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Developing a framework for the use of computable general equilibrium economic and ecological models for fisheries management in the Chesapeake Bay

Final Report to Maryland Sea Grant

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0. Introduction and Summary

For centuries the Chesapeake Bay as the largest estuary in the United States has provided its neighboring human populations with ecosystem services. When human populations were small and the Bay's ecosystems intact, the per capita services were abundant and may have appeared limitless. However, as populations grew and agriculture and industries expanded around the Bay, ecosystem health plummeted and per capita services were greatly diminished. Reversing this trend by restoring the Bay ecosystem's health would seem to be an obvious goal; however, the human activities that have caused diminished services are often the source of other benefits. Thus there are tradeoffs between ecosystem services from the Bay and other benefits that are not dependent on a healthy Bay ecosystem. For example, factory chicken farms in the region provide inexpensive protein for consumers; but also by discharging excessive nitrogen runoff, they reduce the amount of protein available from aquatic species in the Bay. Restoring the Chesapeake to protect aquatic species' protein may mean altering factory farming methods and increasing the cost of chicken protein.

Policymakers need to understand the tradeoffs between securing a healthy, productive Chesapeake Bay and engaging in other economic activities in the Chesapeake's watershed. But understanding the tradeoffs means understanding the complex interactions between the Bay's ecosystem services and the markets for goods produced in the Chesapeake Bay watershed. Moreover, understanding how ecosystem services are generated means understanding the complex interactions among the plant and animal species that comprise the Bay's biodiversity.

The below schematic illustrates the challenge of understanding how the ecosystem and the economy interact:
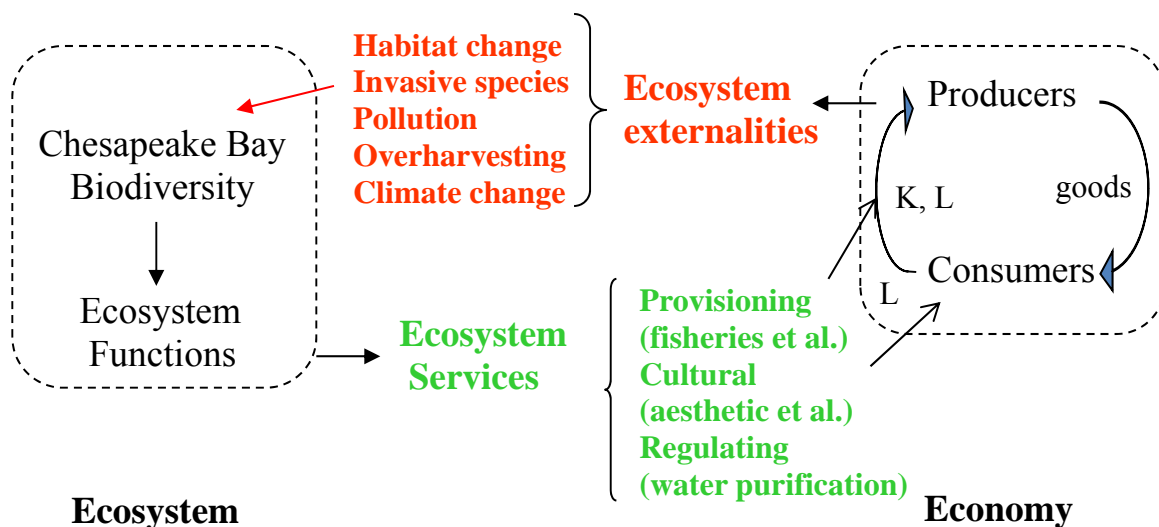
The schematic shows the economy-ecosystem interface which contains the basic trade-off that anthropogenic activity depends on ecosystem services but generates ecosystem externalities. On

the left, biodiversity underpins ecosystem functions from which flow values to humans that economists label direct use, indirect use, and existence (Goulder and Kennedy 1997). These values can be conveniently, if not neatly, divided into the Millennium Ecosystem Assessment's (MEA 2005) classification of ecosystem services: supporting (e.g., soil formation, nutrient cycling), regulating (e.g., climate regulation, water purification), provisioning (e.g., food, wood), and cultural (e.g., recreation, aesthetic). Three important services from the Bay are listed. The provisioning ecosystem services are inputs either into firms' production activities (e.g. commercial fishing) or into consumer activities directly (e.g. recreational fishing). The cultural services typically flow directly to consumers (e.g. swimming). The economic activities, both those dependent on the Bay and those that are not, generate ecosystem externalities, which are distinguished from traditional externalities because they involve internal adjustments within ecosystems (Crocker and Tschirhart 1992). In the schematic the ecosystem externalities are divided into the five main drivers of biodiversity loss (MEA); and biodiversity loss leads to diminished flows of services. To varying degrees all five externalities are germane for the Chesapeake and its watershed.

Either the ecosystem or economy by itself is a highly complex system made up of millions of individuals engaged in unaccountably many actions. Understanding either system alone is extremely difficult, understanding both systems and their interactions is daunting. There are numerous ecological studies of individual species such as oysters or striped bass that have yielded important insights into their life cycles and vulnerabilities to human activities. There are numerous economic studies of individual firms or industries, or individual groups of consumers that also have yielded important insights into production and consumption activities and into the prices and quantities observed in individual markets. These studies could be labeled partial equilibrium in that they examine a small portion of either system, and assume that that portion is isolated from the rest of its system.

The approach discussed herein is general equilibrium. That is, important economic variables that include consumer incomes, firm profits, and the prices and quantities of both consumer goods and the inputs needed to produce them, and important ecological variables that include species populations, individual animal predations, and individual plant biomasses are determined simultaneously. The variables are endogenous in the modeling. Ideally, a general equilibrium approach gives the policymaker the most complete picture of how a policy will change the ecosystem variables and biodiversity, and how it will change the prices and quantities throughout the economy, and ultimately how the policy will impact broad measures of societal wellbeing.

General equilibrium models in economics have a long history, and with the advent of computers, applied models referred to as computable general equilibrium (CGE) models have become commonplace. General equilibrium models in ecology are relatively new and one such a model is referred to as a general equilibrium ecosystem model (GEEM). However, general equilibrium models do not come without their own set of strong assumptions that are needed to determine the

variables. For examples, in a CGE model consumers and firms are assumed to be price takers; that is, they have no control over the prices they pay or charge. The markets are assumed to be perfectly competitive, production is usually assumed to exhibit constant returns to scale, and producers and consumers are assumed to have perfect information about prices and quantities. On the plus side, linearity is not assumed as it is in input-output models. A GEEM is also subject to simplifying assumptions that will be laid out in section I.

In spite of the simplifying assumptions, CGE models have been used to determine the impacts of tax changes, of international trade policies, of environmental regulations, et al.. A CGE model of the Chesapeake Bay watershed, coupled with a GEEM of the Bay, can potentially yield numerous insights into how alternative policies designed to restore the Bay ecosystem will enhance the ecosystem services delivered by the Bay, and how industries in the watershed that are not dependent on these ecosystem services will be affected.

Summary – The next section presents the Chesapeake Bay GEEM. The food web in it draws on previous work by Baird and Ulanowicz (1989) and upon NOAA's Chesapeake Bay Fisheries Ecosystem Model (Christensen, *et al.* 2009). The linkages in the food web highlight predator/prey and competitive ecological relationships across fifteen species, or collections of species, including the targeted species: blue crab, eastern oysters, striped bass, Atlantic Menhaden, and various alosines. Although our proposal was to outline the model and identify data sources, we instead went further and built a partially-working GEEM.

A very time intensive aspect of building GEEM is gathering the data for the species in the food web. Typically, this means consulting many journal or book sources for each species and the sources tend to be scattered throughout the literature. The result of the data gathering effort is shown in Table I.1. The data in the table are similar to a social accounting matrix used in CGE models. The explanations for the entries in each cell in the table are in Appendix A, and the references for the data are in Appendix B.

All the GEEM equations are completed for this food web and shown in Appendix C. The equations have been used to run simulations, the results of which are shown in Figures 2 and 3. The simulations show species densities over time following fixed fish harvests, and also show energy prices which are explained below. Numerous other results can be generated for any levels of harvests and for any combinations of species, now that the model is built. All simulations are run using Mathematica software. In other work GAMS has also been used to run GEEMs.

However, the GEEM is not fully operational. The dynamics perform well in the short run, but the in the long run the model fails to converge. This is consistent with our experience in building a GEEM; that is, small coding errors or unreasonable data can yield non convergence over longer time periods. We have found that a good procedure in "debugging" GEEM is to use Mathematica software, and then in combining GEEM with a CGE, to use GAMS software.

In section II, the outline of an economic CGE model is presented. The first consideration is the economic region to be modeled, which we assert should be the Bay watershed. Obviously, the entire watershed is within U.S. borders, although there are multiple states involved. But the U.S. states are highly integrated, have similar business cycles, and subject to similar fluctuations in employment and inflation. Different areas within the watershed may have different primary industries and this will increase the size of the model. But the important point is that all the economic regions contribute to the quality of the Chesapeake's ecosystem, and any environmental policy ideally will take account of all major pollution sources. One possible extension would be to run the combined GEEM-CGE with all or a portion of the states participating in clean up efforts to determine the costs of not succeeding in setting cross-state policies.

Ecosystem services are discussed followed by ecosystem externalities. We limited the discussion to the main services that include recreational and commercial fisheries and the water quality of the Bay. The fisheries services are then elaborated on by showing how they might be modeled. Recreational fishing is presented in some detail.

Section III provides more detail on the structure of a CGE. In the CGE, economic dynamics are recursive, consistent with the evolution of species populations. The time path of the economy is represented by a sequence of annual competitive equilibria, and the GEEM is represented by a sequence of general equilibriums over the species. (Note the latter does not imply steady state for the species. Equilibrium simply means all individual plants and animals are maximizing their net energies, and predator demands equal prey supplies of biomass. In fact, unless harvests are equal over time, steady states are unlikely.) Years are linked through factor accumulation in the economy, where regional investment expands the capital service endowment for the subsequent period, and the effective labor force grows at an exogenous rate.

Section III begins with the Social Accounting Matrix (SAM). It then goes into more detail on producers, consumers, trade, and the role of government. Finally, a brief description of societal welfare measures is provided.

The last section, IV, draws on a recent EPA report that studied alternative pollution control projects that are divided into gray and green where the former are conventional projects such as waste-water treatment plants, and the latter are projects that work directly with the ecosystems such as wetland restoration. Gray projects would be incorporated into the CGE, while green projects would also be incorporated into the CGE, but in addition be incorporated into GEEM. Basically, the EPA report uses a partial equilibrium framework to assess alternative projects, and expanding it to a general equilibrium framework in the CGE-GEEM may be very useful.

