 $percent_model_run_phyto_removed =$
 $(Phyto_removal_kg/Phyto_Model_Run_Prod_Kg)*100$
 $Prod_Rate_Daily = 2.75 \{ gC/m^2/d \}$
 $P_Conversion = 0.0002 \{ \text{proportion of P in phytoplankton by (wet) wt} \}$
 $K = 0.0064$
 $Linf = 215.96$
 $Lt = Linf * (1 - EXP (-K * (TIME-t0))) \{ \text{length, mm} \}$
 $t0 = -33.21$
 $Wt = 7.1e-06 * (Lt^{3.07})$

APPENDIX B: Stella model structure and equations for age 1-3 Atlantic menhaden as described in Chapter III.

Bioenergetics Constants

ac[Cohorts] = 1.294 {g/g/d Intercept of Cmax}
activity_const[Cohorts] = 1.5 {activity multiplier}
ar[Age_1] = 0.00294 {g O2/g/d, Intercept of maximum respiration}
ar[Age_2] = 0.0027 {g O2/g/d, Intercept of maximum respiration}
ar[Age_3] = 0.003 {g O2/g/d, Intercept of maximum respiration}
bc[Age_1] = -0.421 {slope of C max}
bc[Age_2] = -0.425 {slope of C max}
bc[Age_3] = If Time < 68 then -0.42
else -0.425 {slope of C max}
br[Age_1] = -0.0085 {slope of maximum respiration}
br[Age_2] = -0.01 {slope of maximum respiration}
br[Age_3] = -0.01 {slope of maximum respiration}
CK1[Cohorts] = 0.1 {proportion of Cmax at CTO, CTM}
CK4[Cohorts] = 0.01 {proportion of Cmax at CTL}
CTL[Cohorts] = 30.1 {degrees Celsius, Temperature for CK4}
CTM[Cohorts] = 29.0 {degrees Celsius, temp. for CK3}
CTO[Cohorts] = 28.0 {degrees Celsius, Temperature for CK2}
FA[Cohorts] = 0.14 {proportion of food consumed egested}
Fit_Data[Cohorts] = TIME
Growth_Data[Cohorts] = TIME
NMFS_Data[Cohorts] = TIME
P_value[Age_1] = 0.0413
P_value[Age_2] = If TIME < 68 then 0.059 else
0.071
P_value[Age_3] = If TIME < 31 then 0.042 else
0.051
Qc[Age_1] = 6.5 {water temperature dependence coefficient}
Qc[Age_2] = 5.2 {water temperature dependence coefficient}
Qc[Age_3] = 6 {water temperature dependence coefficient}
Qr[Cohorts] = 2.5 {slope of temperature dependence}
RTM[Cohorts] = 36.0 {Degrees Celsius, maximum temperature for respiration}
RTO[Cohorts] = 33.0 {Degrees Celsius, optimum temperature for respiration}
SDA[Cohorts] = 0.10 {Specific Dynamic Action coefficient}
Temp_Function = 11 - (0.417*(TIME+150)) + (0.00624*(TIME+150)^2) -
(0.0000245*(TIME+150)^3) + (0.0000000285*(TIME+150)^4) +
RANDOM(-0.5,0.5,5)
UA[Cohorts] = 0.10 {Proportion of food assimilated excreted}
FB_specific_cons = GRAPH(TIME)
(0.00, 0.073), (13.3, 0.076), (26.6, 0.065), (39.9, 0.055), (53.2, 0.049), (66.5, 0.041),
(79.8, 0.038), (93.1, 0.035), (106, 0.03), (120, 0.027), (133, 0.023)
FB_specific_growth = GRAPH(TIME)

(0.00, 0.075), (13.3, 0.07), (26.6, 0.051), (39.9, 0.039), (53.2, 0.0325), (66.5, 0.025),
 (79.8, 0.022), (93.1, 0.019), (106, 0.0163), (120, 0.0139), (133, 0.014)