I. The Ecological Model

The ecology of the Bay is modeled using a General Equilibrium Ecosystem Model (GEEM). The starting point in GEEM is to choose a number of plant and animal species to be included in a food web, and assume that individuals within each species are identical. Both individual predator and prey animals within each species are postulated to behave as if they maximize net energy intake by optimally foraging. Individual plants are postulated to behave as if they maximize incoming net energy by optimally setting the amount of green biomass that is used to "forage" on the sun. Net energy gains are converted into reproduction (Fausch 1984, Hill and Grossman 1993). Individual plants compete among themselves for access to sunlight, and individual heterotrophs compete for food. Energy maximization for individual animals consists of trading off the benefits of energy gained from consumed biomass against the costs of energy lost to predators, to respiration, and to the energy expenditures for capturing prey. Maximization for individual plants trades off the benefits of energy gained from sunlight against the costs of energy lost to herbivores, to respiration, and to the energy expenditures for growing green biomass that is lost to competition with other plants for light. That is, plants grow biomass that shades other biomass in competitive environments, and the loss due to the competition is expressed as energy expenditure (Tschirhart 2002, Pethig and Tschirhart 2002, Finnoff and Tschirhart 2005). These expenditures are emergent properties determined by the collective behaviors of the entire populations of plants and animals. The energy expenditures are signals that the plants, herbivores and predators use to forage optimally, and that herbivores use to balance food intake with predation risk (Luttbeg and Schmitz 2000).

Time in GEEM is in increments of one year which is the length of a reproductive cycle for most species. This assumption could be modified without major effects on outcomes. Within each period all populations are constant and all plant and animal individuals optimally forage. A general equilibrium is defined as a state where all plants and animals are optimally foraging and the biomass demands of herbivores (predators) equal the biomass supplies of plants (prey). Yearly general equilibrium calculations yield the optimum plant biomasses, the optimum consumer consumptions, and the energy expenditures. These results are substituted into the individuals' net energy functions to yield optimum net energies for that year. The net energies then are used to update the populations of each group via reproduction prior to the next time period, when the general equilibrium calculations are repeated with the new populations. If, over time, the populations of every group stabilize, then a steady state is attained. At that point, further general equilibrium calculations produce no changes in populations. Thus, there are two equilibrium concepts in the model: the general equilibrium that is calculated within each period for fixed populations, and the population equilibrium or steady state that may or may not be attained over multiple periods.

In the remainder of section I, a Bay food web and its species are identified and used to demonstrate how a GEEM works, data for the GEEM is discussed, and extensions are suggested

for a complete model that could eventually be integrated with an economic model. The impact of some preliminary harvesting is also demonstrated.

I.a The Food Web

The food web used draws upon the work of Baird and Ulanowicz (1989) posted on the UMSG website (http://www.mdsg.umd.edu/issues/chesapeake/food_web/). In addition, for data we draw heavily upon NOAA's Chesapeake Bay Fisheries Ecosystem Model that employs Ecopath/Ecosim (Christensen, *et al.* 2009, CBFEM, http://chesapeakebay.noaa.gov/ecosystem-modeling/chesapeake-bay-fisheries-ecosystem-model). CBFEM uses biomass and population density estimates of 45 trophic groups in the Bay as they existed in 1950. Both the Ulanowicz and Baird and the CBFEM food webs contain benthic and pelagic species beginning with phytoplankton at the bottom and ending with striped bass and other predator fish at the top.
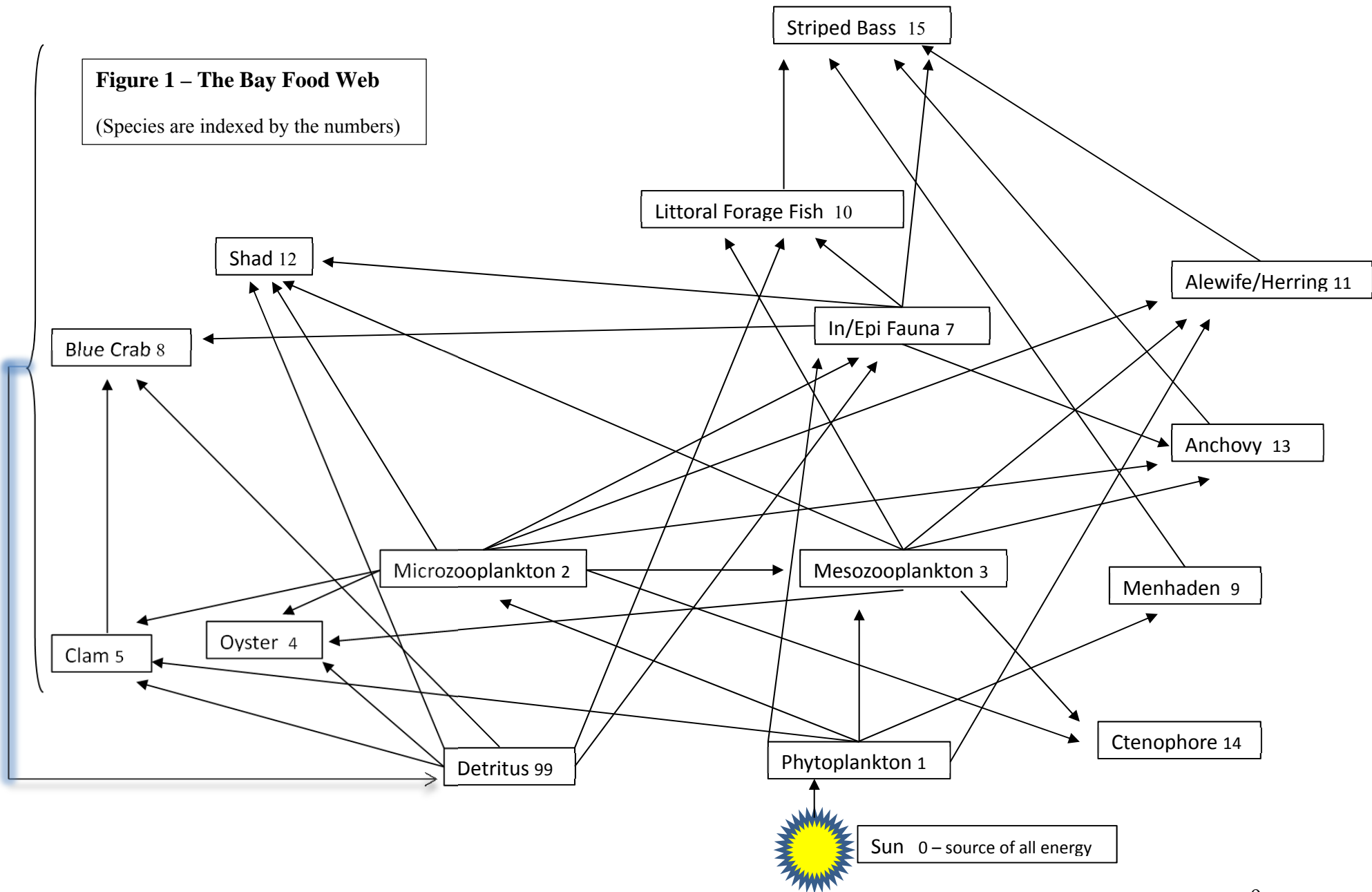
The GEEM web includes phytoplankton and zooplankton at the bottom as well as detritus, and also includes the five species of most interest: blue crab, eastern oysters, striped bass, Atlantic Menhaden, and various alosines that are divided into two components labeled alewife/herring and shad. Note that the compartments in the food web are in some cases a single species but in other cases a collection of species such as in the case of alewife/herring or in the case of mesozooplankton which is made up of various copepods.

The food web is shown in Fig. 1. The fifteen species in the food web, including detritus which for convenience is referred to as a species, were chosen based on several criteria. Phytoplankton are included since they are the base of the marine food web, and because they are plants we have a connection between incoming energy from the sun and all outgoing energy lost to respiration and detritus. Because GEEM models transfer of energy, phytoplankton is a key species as all energy enters the system via phytoplankton photosynthesis. Energy created by phytoplankton is then transferred to species higher in the food web through predation. Also, some ecosystem externalities, such as habitat losses can best be modeled as shocks to the ecosystem in the form of fewer phytoplankton available to the zooplankton, which makes for changes throughout the ecosystem.

Also included in the food web are the five species of most interest mentioned above. Beyond the five, other species were chosen based on energy flows and biomasses shown either in Ulanowicz and Baird or in CBFEM. That is, we tended to include species with a large presence in the Bay based on their total biomass. In this way we hope to capture more of the major ecological interactions among species. Although as discussed below, a GEEM that includes more species may be desirable.

Figure 1 – The Bay Food Web

(Species are indexed by the numbers)

Striped Bass 15

Littoral Forage Fish 10

Shad 12

Alewife/Herring 11

In/Epi Fauna 7

Blue Crab 8

Anchovy 13

Microzooplankton 2

Mesozooplankton 3

Menhaden 9

Oyster 4

Clam 5

Ctenophore 14

Detritus 99

Phytoplankton 1

Sun 0 – source of all energy

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	Variables			Non-calibrated Parameters				Calibrated Parameters			
	Populations N_i[a] (units km^{-2})	x_{ij} Biomass (plants: kg unit^{-1}) Biomass flow (animals: kg unit^{-1} y^{-1}) (% diet composition)		Energy content e_i kcal kg^{-1}	Light absorption e_{0i} kcal kg^{-1} y^{-1}	Resting Metabolic Rate b_i kcal unit^{-1} y^{-1}	Wet weight(w_i)/ age(s_i) kg unit^{-1}/ y	Predation		Plant congestion τ_i[br]	Var. resp. r_i[bs] (kcal y^{-1})
		PREY	x_{ij}					PREDATOR	d_{ij}[bq]		
PHYTOPLANKTON (1)	61.98[b] 1 unit = 1x10^{12} ind.	435.6[o]		1200[ad]	930440[an]	636565.8[aq]	435.6/ 0.219[bd]	MICROZOO	1688.06	0.269985	304.521
								MESOZOO	186.445		
								OYSTERS	28.3862		
								CLAMS	11.7478		
								IN/EPI FAUNA	103.085		
								MENHADEN	198.982		
								ALE/HERR	31.7693		
MICRO-ZOOPLANKTON (2)	2.4956[c] 1 unit = 1x10^{12} ind.	PHYTO.	875000 (100%)[p]	1740[ae]	NA[ao]	580064[ar]	2500/ 0.0329[be]	MESOZOO	265.492	NA	0.000660
								OYSTERS	1.57386		
								CLAMS	1.02129		
								IN/EPI	11.4247		
								ALE/HERR	4.14194		
								SHAD	0.11067		
								ANCHOVY	5.87284		
								CTENOPHORE	17.0893		
MESO-ZOOPLANKTON (3)	154.9423[d] 1 unit = 1x10^9 ind	PHYTO.	1555.6 (28%)[q]	1274[af]	NA[ao]	1181062[as]	66.67/ 0.137[bf]	LITTORAL	0.0721571	NA	0.142365
								ALE/HERR	0.837159		
								SHAD	1.38874		
		MICROZOO	4000 (72%)[q]					ANCHOVY	1.79759		
								CTENOPHORE	6.90804		
OYSTERS (4)	205.025[e] 1 unit = 1000 ind	MICROZOO	17.92 (9%)[r]	147[aj]	NA[ao]	54486[at]	99.5/15[bg]	NA		NA	3.02671
		PHYTO.	179.10 (90%)%[r]								
		DETRITUS	1.99 (1%)[r]								
CLAMS (5)	162.185[f] 1 unit = 1000 ind.	MICROZOO	14.7 (4.5%)[t]	354[aj]	NA[ao]	38924[au]	59.974/8[bh]	BLUE CRABS	2.59968	NA	5.9735
		PHYTO	93.7 (57.5%)[t]								
		DETRITUS	21.2[t] (13%)[t]								
IN/EPI FAUNA (7)	13.0275[h] 1 unit = 1 x 10^8 ind.	MICROZOO	2047.21 (8%)[v]	1035[ai]	NA[ao]	7039977[aw]	5120/1.2[bj]	IN/EPI	3.82398	NA	0.0735964
		IN/EPI FAUNA	511.80 (2%)[v]					CRABS	6.42339		
		PHYTO	10236.04 (40%)[v]					LITTORAL	7.17012		
								SHAD	0.35332		
		DETRITUS	5118.02 (20%)[v]					ANCHOVY	1.49904		
								BASS	0.185005		
BLUE CRABS	235.29[i]	CLAMS	20.40 (15%)[x]	1114[aj]	NA[ao]	15579[ax]	17/3[bk]	NA			5.77833

(8)	1 unit = 100 ind	IN/EPI FAUNA	47.60 (35%)[x]								
		DETRITUS	13.60 (10%)[x]								
MENHADEN (9)	104.762 [j] 1 unit = 1000 ind.	PHYTO	2457 (100%)[y]	2083[ap]	NA [ao]	932677[ay]	315/9 [bl]	BASS	1.16671	NA	0.32920
LITTORAL FORAGE FISH (10)	26.15 [k] 1 unit = 1000 ind.	MESOZOO	31.87 (4%)[z]	956 [ak]	NA [ao]	78798. [az]	199.2/3 [bm]	BASS	0.455609	NA	0.41494
		IN/EPI FAUNA	478.08 (60%)[z]								
		DETRITUS	223.10 (28%)[z]								
ALEWIFE/ HERRING (11)	296.96 [l] 1 unit = 100 ind.	PHYTO.	138.39 (68%)[aa]	5653 [al]	NA [ao]	91876. [ba]	20.15/8 [bn]	BASS	0.272737	NA	6.59998
		MICROZOO	32.56 (16%)[aa]								
		MESOZOO	32.56 (16%)[aa]								
AMERICAN SHAD (12)	2.813 [m] 1 unit = 100 ind.	MICROZOO	91.84 (13%)[ab]	1492.8 [am]	NA [ao]	162487. [bb]	142.2/8 [bo]	NA		NA	2.21173
		MESOZOO	91.84 (13%)[ab]								
		IN/EPI FAUNA	219.00 (31%)[ab]								
		DETRITUS	70.65 (10%)[ab]								
BAY ANCHOVY (13)	197.2615 [n] 1 unit = 1x10^4 ind.	MICROZOO	69.5 (37%)[ac]	956 [ah]	NA [ao]	76568. [bc]	17.236/3 [bp]	BASS	0.158296		6.03649
		MESOZOO	105.25 (56%)[ac]								
		IN/EPI FAUNA	13.25 (7%)[ac]								
CTENOPHORES (14)	68 [cf] 1 unit = 10000 ind.	MICROZOO	586.67 (33%)[ct]	111.41[ag]	NA [ao]	8072.12 [ch]	50/0.5 [ci]	NA		NA	0.006701
		MESOZOO	1173.33 (67%)[ct]								
STRIPED BASS (MIG + RES) (15)	117.3 [cj] 1 unit = 1 ind.	MENHADEN	51.6 5 (58%)[cu]	1673[cl]	NA [ao]	25505. [cm]	25.25/30 [cn]	NA		NA	13.1053
		ALE/HERR	9.85 (11%)[cu]								
		ANCHOVY	3.65 (4%)[cu]								
		LITTORAL	2.75 (3%)[cu]								
		IN/EPI FAUNA	2.75 (3%)[cu]								
DETRITUS (99)	27076.817 = $\Sigma N_J W_J / S_J$	NA	NA	1293[ck]	NA	NA	NA	OYSTER	0.0150682	NA	NA
								CLAMS	0.126984		
								IN/EPI FAUNA	2.46244		
								BLUE CRABS	0.11818		
								LITTORAL	0.215463		
								SHAD	0.0073398		

Table I.1 Parameter data for GEEM ecosystem

I.b Food Web Data

A GEEM updates species populations by way of energy transfers from prey to predator; therefore the model requires information about species population, diet composition, respiration and energy content of species biomass. The parameter data for the species in GEEM are presented in Table I.1. Unlike other population models, most of the data for GEEM pertain to an individual plant or animal. Thus, where the many extensions of the Lotka-Volterra framework for dynamic predator prey or competition models rely on estimates of species-level or lumped parameters, GEEM relies more on field or laboratory data that describe individual plants or animals. Constructing Table I.1 is analogous to constructing a social accounting matrix for a CGE model in economics. Gathering the data is time intensive, but indispensable for the modeling. The contents of every cell in Table I.1 are explained in footnotes that in Appendix A. The extensive footnotes give data sources and in most cases give the method for calculating the parameters.

By way of example of data usage, consider alewife/herring (species 11) in Table I.1. The population of 296.96 units per km^2 was obtained from CBFEM estimates of 1950 populations. CBFEM uses 1950 for a base so we do the same. Using the same data when possible in both GEEM and CBFEM will be useful for future comparability of GEEM and Ecopath - basically the two models can provide checks on one another. Each alewife/herring unit represents 100 individual fish, thus, there are 29,696 alewife/herring per km^2. Following population in the alewife/herring row of Table I.1 are the species consumed by alewife/herring and the amount of biomass of each species consumed. These values are also from CBFEM diet estimates. The biomasses consumed are in kg unit^{-1} y^{-1} which is consistent with the yearly general equilibrium calculations. For example, phytoplankton comprises 68% of the alewife/herring diet, or 138.39 kg of phytoplankton consumed per unit of alewife/herring per year. This implies one alewife/herring consumes 1.3839 kg of phytoplankton annually. The total consumption of alewife/herring over all species consumed (phytoplankton, microzooplankton and mesozooplankton) is 100% of the alewife/herring diet. For some species, however, not all the diet is included in the model. For example, for blue crabs only 60% of their diet is included, which can be seen by summing the percentages in the x_{ij} column for crabs. The other 40% of the crab diet consists of prey not included in the model. This omission requires certain adjustments to other parameters as indicated below. For most species, their diets in the model are less than 100% of actual diets owing to insufficient data.

The third alewife/herring cell is the energy content of their biomass which is 5653 kcal/kg. This energy content is from Flath and Dana (2011) and it is needed because alewife/herring are consumed by striped bass; therefore in determining the maximized net energy of bass, it is necessary to know how much energy bass acquire when consuming alewife/herring biomass.

The resting metabolic rate (RMR) for alewife/herring in the next cell is 91,876 kcal unit^{-1} y^{-1}. As explained below, each individual animal has a RMR and a variable respiration. Each RMR for the different species requires searching a variety of data sources, because there seems to be no one location that summarizes the RMR, or for that matter, some of the other parameters needed in GEEM. In addition, data usually requires several conversions to get it into a usable form. For example, alewives and herring are very similar and data from alewives was used for both species. From Stewart and Binkowski (1986) the RMR for alewives can be determined using the formula: $\ln R$ (mL O$_2$/kg h^{-1}) = 4.894 - 0.215$\ln$W(g) + 0.0548Temp (deg C). Using an average Bay temperature of 18 degrees C and average alewife/herring weight of 20.15 g (weight is in note bn in Table 1), R = 107.765 mL O$_2$/kg h. Furthermore, (107.765 mL O$_2$/kg h) (8760 h/y)(4.83 cal/mL O$_2$)(kcal/1000 cal)(0.2015 kg/ind)(100 ind/unit) = 91,876.42 kcal/unit y. This RMR constitutes about 35% of an alewife's incoming net energy from predation in the initial steady state discussed below.

Following RMR is the cell containing the weight and lifespan of alewife/herring. Like all other biomass terms, weight is given as wet weight (as opposed to dry weight or ash free dry weight). Dividing the weight of in kg unit^{-1} by the number of individuals per unit reveals that an individual alewife/herring weighs 0.2015 kg (fishbase.org). Lifespans are taken as the longest lifespans known for animals and plants in the wild (fishbase.org). Of course, not all individuals will live that long since they may fall to predation.

The final two cells for alewife/herring are not drawn from the literature. Instead they are obtained by calibration as described below. The penultimate cell for alewife/herring indicates that they are consumed by striped bass only, and the demand/supply coefficient is the unitless term d1115 = 0.2727. Note that in d1115, the 11 is the index for alewife and the 15 is the index for bass. The final cell in Table I.1 for alewife/herring is the coefficient for variable respiration of alewife/herring in kcal y^{-1} which is explained below.

To summarize Table I.1, the first two columns of data on densities and biomass of plants, or biomasses consumed by animals, contain values that are assumed to hold at a particular point in time, in this case 1950. This data obtained from the literature are referred to as benchmark values, and they are assumed to be from a steady state. The steady-state assumption can be relaxed with more programming effort as described in GEEM Extensions below. The data in the first two columns, along with the data in columns 3-6, are used in the calibrations to calculate the parameters in the last three columns. Once the calibration is done, then the parameters in the last seven columns do not change in simulations. However, the density and biomass values in the first two columns can change period to period depending on human activities such as harvesting or polluting.

I.c Equations for a General Equilibrium

This section contains the equations and method of calculating a general equilibrium. Readers familiar with GEEM may want to skip to the next section. All GEEM simulations described herein are run using Mathematica 9 software.

Following Tschirhart (2002, 2004) and Finnoff and Tschirhart (2003), plants and animals in GEEM are assumed to behave as if they maximize net energy. In each period all individuals of every species maximize net energy by choosing their biomass (plants) or biomass consumption (animals). When the transfer of energy (biomass) between species is in balance, meaning the amount of energy consumed by each predator species is the same as energy lost by its prey species, the ecosystem is in general equilibrium. Once the system is in a general equilibrium, the net energy gained by each individual is used to update populations in the dynamic model.

GEEM uses four sets of equations: i) individual's net energy-maximizing objective functions, ii) first-order conditions for a maximum, iii) predator biomass demand/prey biomass supply equations, and iv) population updating equations. These are explained in detail.

For set i), the net energy objective functions, consider a member of species i that preys on organisms in lower numbered species and is preyed upon by members of higher numbered species. The individual chooses an x_{ij} for each prey species to maximize

$$R_i = \sum_{j=1}^{i-1} [e_j - e_{ij}] x_{ij} - f^i (\sum_{j=1}^{i-1} x_{ij}) - \sum_{k=i+1}^{m} e_i [1 + t_i e_{ki}] y_{ik} - \beta_i \tag{1}$$

where R_i is net energy in power units (e.g., watts or kilocalories/time). The first term on the right side of (1) is the total inflow of energy from members of prey species to the representative individual of species i. The parameters e_j are the energy content of one unit of biomass (e.g., in kcal/kg) from a member of prey species j, and e_{ij} are the energies the member species of i must spend to locate, capture, and handle units of biomass of species j so that $(e_j - e_{ij})$ is the net energy species i receives from preying on j. These e_{ij} values can be considered 'energy prices', and there is one price for each predator/prey relationship. As in economic CGE models, the prices play a central role in each individual's maximization problem, because the individual's choice of prey will depend on the relative energy prices it pays. Predators are assumed to be energy price takers: they have no control over the price paid to capture prey, because each predator is only one among many individuals in a species capturing one of many individuals in a prey species. The choice variables or demands, x_{ij}, are the biomasses (in kg/y) transferred from the prey species j to the individual of species i.