Fit_Data[Cohorts] = TIME

Growth_Data[Cohorts] = TIME

NMFS_Data[Cohorts] = TIME

Bioenergetics Equations

$C_{max}[Cohorts] = ac[Cohorts] * EXP(bc[Cohorts] * LOGN(Growth_Data[Cohorts]))$
 {g/g/d}

$fT_{cons}[Cohorts] = Ka[Cohorts] * Kb[Cohorts]$

$fT_{resp}[Cohorts] = EXP(X[Cohorts] * LOGN(V[Cohorts])) * EXP(X[Cohorts] * (1 - V[Cohorts]))$

$G1[Cohorts] = (1 / (CTO[Cohorts] - Qc[Cohorts])) * LOGN((0.98 * (1 - CK1[Cohorts])) / (CK1[Cohorts] * 0.02))$

$G2[Cohorts] = (1 / (CTL[Cohorts] - CTM[Cohorts])) * LOGN((0.98 * (1 - CK4[Cohorts])) / (CK4[Cohorts] * 0.02))$

$Ka[Cohorts] = (CK1[Cohorts] * L1[Cohorts]) / (1 + CK1[Cohorts] * (L1[Cohorts] - 1))$

$Kb[Cohorts] = (CK4[Cohorts] * L2[Cohorts]) / (1 + CK4[Cohorts] * (L2[Cohorts] - 1))$

$L1[Cohorts] = EXP(G1[Cohorts] * (Temp_Function - Qc[Cohorts]))$

$L2[Cohorts] = EXP(G2[Cohorts] * (CTL[Cohorts] - Temp_Function))$

$V[Cohorts] = (RTM[Cohorts] - Temp_Function) / (RTM[Cohorts] - RTO[Cohorts])$

$W[Cohorts] = Z[Cohorts] * (RTM[Cohorts] - RTO[Cohorts])$

$X[Cohorts] = (W[Cohorts]^2 * (1 + (1 + (40/Y[Cohorts]))^0.5)^2) / 400$

$Y[Cohorts] = LOGN(Qr[Cohorts]) * (RTM[Cohorts] - RTO[Cohorts] + 2)$

$Z[Cohorts] = LOGN(Qr[Cohorts])$

Fish Pop Sector

$Fish_Catch_#[Cohorts](t) = Fish_Catch_#[Cohorts](t - dt) + (Fishing_Mortality_daily[Cohorts]) * dt$

INIT Fish_Catch_#[Cohorts] = 0

Fishing_Mortality_daily[Cohorts] = If TIME < open_season THEN
 (Number_of_Fish[Cohorts] * 0)

ELSE (Number_of_Fish[Cohorts] * (-1 * (LOGN(1 - Fmort[Cohorts]) / 365)))

Number_of_Fish[Cohorts](t) = Number_of_Fish[Cohorts](t - dt) + (-
 Natural_Mortality[Cohorts] - Fishing_Mortality_daily[Cohorts]) * dt

INIT Number_of_Fish[Cohorts] = Initial_Number[Cohorts]

Natural_Mortality[Cohorts] =

Number_of_Fish[Cohorts] * (-1 * (LOGN(1 - Mmort[Cohorts]) / 365))

```

Fishing_Mortality_daily[Cohorts] = If TIME<open_season THEN
(Number_of_Fish[Cohorts]*0)
ELSE (Number_of_Fish[Cohorts]*(-1*(LOGN(1-Fmort[Cohorts])/365)))
Pop_consumption_kg[Cohorts](t) = Pop_consumption_kg[Cohorts](t - dt) +
(Pop_cons_rate[Cohorts]) * dt

INIT Pop_consumption_kg[Cohorts] = 0
Pop_cons_rate[Cohorts] =
Number_of_Fish[Cohorts]*individual_consumption[Cohorts]/1000 {kg}
Catch_biomass_t[Cohorts] = (Fish_Catch_#[Cohorts]*Growth_g[Cohorts])/1000000
{tons}
Catch_proportion[Age_1] = (Fish_Catch_#[Age_1]/(SUM_Fish_Catch_# + 0.001)
)*100 {%}
Catch_proportion[Age_2] = (Fish_Catch_#[Age_2]/(SUM_Fish_Catch_# + 0.001)
)*100 {%}
Catch_proportion[Age_3] = (Fish_Catch_#[Age_3]/(SUM_Fish_Catch_# + 0.001)
)*100 {%}
Fmort[Age_1] = 0.25
Fmort[Age_2] = 0.5
Fmort[Age_3] = 0.5
Gross_value_of_catch[Cohorts] = Price[Cohorts]{$/ton}
*Catch_biomass_t[Cohorts]{t}
Initial_Number[Age_1] = 2.2e+09
Initial_Number[Age_2] = 1.2e+09
Initial_Number[Age_3] = 2.4e+08
Initial_proportion[Cohorts] = (Initial_Number[Cohorts]/SUM_Initial_Number)*100
{%}
Mmort[Cohorts] = 0.45
open_season = 0
Pop_biomass_kg[Cohorts] = Number_of_Fish[Cohorts]*Growth_g[Cohorts]/1000
{kg}
Price[Cohorts] = 116{$/metric ton}
SUM_catch_biomass_t = ARRAYSUM(Catch_biomass_t[*]){tons}
SUM_Fish_Catch_# = ARRAYSUM(Fish_Catch_#[*])
SUM_Gross_value_of_catch = ARRAYSUM(Gross_value_of_catch[*])
SUM_Initial_Number = ARRAYSUM(Initial_Number[*])
SUM_number_of_fish = ARRAYSUM(Number_of_Fish[*])
SUM_pop_biomass = ARRAYSUM(Pop_biomass_kg[*])
SUM_pop_cons = ARRAYSUM(Pop_consumption_kg[*])
SUM_pop_cons_rate = ARRAYSUM(Pop_cons_rate[*])

```

Menhaden Bioenergetics Sector

$$\text{Activity}[\text{Cohorts}](t) = \text{Activity}[\text{Cohorts}](t - dt) + (\text{activity_eq}[\text{Cohorts}]) * dt$$

$$\text{INIT Activity}[\text{Cohorts}] = \text{activity_eq}[\text{Cohorts}]$$

$$\text{activity_eq}[\text{Cohorts}] = \text{SDA}[\text{Cohorts}] * (\text{C}[\text{Cohorts}] - \text{F}[\text{Cohorts}]) \{ \text{g/g/d} \}$$

$$\text{Consumption_g}[\text{Cohorts}](t) = \text{Consumption_g}[\text{Cohorts}](t - dt) + (\text{individual_consumption}[\text{Cohorts}]) * dt$$

$$\text{INIT Consumption_g}[\text{Cohorts}] = \text{individual_consumption}[\text{Cohorts}]$$

$$\text{individual_consumption}[\text{Cohorts}] = \text{consumption_eq}[\text{Cohorts}]$$

$$\text{Egestion_g}[\text{Cohorts}](t) = \text{Egestion_g}[\text{Cohorts}](t - dt) + (\text{egest_eq}[\text{Cohorts}]) * dt$$

$$\text{INIT Egestion_g}[\text{Cohorts}] = \text{egest_eq}[\text{Cohorts}]$$

$$\text{egest_eq}[\text{Cohorts}] = \text{Growth_g}[\text{Cohorts}] * (\text{FA}[\text{Cohorts}] * \text{C}[\text{Cohorts}]) \{ \text{g waste/d} \}$$

$$\text{Excretion_g}[\text{Cohorts}](t) = \text{Excretion_g}[\text{Cohorts}](t - dt) + (\text{excretion_eq}[\text{Cohorts}]) * dt$$

$$\text{INIT Excretion_g}[\text{Cohorts}] = \text{excretion_eq}[\text{Cohorts}]$$

$$\text{excretion_eq}[\text{Cohorts}] = \text{Growth_g}[\text{Cohorts}] * (\text{UA}[\text{Cohorts}] * (\text{C}[\text{Cohorts}] - \text{F}[\text{Cohorts}])) \{ \text{g waste/d} \}$$