The second and fourth terms in (1) represent respiration energy lost to the atmosphere which, following Gurney and Nisbet (1998), is divided into a variable component, $f^i(\cdot)$, that depends on energy intake and includes feces, reproduction, defending territory, etc., and a fixed component, β_i, that is basal metabolism or RMR.

The third term is the outflow of energy to animals of species k that prey on i. The e_i is the embodied energy in a unit of biomass from the representative individual of species i, and y_{ik} is the biomass supplied by i to k. The term in brackets is the energy the individual i uses in attempts to avoid being preyed upon. It is assumed to be a linear function of the energy its predators use in capture attempts: the more energy predators expend, the more energy the individual expends escaping. t_i is a tax on the individual because it loses energy above what it loses to being captured since the individual sometimes escapes but expends energy in the process.

To better understand the above equations, by way of example the alewife/herring (indexed as 11) net energy objective function is shown in (2). Unlike equation (1) the indices for predators and prey for any individual are not necessarily higher or lower numbered, because the food web is not a simple food chain. As seen in Fig. 1, alewife/herring prey on phytoplankton, microzooplankton, and mesozooplankton and are preyed upon by striped bass. Function (2) shows that the alewife/herring (11) consumes x_{1101}, x_{1102}, and x_{1103} units of phytoplankton (01), microzooplankton (02) and mesozooplankton (03), respectively, in the first three terms on the right side. (On the x consumption terms, the first two subscripted digits indicate the predator index, and the second two subscripted digits indicate the prey index.) The variable respiration is comprised of the fourth and fifth terms on the right side of (2). This respiration is assumed to be a quadratic function that depends on the alewife/herring consumptions of its three prey. The r_{11} is the variable respiration parameter from the penultimate column of Table 1 that is obtained via calibration as explained above. The quadratic functional form is chosen for variable energy because it is strictly convex in the consumption terms, and in economics it is a commonly chosen cost function for firms with multiple outputs. The form allows for substitution between prey items and for zero consumption of some prey. Also, for any given quantity of total biomass of multiple species consumed, the respiration cost is lower if the predator consumes multiple species as opposed to specializing in one species. Thus there are benefits to a diverse diet.

$$R_{11} = (e_{01} - e_{1101})x_{1101} + (e_{02} - e_{1102})x_{1102} + (e_{03} - e_{1103})x_{1103} - r_{11}(x_{1101} + x_{1102} + x_{1103})$$

$$-0.5r_{11}(x_{1101}^2 + x_{1102}^2 + x_{1103}^2 + x_{1101}x_{1102} + x_{1101}x_{1103} + x_{1102}x_{1103})$$

$$-d_{1115}(1 + t_{11}e_{1511})(x_{1101} + x_{1102} + x_{1103})^{.5} - \beta_{11} \qquad (2)$$

The fifth term shows that the alewife/herring is prey for striped bass (15). The term $(x_{1101} + x_{1102} + x_{1103})^{.5}$ is the functional form used for alewife/herring energy losses to predation. It is an increasing function of the biomass alewife/herring consume from its prey species owing to predation risk. An exponent that is positive and less than one is needed to allow for correct population movements between predators and prey (see Tschirhart, 2000). The value 0.5 facilitates numerical solutions. The final term in (2) is RMR.

The net energy objective functions for the 15 species are in Appendix E.

For set ii), the first-order conditions for the maximums, each individual in a general equilibrium chooses optimal intake energy to maximize its net energy. In mathematical terms, each individual chooses an optimal x_{ij} to maximize its net energy objective function. For each species, the individual's objective function will have one first-order condition for each prey species. In the Chesapeake 15 species ecosystem, there are 38 predator-prey pairs in the food web, which yields 38 x_{ij} choice variables and 38 first-order conditions. For example, the first-order condition for alewife/herring preying on microzooplankton is:

$$\frac{\partial R_{11}}{\partial x_{1102}} = e_{02} - e_{1102} - r_{11} - 0.5r_{11}(2x_{1102} + x_{1101} + x_{1103})$$

$$- 0.5d_{1115}(1 + t_{11}e_{1511})(x_{1101} + x_{1102} + x_{1103})^{-.5} = 0 \qquad (3)$$

In equation (3) the individual alewife/herring is choosing the quantity of microzooplankton to consume by equating the marginal energy gained from consuming an additional unit of microzooplankton with the marginal energy lost to respiration and potential energy lost to predation. Marginal energy is lost to predation because if the individual chooses to forage more on microzooplankton it is exposed more to predators. In other words, in consuming another unit of prey the organism is weighing the marginal benefit of energy gained against the marginal cost of energy lost to respiration and exposure to predators.

Like equation (3), the other 37 first-order conditions are simply derivatives of the net energy objective functions and are omitted for brevity.

A general equilibrium also requires mass and energy balance. Energy balance means that the total energy entering the food web via photosynthesis must equal the total energy lost to all respiration, to escaping predators, and to non-consumed detritus. This balance does not play a role in the general equilibrium calculations but holds in the model as shown in Tschirhart (2000).

With respect to mass balance and equation set iii), for each predator/prey relationship the biomass consumed by the total population of the predator species must equal the biomass sacrificed by the total population of the prey species. If N_k, $k = 1,\dots,15$, is the density of species i, then an equilibrium condition is written as:

$$N_i x_{ij}(e_i) = N_j y_{ji}(x_j(e_j)) \qquad (4)$$

where the left side is the total consumption by species i of species j and the right side is the total biomass lost by species j to species i. There is one condition for every one of the 38 predator/prey relationships. Equation (5) shows the condition for biomass balance between the alewife/herring predator species and the microzooplankton prey species.

$$N_{11} x_{1101} = N_{01} d_{0111} x_{0100}^{.5} \qquad (5)$$

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The balance condition between phytoplankton and the sun is different from the other predator/prey conditions. Basically, the amount of biomass generated by the plankton is set equal to the total available space in the Bay. Because phytoplankton experiences swings in its total biomass, this condition should be relaxed as discussed below. As the model stands now, the implication is that the total biomass of phytoplankton, $N_{01}x_{0100}$, is a constant so that that if density increases then the biomass of an individual phytoplankton must decrease, and vice versa.

The remaining biomass balance conditions are in Appendix E.

There are 38 equations from the first-order conditions of the net energy maximizations and 38 mass balance equations. This system of 76 equations can be simultaneously solved for 38 energy prices, the e_{ij}, and 38 biomass demands for the general equilibrium. The prices and demands are dependent on the species populations, which are entered in the model as parameters in the mass balance equations. Consider any predator/prey relationship. A larger predator species density will increase the energy price of foraging and decrease biomass demand because there are more predators after prey species. Alternatively, a higher prey population will decrease the predator's energy price of foraging and increase biomass demand because there is more prey to catch. These movements in prices and demands are the essence of competition in the model. The individual plant or animal maximizes net energy by choosing biomasses in response to the prices it observes, and which it has not control over as an individual. Although the aggregate action of all individuals determines the prices via the balance equations.

In many standard population models that depict each species with a differential equation, each predator species population is a direct function of a prey species population. And the parameters relating the species are lumped in the sense that they capture a variety of biological interactions unspecified in the model. For example, a predator population in a simple Lotka-Volterra system may be given by:

$$\dot{N}_i = \alpha N_j N_i - \beta N_i$$

where N_i is the predator and N_j the prey densities. Any notion of competition is buried in the mass action term consisting of both species and in the lumped α and β parameters. GEEM adds a behavioral component in that individuals make decisions. These decisions are not based directly on predator and prey populations, but rather on energy prices which are determined by the populations as parameters in the solution to the first-order conditions and mass balance equations. The GEEM approach is a more realistic depiction of competition because individuals are more likely to gauge the cost of locating and catching prey by observing energy prices, than they are to take an inventory of surrounding populations.

As discussed above, Table 1 indicates which parameters in GEEM are taken from the literature and which are determined during calibration. The calibration procedure is to use biomasses and

populations (the x_{ij} and N_i values), taken from an assumed steady state period, combined with literature parameters for embodied energies, light absorption, metabolic rates, weights, predation risk values, and taxes t_{ij}, to solve the 76 equations plus the 14 net energy R_i expressions set to zero, for the d_{ij}, r_j and the energy prices. After the d_{ij} and r_j are found, then simulations are run with the biomasses and energy prices as variables and the populations as parameters. When the general equilibrium simulations are run by using the d_{ij} and r_j terms, and using the assumed steady-state populations, then the steady-state biomasses and energy prices must be reproduced.

I.d Population Updating

Species populations as parameters are important in determining the optimum energy prices and demands in the general equilibrium. Over time the populations may change, meaning that energy prices and demands also change. The changes in populations are dependent on the optimum net energy each period's general equilibrium calculations. If the net energy is nonzero then the population will change for the next period, because zero net energy is associated with a steady state. How much net energy individuals obtain in any period is determined by substituting the general equilibrium energy prices and demands into the net energy objective functions from above.

After substitution, the values of net energy objective functions may be positive, zero, or negative. GEEM uses the economics general equilibrium convention that the numbers of firms in an industry increase, remain constant, or decrease depending on whether profits are positive, zero or negative. Thus a species' population increases, remains constant, or decreases depending on whether the representative individual in that species has positive, zero or negative optimum net energy. If a species has zero net energy every period then its population is unchanging and it is in steady state. However, owing to the interconnectedness of the food web, it will be the case that either all species or no species are in steady state. A steady state in GEEM is, therefore, characterized by a system in which there is a general equilibrium in each period, and populations are unchanging over periods. A system not in steady state is still characterized by general equilibrium in each period.