$$\text{Growth_g}[\text{Age_1}](t) = \text{Growth_g}[\text{Age_1}](t - dt) + (\text{consumption_eq}[\text{Age_1}] - \text{resp_eq}[\text{Age_1}] - \text{activity_eq}[\text{Age_1}] - \text{egest_eq}[\text{Age_1}] - \text{excretion_eq}[\text{Age_1}]) * dt$$

$$\text{INIT Growth_g}[\text{Age_1}] = 98$$

$$\text{Growth_g}[\text{Age_2}](t) = \text{Growth_g}[\text{Age_2}](t - dt) + (\text{consumption_eq}[\text{Age_2}] - \text{resp_eq}[\text{Age_2}] - \text{activity_eq}[\text{Age_2}] - \text{egest_eq}[\text{Age_2}] - \text{excretion_eq}[\text{Age_2}]) * dt$$

$$\text{INIT Growth_g}[\text{Age_2}] = 170$$

$$\text{Growth_g}[\text{Age_3}](t) = \text{Growth_g}[\text{Age_3}](t - dt) + (\text{consumption_eq}[\text{Age_3}] - \text{resp_eq}[\text{Age_3}] - \text{activity_eq}[\text{Age_3}] - \text{egest_eq}[\text{Age_3}] - \text{excretion_eq}[\text{Age_3}]) * dt$$

$$\text{INIT Growth_g}[\text{Age_3}] = 284.3$$

$$\text{consumption_eq}[\text{Cohorts}] =$$

$$\text{Growth_g}[\text{Cohorts}] * (\text{Cmax}[\text{Cohorts}] * \text{P_value}[\text{Cohorts}] * \text{fT_cons}[\text{Cohorts}]) \{ \text{g/d} \}$$

$$\text{resp_eq}[\text{Cohorts}] =$$

$$\text{Growth_g}[\text{Cohorts}] * ((\text{ar}[\text{Cohorts}] * \text{Growth_g}[\text{Cohorts}]^{\text{br}[\text{Cohorts}]) *$$

$$\text{fT_resp}[\text{Cohorts}] * \text{activity_const}[\text{Cohorts}]) \{ \text{g/d} \}$$

$$\text{activity_eq}[\text{Cohorts}] = \text{SDA}[\text{Cohorts}] * (\text{C}[\text{Cohorts}] - \text{F}[\text{Cohorts}]) \{ \text{g/g/d} \}$$

$$\text{egest_eq}[\text{Cohorts}] = \text{Growth_g}[\text{Cohorts}] * (\text{FA}[\text{Cohorts}] * \text{C}[\text{Cohorts}]) \{ \text{g waste/d} \}$$

$$\text{excretion_eq}[\text{Cohorts}] = \text{Growth_g}[\text{Cohorts}] * (\text{UA}[\text{Cohorts}] * (\text{C}[\text{Cohorts}] - \text{F}[\text{Cohorts}])) \{ \text{g waste/d} \}$$

$$\text{Respiration_g}[\text{Cohorts}](t) = \text{Respiration_g}[\text{Cohorts}](t - dt) + (\text{resp_eq}[\text{Cohorts}]) * dt$$

INIT Respiration_g[Cohorts] = resp_eq[Cohorts]
 resp_eq[Cohorts] =
 Growth_g[Cohorts]*((ar[Cohorts]*Growth_g[Cohorts]^br[Cohorts]) *
 fT_resp[Cohorts] * activity_const[Cohorts]) {g/d}
 C[Cohorts] = consumption_eq[Cohorts]/Growth_g[Cohorts]
 F[Cohorts] = egest_eq[Cohorts]

Miscellaneous Calculations

Growth_SS_error[Cohorts](t) = Growth_SS_error[Cohorts](t - dt) +
 (Growth_Sq_error[Cohorts]) * dt

INIT Growth_SS_error[Cohorts] = 0
 Growth_Sq_error[Cohorts] = (Growth_g[Cohorts]-Fit_Data[Cohorts])^2
 Average_error[Cohorts] = Growth_SS_error[Cohorts]/154