The population updating equations, set iv), are derived as follows. Consider striped bass, a top predator in the model. In steady-state the number of striped bass births must equal deaths. Therefore, if s_{15} is the lifespan of the representative striped bass, then the total number of births and deaths must be N_{15}/s_{15}. Dividing the total births and deaths by the species population N_{15} yields the per capita steady-state birth and death rates:

$$1/s_{15} \qquad\qquad (6)$$

The maximized energy of a striped bass is given by $R_{15}(x^d(N), e(N)) = R_{15}(\cdot)$ which is obtained by substituting the striped bass biomass demand and energy prices, as functions of the populations, into its net energy objective function (1-Bas). N is a vector of all species'

populations, and the demands and prices are the solutions to a general equilibrium solution. In the steady state, energy incoming and outgoing sums to 0, $R_{15}(\cdot) = R_{15}^{ss}(\cdot) = 0$. Reproduction requires energy and by the setup of the terms in (1-Bas), that energy is contained in variable respiration. Let be v_{15}^{ss} be the steady-state variable respiration and let qv_{15}^{ss} be the proportion of this variable respiration devoted to reproduction. Thus in steady state the energy given to reproduction by qv_{15}^{ss} yields a per-capita birth rate of $1/s_{15}$. Next, suppose the striped bass is not in steady state so that $R_{15}(\cdot) \neq 0$ and let variable respiration be v_{15}. Assuming that the proportion of net energy available for reproduction is the same as the proportion of variable respiration available for reproduction, the energy available out of steady state for reproduction is $q[R_{15}(\cdot)+v_{15}]$. Finally, assuming that reproduction is linear in available energy, then it follows that if qv_{15}^{ss} yields a per capita birth rate $1/s_{15}$, then $q[R_{15}(\cdot)+ v_{15}]$ yields a per capita birth rate of

$$(1/s_{15}) \, [R_{15}(\cdot)+ v_{15}] \, / \, v_{15}^{ss}. \tag{7}$$

An updated population is obtained by multiplying the population by the difference between the birth and death rates, where the latter rate is assumed to be independent of energy available for reproduction. Therefore, using (7), the population adjustment equation is

$$N_{15}^{t+1} = N_{15}^t + N_{15}^t \left[\frac{1}{s_{15}} \frac{R_{15}(\cdot) + v_{15}}{v^{ss}} - \frac{1}{s_{15}} \right]$$

$$= N_{15}^t + N_{15}^t \frac{1}{s_{15}} \left[\frac{R_{15}(\cdot)+v_{15}}{v^{ss}} - 1 \right] \tag{8}$$

Equation (8) reduces to the steady state if $R_{15}(\cdot) = R_{15}^{ss}(\cdot) = 0$ which means $v_{15} = v_{15}^{ss}$, making the bracketed term zero. Alternatively, $R_{15}(\cdot) > (<) 0$ implies that $v > (<) v_{15}^{ss}$, in which case population increases (decreases). Because of the form of (8), the optimum net energy plays the key role in determining population movements. Additionally from the general equilibrium solution we know that the optimum net energy is a result of individual behavior and competition.

If the species is not a top predator, then in steady state the births must equal the deaths *plus* any individuals lost to predation. Consider alewife/herring, which is consumed by striped bass, as the prey species. Define the predation rate on alewife/herring in period t as the total biomass a representative individual loses to its predators divided by the individual's weight. Dividing by weight gives the percent of the individual's biomass lost to striped bass. (Of course, in reality when a fish is preyed on it loses 100% of its biomass, so we interpret predation losses of an individual as the average biomass lost over all individuals.) The alewife/herring biomass loss as a percent of weight, w_{11}, that is, the alewife/herring predation rate, is taken from the species' net energy objective function in (1-Ale)

$$pred_{11}^t = \frac{d_{1115}(x_{1101}^t + x_{1102}^t + x_{1103}^t)^{.5}}{w_{11}}$$

The population update equation is

$$N_{11}^{t+1} = N_{11}^t + N_{11}^t \left[\frac{R_{11}(\cdot)+v}{v^{ss}}\right] pred_{11}^t + N_{11}^t \left[\frac{R_{11}(\cdot)+v}{v^{ss}}\right][1 - pred_{11}^t]\frac{1}{s_{11}} \qquad (9)$$

$$-N_{11}^t pred_{11}^t - N_{11}^t[1 - pred_{11}^t]\frac{1}{s_{11}}$$

Where the second term in the right side is the number of births to offset the deaths from predation, the third term is births to replace old-age deaths noting that old age deaths are individuals that are not preyed upon. The fourth term is deaths to predation and the last term is deaths to old age. Expression (9) reduces to:

$$N_{11}^{t+1} = N_{11}^t + N_{11}^t \left[\frac{R_{11}(\cdot)+v}{v^{ss}} - 1\right]\left[pred_{11}^t\left(1 - \frac{1}{s_{11}}\right) + \frac{1}{s_{11}}\right] \qquad (10)$$

Equation (9) also follows by noting that if $v_{11}{}^{ss}$ yields a birth rate that covers predation and old age deaths, or covers $pred_{11}^t\left(1 - \frac{1}{s_{11}}\right) + \frac{1}{s_{11}}$, then $R_{11}(\cdot) + v_{11}$ must cover predation and deaths equal to $\frac{R_{11}(\cdot)+v_{11}}{v_{11}^{ss}}\left[pred_{11}^t(1 - pred_{11}^t)\frac{1}{s_{11}}\right]$.

For some species with very short lifespans such as the plankton, the update equations are modified. Currently the method used is to replace the lifespan in years by a term that equals the lifespan divided by the time for reproduction. For example, if phytoplankton reproduces every 9 days and lives for 90 days, the *s* term in the above update equations would be 90/9 = 10. Details of how this procedure is carried out are in the footnotes to Table 1 in Appendix A. Further study of updating for short-lived species is ongoing.

Finally, detritus is indexed as one of the 15 species, but, of course, it does not reproduce. However, each period detritus biomass is updated. The biomass is assumed to be the sum over all species of the individuals' biomasses for those individuals that die of at the end of their lifespan. Thus, detritus is:

$$detritus = N_1{}^*w_{01}/s_{01} + N_2{}^*w_{02}/s_{02} + N_3{}^*w_{03}/s_{03} + N_4{}^*w_{04}/s_{04} + N_5{}^*w_{05}/s_{05} + N_7{}^*w_{07}/s_{07} +$$
$$N_8{}^*w_{08}/s_{08} + N_9{}^*w_{09}/s_{09} + N_{10}{}^*w_{10}/s_{10} + N_{11}{}^*w_{11}/s_{11} + N_{12}{}^*w_{12}/s_{12} + N_{13}{}^*w_{13}/s_{13} +$$
$$N_{14}{}^*w_{14}/s_{14} + N_{15}{}^*w_{15}/s_{15} \qquad (11)$$

This expression updates each period with population updates.

I.e Impacts of Human Activities

I.e.1 Water Quality Species may be impacted by numerous human activities. Nutrient loading from agriculture and transportation, pollution from industry and urban sources, and sediments are prime examples. The impact of these externalities can be incorporated into GEEM, although how best to do this is the subject of ongoing research. One possibility, for example, is to recognize that nutrient loading can stress plants and animals and this can lead to increased respiration. This approach was taken by Finnoff and Tschirhart (2011) in a study of the

Neus estuary in North Carolina. Phytoplankton and blue crabs were assumed to be stressed by nitrogen loading from agriculture, and this stress increased the variable respiration in their net energy functions. In turn, increased respiration for any given phytoplankton photosynthesis or crab consumption lowers the net energies and lowers phytoplankton and crab fitness and reproductions.

The phytoplankton net energy function was augmented by changing the variable respiration. The original variable respiration is given by $r_{01}x_{0100} + 0.5\, r_{01}x_{0100}^2$. This becomes:

$$(r_{01}x_{0100} + 0.5\, r_{01}x_{0100}^2)((N - N_1)^2 + 1) \tag{12}$$

In (12), N is the ambient nitrogen level and N_I is an "ideal" level of nitrogen for phytoplankton. As the ambient level diverges from the ideal level, the total respiration increases.

Excess nitrogen leads to increased sediment oxygen demand (SOD) and less dissolved oxygen (DO). The increased stress on blue crabs (and other species) can be incorporated as follows. First, phytoplankton blooms are linked to SOD following Smith and Crowder (2005). The method calculates an elasticity of SOD to phytoplankton biomass, $\varepsilon_{n_1}^{SOD}$, from the derivation of SOD provided in Borsuk et al. (2001). The value $\varepsilon_{n_1}^{SOD} = 0.7071$ was calculated using Neuse data. DO is assumed to respond perfectly to changes in SOD so that the elasticity of DO to changes in phytoplankton biomass is inferred to be $\varepsilon_{n_1}^{DO} = -0.7071$. Second, DO changes are related to stress on animal species. Studies exist that show reduced DO lead to increased, non predatory, mortality, although a study specific to the Neuse only address clams and SOD (Borsuk et al., 2002). Borsuk et al. calculate mean survival probabilities for various reductions in SOD. Employing their results for crabs, the elasticity of crab mortality with respect to SOD can be estimated as $\varepsilon_{SOD}^{M} = 0.7592$. Third, assume that the stress from low DO implies that a crab will lose additional respiration energy for any biomass it demands, and because DO is the negative of SOD, SOD can be used directly in the respiration expression. Letting the change in phytoplankton biomass be denoted Δ^{n_1} the variable crab respiration energy is augmented with the term:

$$\Omega^w = \left(1 + \Delta^{n_1}\, \varepsilon_{n_1}^{SOD}\, \varepsilon_{SOD}^{M}\right) \tag{13}$$

Basically, crab variable respiration is increased by the percentage change in mortality that follows from nutrient loading. The augmented crab variable respiration becomes:

$$r_{08}\big(\Omega^W(x_{0805} + x_{0806} + x_{0807} + x_{0899})\big)$$

$$+ 0.5r_{08}\big(\Omega^{W2}(x_{0805}^2 + x_{0806}^2 + x_{0807}^2 + x_{0899}^2 + x_{0805}x_{0806} + x_{0805}x_{0807}$$

$$+ x_{0805}x_{0899} + x_{0806}x_{0807} + x_{0806}x_{0899} + x_{0807}x_{0899})\big)$$

I.e.2 Harvesting   Harvesting has a long history in the Chesapeake Bay, with productive fisheries going back at least into the early 1800s. Today there are forty-one fisheries in the Chesapeake, each harvesting one or more of the above five species, or other species not in the model. Any number of the species in GEEM can be harvested simultaneously. The species of immediate interest are the blue crab, eastern oysters, striped bass, Atlantic Menhaden, and alosines (shad, alewife/ herring). GEEM can be set up to harvest fixed or varying catches in each period (likely one year). A varying catch might be designed to harvest the same percent of a stock each period, or other criteria based on current stocks. Harvesting any species will have slight or substantial impacts on the stocks of other species depending on the linkages in the food web, and these impacts are easily tracked in GEEM. Understanding the linkages is crucial for EBFM.

In addition, recreational fishing in the Bay is an important ecosystem service and can have significant impacts on the stocks. For GEEM purposes the recreational and commercial catches can be added to obtain their full effect on the stocks; however, on the economic side there are major differences in valuing the benefits and costs of commercial versus recreational that need to be taken into account.

Harvesting can be incorporated into GEEM using the population updating equations. Thus, if alewife/herring were harvested by quantity H_{11} in period t, then the population update equation from (10) is changed to:

$$N_{11}^{t+1} = N_{11}^t + N_{11}^t \left[\frac{R_{11}(\cdot)+v}{v^{ss}} - 1\right]\left[pred_{11}^t\left(1 - \frac{1}{s_{11}}\right) + \frac{1}{s_{11}}\right] - H_{11} \tag{14}$$

A simple demonstration of a one-period harvest is shown in Fig. 2. All populations begin at their calibrated steady-state values, and then in period two a 30% harvest of alewife/herring is carried out. The immediate affect is the drop in the alewife/herring density as shown in the graph in the fourth row, first column. Because the harvest in only one period, the alewife/herring rebound quickly in period three and briefly oscillate before settling back to the original steady state.

The reason the alewife/herring rebound can be traced with GEEM output. In Fig. 3 are the energy prices for selected predator/prey relationships. The second row of cells in the Fig. show the prices alewife/herring "pay" for their consumption of phytoplankton, micro zooplankton and

meso zooplankton. As can be seen, all three prices fall following the harvest. This follows because the lower alewife/herring density following harvest means there is less competition among alewife/herring for their prey, and prices fall in response. The lower prices mean more biomass (not shown) will be consumed by alewife/herring which raises their net energy and then raises their density via the population update equations. As their density increases as in Fig. 2, the prices they must pay for micro and meso zooplankton begin to rise with the rising competition. Interestingly, the price for phytoplankton fell with the other two prices, but in this case the price fell to zero. The reason is that a corner solution is obtained whereby alewife/herring biomass demand for phytoplankton is equal to phytoplankton supply to alewife/herring only at a negative price. Negative prices are, of course, ruled out, and a corner solution at price equals zero applies at which demand is less than the biomass phytoplankton are willing to supply. For the six periods shown alewife/herring demand remains less than supply, although price will eventually turn positive when the alewife/herring density increases and alewife/herring competition for phytoplankton drives up the price. Corner solutions in GEEM are explained in Appendix C.

A few other noteworthy results can be seen in Figures 2 and 3. Following the alewife/herring drop in density in period two, the striped bass density decreased in period three. As can be seen in the bottom row of Fig. 3, the drop in alewife/herring meant an increase in bass competition for the remaining alewife/herring, and this caused the bass energy price for alewife/herring to increase in period two. The higher price meant lower bass consumption of alewife/herring and a lower net energy which was followed by the fall in the bass density in period three.
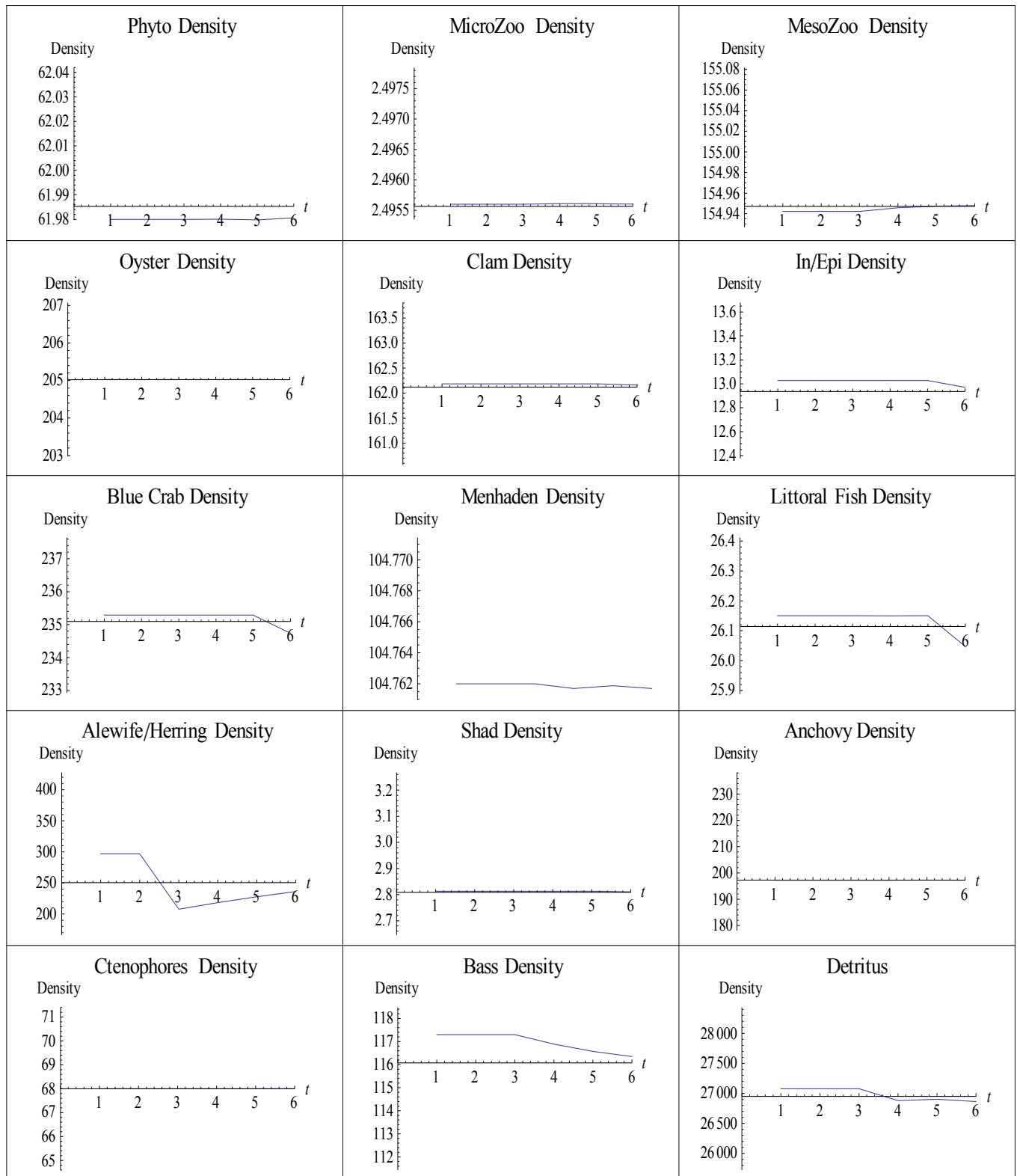
Figure 2. Density of the 15 species following a one-time harvest of alewife-herring in period two.
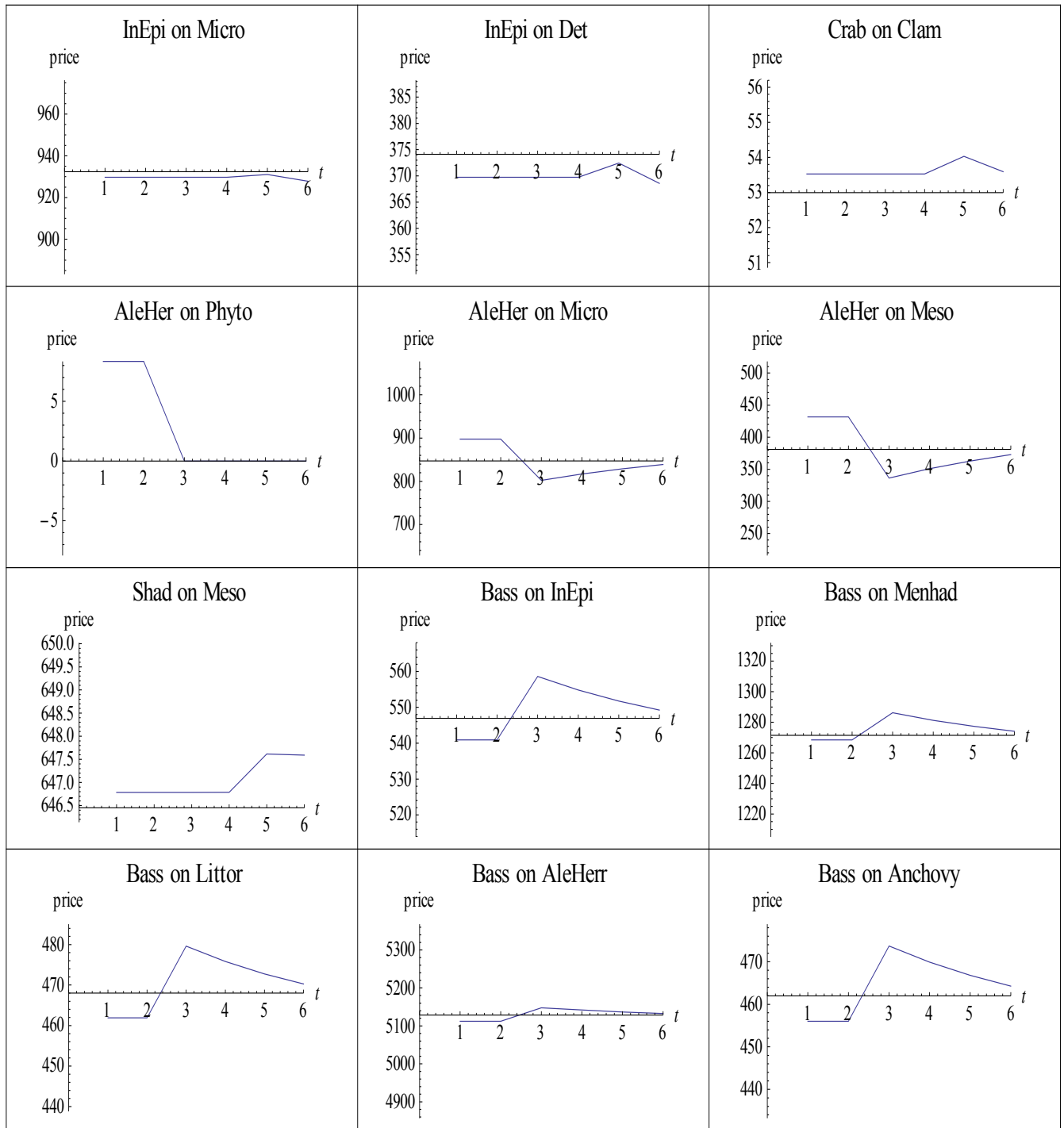
Figure 3. Selected energy prices for predator on prey following a one-time harvest of alewife-herring in period two.

Also following the alewife/herring fall in density after the harvest there are almost imperceptible increase in the plankton densities. Alewife/herring consume all three plankton so the lower alewife/herring density would allow the plankton densities to increase, but the alewife/herring consumption is small relative to the plankton populations so the changes are slight. The alewife/herring drop in density also decrease detritus in the following period, and this leads to small decreases in densities for detritus consumers such as in/epi, littoral fish and blue crab.

Figures 2 and 3 are meant to be suggestive as to how GEEM can be used to track species densities, consumptions and energy prices for all predator/prey relationships in the food web. Only one harvest is presented here, but any combination of harvests over any species can be implemented as well as water quality changes, while densities, consumptions and prices are tracked. Like in an economic model, GEEM users can determine how predator species substitute among prey species as prices change, which has implications for how harvesting policies can have complimentary or substitutable effects on densities. What is very clear is that harvesting of any species will have significant impacts across the ecosystem.

I.f GEEM Extensions

There are important extensions that could be made to the preliminary GEEM presented here. Several key extensions are as follows:

a) Age structuring. The technique for this extension has already been developed for an Alaskan marine food web and fishery (Finnoff et al. 2007). It was important for the Alaska study because pollock is a very important ecosystem and economic species in the model, and adult pollock cannibalism of their young constitutes a substantial predator/prey relationship. A similar effort may be important for the Chesapeake Bay because tributaries and sea grass areas of the Bay are important breeding grounds for the food web species. In fact, sea grasses may be an important species to add into the food web so that impacts of nutrient loading on spawning grounds can be tracked in the modeling.

b) Natural Steady State. GEEM calibration establishes values for some respiration and biomass transfer parameters of individual plants or animals. Because the parameters are individual based, presumably they are inherent properties of the individuals that are not subject to human activities. For example, a variable respiration coefficient (r_i) is assumed to be invariant to human activities, although the total respiration of the individual may very much depend on human activities. Because the parameters will depend on the initial population and consumption values inserted into the model, they will be biased owing the realization that the initial population and consumption values used are taken from periods when humans were already active in the ecosystem. Thus, the initial values used in the report were taken from CBFEM where 1950 was estimates were used. Obviously, human were already active at this time. To address this problem it is possible to calibrate using current data, but 'back out' the impacts of

human activity. In a sense, the calibrations could be used to generate historical population and consumption values. The method would entail solving the same sets of equations described above, in addition to appending the update equations into the calibration. Data would be needed from multiple time periods when harvesting or other human activities were impacting the ecosystem, and the update equations would be updated "backward" to account for the observed changes in data. To date, this method has not been worked into GEEM on a large scale.

 c) <u>Modeling Changes</u>. Minor changes to the procedures outlined above could include: i) changing the individual weights from constants to variables that depend on consumption; ii) when biomass demand is less than supply the net energies could be calculated based on actual demands and not on supply as is done now; and iii) modifying the longevity parameters and update equations for species with very short lifespans (< 1 year).