N-Phytoplankton Sector

\$ _Value_of_Removal_of_N_by_Menhaden[Cohorts](t) =
 \$ _Value_of_Removal_of_N_by_Menhaden[Cohorts](t - dt) + (N_to_\$[Cohorts]) * dt

INIT \$ _Value_of_Removal_of_N_by_Menhaden[Cohorts] = 0 {\$}
 N_to_\$[Cohorts] = \$ _per_Kg_N*phyto_to_N[Cohorts] {kg N}
 C_Removed_by_Menhaden_kg[Cohorts](t) =
 C_Removed_by_Menhaden_kg[Cohorts](t - dt) + (phyto_to_C[Cohorts]) * dt

INIT C_Removed_by_Menhaden_kg[Cohorts] = 0
 phyto_to_C[Cohorts] = Pop_cons_rate[Cohorts] * C_Conversion {kg C/d}
 N_Removed_by_Menhaden_kg[Cohorts](t) =
 N_Removed_by_Menhaden_kg[Cohorts](t - dt) + (phyto_to_N[Cohorts]) * dt

INIT N_Removed_by_Menhaden_kg[Cohorts] = 0 {kg N}
 phyto_to_N[Cohorts] = (Pop_cons_rate[Cohorts]{kg/d}*N_Conversion{proportion
 N}) {kg N/d}
 Phyto_Model_Run_Prod_Kg(t) = Phyto_Model_Run_Prod_Kg(t - dt) +
 (Phyto_Daily_Prod_Kg) * dt

INIT Phyto_Model_Run_Prod_Kg = 1
 Phyto_Daily_Prod_Kg = (Prod_Rate {gC/m^2/d} * 8.52e+09{m^2})/1000 {kg C}
 Phyto_removal_kg[Cohorts](t) = Phyto_removal_kg[Cohorts](t - dt) +
 (Removal_rate[Cohorts]) * dt

```

INIT Phyto_removal_kg[Cohorts] = 0
Removal_rate[Cohorts] = Pop_cons_rate[Cohorts] {consumption kg}
P_Removed_by_Menhaden_kg[Cohorts](t) =
P_Removed_by_Menhaden_kg[Cohorts](t - dt) + (phyto_to_P[Cohorts]) * dt

INIT P_Removed_by_Menhaden_kg[Cohorts] = 0
phyto_to_P[Cohorts] = Pop_cons_rate[Cohorts] {kg/d} * P_Conversion {kg P/d}
$_per_Kg_N = 6.00 {$/kg N removed}
annual_pp_kg = annual_pp_per_vol {gC/m^2/yr} * bay_volume {m^2} / 1000 {g/kg}
annual_pp_per_vol = 82 {gC/m^2/yr}
bay_volume = 8.52e+09 {m^2 in Chesapeake Bay}
C_Conversion = 0.0185 {proportion of C in phytoplankton by (dry) wt}
N_Conversion = .003 {proportion of N in phytoplankton by (dry) weight}
percent_annual_phyto_removed[Cohorts] =
(Phyto_removal_kg[Cohorts]/annual_pp_kg)*100
percent_model_run_phyto_removed[Cohorts] =
(Phyto_removal_kg[Cohorts]/Phyto_Model_Run_Prod_Kg)*100
Prod_Rate = 1.37 {gC/m^2/d}
P_Conversion = 0.0002 {proportion of P in phytoplankton by (dry) wt}
SUM_$_value_removal_of_N =
ARRAYSUM($_Value_of_ReMOval_of_N_by_Menhaden[*])
SUM_%_annual_phyto_removed = ARRAYSUM(percent_annual_phyto_removed[*])
SUM_%_model_run_phyto_removed =
ARRAYSUM(percent_model_run_phyto_removed[*])
Sum_C_Removed = ARRAYSUM(C_Removed_by_Menhaden_kg[*])
SUM_N_Removed = ARRAYSUM(N_Removed_by_Menhaden_kg[*])
SUM_phyto_removal = ARRAYSUM(Phyto_removal_kg[*])
Sum_P_Removed = ARRAYSUM(P_Removed_by_Menhaden_kg[*])

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