II. The Economy

In our interm report we detailed 9 basic steps in building a computable general equilibrium (CGE) model to link with the GEEM model of the Chesapeake Bay. The steps were to:

1. define the relevant economic region;
2. define the direct ecosystem services;
3. define the indirect ecosystem services;
4. review the related economic literature;
5. build a regional Social Accounting Matrix (SAM);
6. basic Economic Structure;
7. institutional details;
8. define the temporal details of the model;
9. define the uncertainties/measurement error of the model.

In this final report we will detail the foundations for future work.

II.a The economic region

The eight watersheds draining into Chesapeake Bay best define the relevant economic region. This includes area immediately surrounding the Bay that derive direct ecosystem services, and areas of economic activity connected to the Bay that indirectly enjoy services, such as effluent disposal. The watershed is defined by the Chesapeake Bay Fisheries Ecosystem Advisory Panel (2006, pp. 341-342). The relevant states and counties in each watershed of Chesapeake Bay were identified using the EPA's 'Surf Your Watershed' tool[1]. This mapping is shown in Table II.1.

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[1] Surf Your Watershed: http://cfpub.epa.gov/surf/locate/index.cfm

Table II.1 States and Counties of the Chesapeake Bay Watersheds

Watershed	State	County
Eastern Shore	Maryland	Caroline, Cecil, Dorchester, Kent, Queen Anne's, Somerset, Talbot, Wicomico, Worcester
James	Virginia	Albemarle , Alleghany , Amherst , Appomattox , Augusta , Bath , Bedford , Botetourt , Buckingham , Campbell , Charles City , Chesterfield , Clifton Forge , Covington , Craig , Cumberland , Fluvanna , Giles , Goochland , Hanover , Henrico , Highland , Hopewell , Isle of Wight , James City , Louisa , Lynchburg , Montgomery , Nelson , New Kent , Newport News , Petersburg , Powhatan , Prince George , Richmond City , Roanoke , Rockbridge , Suffolk , Surry , Williamsburg , York
James	West Virginia	Greenbrier, Monroe, Pendleton, Pocahontas
Patuxent	Maryland	Anne Arundel, Calvert, Charles, Frederick, Howard, Montgomery, Prince Georges, St. Marys
Potomac	DC	Washington
	Maryland	Allegany, Charles, Frederick, Garrett, Montgomery, Prince Georges, St. Mary's, Washington
	Pennsylvania	Bedford, Somerset
	Virginia	Alexandria, Arlington, Augusta, Clarke, Fairfax, Fairfax City, Falls Church, Fauquier, Highland, King George, Loudoun, Manassas City, Manassas Park City, Northumberland, Prince William, Richmond, Rockingham, Stafford, Warren, Westmoreland
	West Virginia	Grant, Hampshire, Hardy, Jefferson, Mineral, Pendleton, Pocahontas, Preston, Randolph, Tucker
Rappahannock	Virginia	Albemarle, Caroline, Culpeper, Essex, Fauquier, Fredericksburg, Greene, King and Queen, King George, Lancaster, Madison, Middlesex, Northumberland, Orange, Page, Rappahannock, Richmond, Rockingham, Spotsylvania, Spotsylvania, Stafford, Warren, Westmoreland
Susquehanna	Maryland	Baltimore, Carroll, Cecil, Harford
	New York	Allegany, Broome, Chemung, Chenango, Cortland, Delaware,

Watershed	State	County
		Herkimer, Livingston, Madison, Oneida , Onondaga, Ontario, Otsego, Schoharie, Schuyler, Stueben, Tioga, Tompkins, Yates
	Pennsylvania	Adams, Bedford, Berks , Blair, Bradford, Cambria, Cameron, Carbon, Centre, Chester, Clearfield, Clinton, Columbia, Cumberland, Dauphin, Elk, Franklin, Fulton, Huntingdon, Indiana, Jefferson, Juniata, Lackawanna, Lancaster, Lebanon, Luzerne, Lycoming, McKean, Mifflin, Montour, Northumberland, Perry , Potter, Schuylkill, Snyder, Somerset, Sullivan, Susquehanna, Tioga, Union, Wayne, Wyoming, York
Western Shore	Maryland	Anne, Arundel, Baltimore, Baltimore City, Calvert, Harford, St. Mary's
York	Virginia	Gloucester, James City, King and Queen, King William, New Kent, Newport News, Williamsburg, York

II.b Ecosystem services and Externalities

Identifying feedback loops between Chesapeake Bay economic activity and the ecosystem defines the linkages of GEEM/CGE. These linkages define the minimum level of detail the CGE must contain for it to be useful in any linked system policy assessment exercise. Ecosystem services for the region have been the basis of many years of research. A detailed description of the services provided by the bay are detailed in the Chesapeake Bay Fisheries Ecosystem Advisory Panel report *Fisheries Ecosystem Planning for Chesapeake Bay* (FEPCB, 2006). The linkages between the ecosystem, fish harvesting, and nutrient/sediment loading are as follows:

II.b.1 Direct ecosystem services – Fisheries. Five species groups in the GEEM, blue crab, Eastern oyster, Atlantic menhaden, various alosines, and striped bass are of most interest for the provisional ecosystem services they provide in the form of commercial harvest and/or recreational fishing. Commercial fisheries propagate value in rents, industry, and exchange. Recreational fisheries generate benefits in the form of trip expenditures like boat rentals, chartered trips, and other related expenses. The value of a sport fishery can be estimated using available catch and effort data in combination with NOAA Fisheries Surveys. EBFM should consider food web interactions and environmental factors in sustainable harvest decisions. Table II.2 displays 2010 catches and revenues from the five species.

Table II.2 2010 reported commercial catch and biomass by species

	Total Catch[2] (millions of pounds)	Revenue[2] (millions $)
Blue Crab	111.95	131.227
Oyster	1.819	10.615
Menhaden	448.997	35.231
Alosine (alewife, shad, herring)	0.98	.332
Striped bass	4.687	9.165

The blue crab commercial and recreational fisheries are economically and culturally important to the region. It is the largest and most valuable shellfish industry in the Bay. The states of Maryland and Virginia independently set the commercial and recreational harvests annually based on abundance estimates. The commercial fishery is managed using entry limitation via license, seasonal closures, and harvest, gear, and size restrictions. Environmental conditions and fishing pressure resulted in an 84% reduction in the biomass between 1988-2004 (Lipcius and Stockhausen, 2002, Miller et al., 2005). The 2012 Chesapeake Bay Blue Crab Advisory Board reports the blue crab stock is not experiencing overfishing.   Though the spawning population has stabilized, it has not rebounded despite management efforts (Chesapeake Bay Blue Crab Stock Replenishment, 2008).

Oyster populations have historically been a significant ecological and socio-economic aspect of Chesapeake Bay. In the latter half of the 19th century, competition over the Bay's rich oyster beds led to deadly conflicts among watermen, and between watermen and the Maryland Oyster Navy. By the late 1800s, a half million tons of Chesapeake Bay oysters were consumed both locally and as far away as Colorado (Wennersten1981).

 Today the bay is one of the last locations of a wild-caught oyster fishery in the world, and the oyster population is roughly 1% of historic levels (Frankenberg 1995, Rothschild et al. 1994). Contributions to the decline include pollution, water quality, overharvesting, and disease. Despite increased stocking strategies and hatchery production for the benefit of commercial, aquaculture, and recreational fisheries, oyster populations remain extremely low. The states of Maryland and Virginia regulate fishing effort via seasonal, gear, and catch limits on public harvesting grounds. Private-harvest lease operations give leaseholders exclusive rights to harvest

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[2] NOAA Annual Commercial Landing Statistics
http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html

in specific locations. Lease operations encourage sustainable harvest and culturing populations. Aquaculture was previously a viable option to replace wild harvest practices, but prevalence of oyster disease has restricted establishment of aquaculture in the bay.

Atlantic menhaden play a crucial role in marine food web linkages as a filter feeder and food source for predators such as striped bass. Chesapeake Bay is a plankton-rich nursery habitat for young of year and juvenile menhaden. Menhaden are a nutrient-rich fish with a large commercial fishery in Chesapeake Bay, but are not sold for human consumption (Lipton 2009). Menhaden are used in nutrition supplements, animal feed, industrial products, and as bait for other fisheries. This creates an industry dependent on menhaden harvest in the Chesapeake regional economy. Though the menhaden stock along the Atlantic seaboard is healthy, Chesapeake Bay population and annual recruitment are estimated to have declined to 10% of historic numbers (2012 Atlantic Menhaden Stock Assessment Update). The causes of population decline have been identified as pollution, nutrient and sediment loading, and habitat destruction. The Atlantic States Marine Fisheries Commission (ASMFC) 2012 Atlantic menhaden stock assessment identified overfishing of the Chesapeake Bay menhaden population.   In 2012 the ASMFC reduced the total allowable catch for menhaden by 20%. This is the first effort to manage the stock along the entire Atlantic seaboard in hopes of increasing the total population and therefore immigration into the bay.

Anadromous alosines (blueback herring, alewife, American shad) are commercially harvested primarily for use as bait or fish meal, though historically harvested as a food fish. Stocks were heavily fished during their migrations to spawning habitats in the early 20th century and declined to 20% of historic populations between years 1965-1985. This resulted in severe restrictions to both commercial and recreational alosine fisheries that currently remain in place. In addition to overfishing, pollution and creation of dams, culverts, and other blockades in the tributaries of has restricted the ability of these fish to reach their preferred spawning habitat.

Striped bass is one of the largest and most profitable recreational sport fisheries in the Chesapeake Bay (see Table II.3). They also play an important role in the food web as a top predator. After a decline in population in the 1980's, striped bass populations have steadily increased due to management efforts and have surpassed target population levels. The species is currently managed by states following an Atlantic coast-wide initiative which sets catch limits. Declines in the Chesapeake Bay menhaden population, an important prey species, are a potential concern for striped bass populations. Uphoff (2003) indicates lack of menhaden in striped bass diet leads to malnutrition and incidence of disease. Therefore efforts to maintain a healthy stock of striped bass must include consideration of the health of prey species populations.

Table II.3   2011 striped bass recreational landings and angling days[3]

	Catch (millions of pounds)	Angling days (millions)
For-hire charter/party boats	0.9362	0.1911
Private/rental boats	2.8337	3.2345
Shore	0.0314	2.2925

II.b.2 Regulatory ecosystem services. The Eastern oyster and other filter feeders have historically played a vital role in maintaining the overall health of the Chesapeake Bay ecosystem. Oysters provide a regulatory ecosystem service by feeding on suspended particles nutrients and sediments at a high volume, clearing the water column (Baird and Ulanowicz, 1989). When oysters eliminate sediment from the water column, light is able to penetrate to deeper depths and encourages growth of sea grass and other submerged aquatic vegetation. These macrophytes are crucial habitat for juvenile fishes and prey species and as these habitats are lost the ecosystem is negatively affected.

Newell (1988) estimated the 1800's bay oyster population filtered the entire bay's water volume in 3.3 days. Current populations are estimated to filter the same volume in 325 days. The reduction in the Chesapeake Bay oyster population in concurrence with increased levels of nutrient and sediment runoff from the watershed has resulted in an overall decline in water quality. Nutrients are a food supply for phytoplankton. Elevated nutrient loads cause algal blooms, which choke submerged aquatic vegetation and reduce oxygen levels in deep-water habitats. Both have negative impacts on the invertebrate and vertebrate communities. Oyster reefs provide forage and refuge habitat for numerous species in Chesapeake Bay (Grabowski et al., 2005 and Peterson et al., 2003). The disappearance of oyster beds therefore has an indirect effect on commercial and recreational fisheries. The loss of reef habitat cannot be isolated from other environmental changes in Chesapeake species health but has been identified as important.

II.b.3 Ecosystem externalities. Elevated levels of nitrogen and phosphorus cause eutrophication, which is the largest threat to Chesapeake Bay ecological stability, having negative impacts on multiple trophic levels. Historical records indicate eutrophication began to occur with European habitation of the geographic region (Boynton, 1998).   Significant increases in nitrogen and phosphorus levels in the bay began in the 1950's. Nutrients enter the bay

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[3] NOAA Recreational Fisheries Statistics Queries http://www.st.nmfs.noaa.gov/st1/recreational/queries/index.html

through wastewater, storm/groundwater runoff, and atmospheric deposition. Economic activities contributing to nutrient loading are detailed in Table II.4. Increased nutrients levels result negative impacts on different aspects of the ecosystem through a variety of mechanisms.

Table II.4   Direct and indirect effects of ecosystem externalities on species of interest

Externality	Effect	Species directly impacted	Species indirectly impacted
Nitrogen/ Phosphorus	Reduced water clarity	sea grass	menhaden, alosines, blue crab
	Oxygen depletion	sea grass, blue crab, oyster, striped bass, menhaden	menhaden, alosines, blue crab, striped bass
	Reduced water quality	oyster, striped bass, menhaden, alosines	striped bass
Chemicals	Habitat loss	oyster	crab
	Reduced water quality	oyster, striped bass, menhaden, alosines	striped bass, crab
Sediment	Reduced water quality	sea grass, oyster	menhaden, alosines, blue crab
Fishery	Habitat destruction	sea grass	menhaden, alosines, blue crab
	Population loss	blue crab, oyster, striped bass, menhaden, alosine	blue crab, striped bass
Spawning habitat loss		American shad	striped bass
Increased temps	Disease	oyster	blue crab

Nitrogen, chemicals and contaminants enter Chesapeake Bay via storm, ground, and wastewater as well as atmospheric deposit. Agriculture, industry, and urban development all contribute to pollution levels through point and non-point sources. Pollution degrades the water quality in the bay, which affects a variety of species directly and through the food web.

Nitrogen-rich water provides food for phytoplankton, causing algal blooms. Spikes in algae populations reduce water clarity and therefore the amount of light submerged aquatic vegetation (SAV) receives. The photosynthesis capabilities of SAV are reduced by lack of exposure to sunlight and reduced plant growth. Prey and juvenile fish species, such as menhaden, shad, and blue crab, use SAV habitat for forage and refuge. As these habitats disappear due to reduced water clarity, populations are more vulnerable to predation and other stressors.

Eventually phytoplankton in algal blooms die and sink to the benthic zone. Bacteria that decompose the bodies of dead algae remove oxygen from the bay floor habitat resulting in hypoxic (low-oxygen) conditions in deeper parts of the bay. Low oxygen levels result in large-scale fish kills and drive adult menhaden and blue crab populations from their preferred habitats. Menhaden compose a large portion of striped bass diet. Declining menhaden in the diet of striped bass is concurrent with greater incidence of lesion-causing bacterial infection is observed in the Chesapeake Bay population (Uphoff, 2003).

Enhanced levels of nitrogen and phosphorus also alter the water chemistry of the bay. This, along with other factors severely decreases the overall water quality. This creates stress for individuals and has generally negative impacts on all levels of the food web, from plants to invertebrates to top predator species.

Particles in the slower-moving areas of the bay eventually settle, covering and suffocating oysters and other benthic inhabitants. Oyster beds again are important habitat for a multitude of species that are significant in health and therefore harvest of commercial and recreational fisheries. Terrestrial runoff in tributaries degrades these freshwater systems that are used by many estuarine species as spawning habitat.

Recent increases in water temperatures in Chesapeake Bay have led to increased levels of two infectious diseases, "MSX" and "Dermo" in oyster populations. Both are highly contagious and cause mass mortalities in oyster beds when exposed. Incidence of infection is greatest during summer months, though unusually warm water temperatures allow for infections to persist year-round. The effect of climate change on Chesapeake Bay year-round temperatures may significantly alter infection rates (Ewart and Ford, 1993). Poor water quality and other stressors have also been linked to increased incidence of oyster infection.

To address water quality issues, the Environmental Protection Agency initiated a Total Maximum Daily Load (TMDL) in 2010 to regulate levels of nitrogen, phosphorus, and sediment in flows into the bay from watershed jurisdictions (2012, U.S. EPA/600/R-11/001). TMDL targets both point and non-point pollution sources. Point source pollution addresses municipal and industrial discharge facilities, storm water and sewer overflows, and animal feeding operations. Nonpoint source pollution targeted by TMDL include agriculture, atmospheric deposition, erosion, non-regulated storm water runoff, and tidal re-suspension. Reducing

nutrient levels is a "bottom-up" approach for restoring the Chesapeake Bay to ecological stability, as the benefits from this action will have effects on the entire food web.

II.c Modeling Ecosystem Services

To incorporate the ecosystem services detailed above into the CGE we will follow methods used in prior work where appropriate, and incorporate additional modeling where necessary. We focus on the following critical ecosystem services described above:

1. Commercial fishing
2. Recreational fishing
3. Nutrient filtration/waste disposal

II.c.1 Commercial fishing. The treatment of Commercial fishing follows methods developed and applied in Finnoff and Tschirhart (2008, 2011). The ecosystem service provision with commercially harvested species is given by the abundances of the harvested species (i.e. the links between the GEEM and CGE are given by species abundances and species harvests). While the methodology of commercial harvests in bioeconomic modeling is well developed (Clark 1991), there are issues when trying to merge these methods into a CGE. These issues require at least two modifications to the standard CGE framework. First, where most of the fishery literature employs effort as the single human factor of production,[4] capital and labor must be included in CGE so that the fishery interacts with other sectors. Second, the fishery may be regulated in a variety of dimensions that have structural implications in the model. The regulations over key species and regulatory agencies responsible for commercial fishing in the Bay are shown in Table II.5.

A primary tool of regulation in the fisheries are the total allowable catch (*TAC*) constraints. Given abundance for species i in period t, N^t_i, from the GEEM, total allowable catches for species i is given by TAC^t_i. Homans and Wilen (HW 1997) develop a model of a regulated, open-access fishery in which fishery managers set *TAC* and firms have free entry. In HW, *TAC's* are based on historical catches and current biological criteria. A simple form is given by the linear relationship

$$TAC^t_i = a_i + b_i N^t_i \tag{15}$$

where parameters a_i and b_i can be estimated as shown in HW and Finnoff and Tschirhart (2003). The TAC^t_i provides an upper bound on harvests of the species i, H^t_i.

Harvests are a function of species abundances and the effort employed by the harvesting sector,

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[4] An exception is Weninger and McConnell (2000), who present an analysis that deliberately separates fixed and variable inputs in a partial equilibrium model of a fishery regulated through *TAC's* and a limited entry program.

E^t_i, with a simple form given by the Schaffer production function

$$H^t_i = d_i E^t_i N^t_i \tag{16}$$

where parameter d_i is the catchability coefficient and can be estimated from data catches, effort and biomass (see Finnoff and Tschirhart (2003) as an example). If harvests are presumed to exhaust the *TAC*, then the production function (16) defines the effort required to harvest the *TAC*.

Table II.5 Commercial fishing regulations

	Striped bass	American Shad	Blueback herring and alewife	Blue crab	Eastern oyster	Atlantic menhaden
Regulations	- commercial license - minimum/maximum size - annual TAC[5] - annual individual quota	- moratorium	- moratorium	- commercial license - minimum size - location - daily quota - gear - life cycle-stage - season	- harvest method-specific license - location - minimum size - annual TAC[6] - daily individual quota	- TAC[7]
Managing organization	Marine Resources Commission	Marine Resources Commission	Marine Resources Commission	Marine Resources Commission	Marine Resources Commission	Atlantic States Marine Fisheries Commission
Sources	http://mrc.virginia.gov/regulations/fr252.shtm http://www.dnr.state.md.us/fisheries/regulations/table.asp?c=commercial	http://mrc.virginia.gov/regulations/fr530.shtm http://www.dnr.state.md.us/fisheries/regulations/table.asp?c=commercial	http://mrc.virginia.gov/regulations/fr1260.shtm http://www.dnr.state.md.us/fisheries/regulations/table.asp?c=commercial	http://mrc.virginia.gov/regulations/fr270.shtm http://www.dnr.state.md.us/fisheries/regulations/table.asp?c=commercial	http://mrc.virginia.gov/regulations/FR720.shtm http://www.dnr.state.md.us/fisheries/regulations/table.asp?c=commercial	http://www.asmfc.org/ http://www.dnr.state.md.us/fisheries/regulations/table.asp?c=commercial

[5] 1,230,110 pounds for entire bay
[6] 50% of standing stock
[7] 170,800 metric tons for entire bay

The next step is to determine the composition of primary factors of production, L^t_i, and capital, K^t_i, in harvesting effort, E^t_i. An economic CGE model with multiple sectors invariably uses capital and labor as inputs; therefore, in order to have movement of inputs between fisheries and other sectors, capital and labor must replace the often used E for effort. The institutional details of the fishery govern how the factors are employed in the fishery. In Homans and Wilen (HW, 1997) fishery managers set TAC and firms have free entry. Here we modify HW, and include the potential for a licensing or capacity limitation program which limits entry to the fishery. In the case of a capacity limitation program, the level of capital directed at a fishery K_i may be fixed at a certain level $\overline{K}_i$ by regulation. The industry is assumed to minimize the cost of harvesting by employing capital and labor to satisfy aggregate effort E, where the effort function exhibits constant returns to scale with efficiency parameter φ_i, distribution parameter δ_i and elasticity of substitution between labor and capital σ_i

$$\text{Minimize } wL^t_i + r\overline{K}^t_i \text{ s. t. } \quad E^t_i = \varphi_i \left[\delta_i L^{t\,\frac{\sigma_i-1}{\sigma_i}}_i + \left(1-\delta_i\right)\overline{K}^{\frac{\sigma_i-1}{\sigma_i}}_i \right]^{\frac{\sigma_i}{(\sigma_i-1)}} \tag{17}$$

where w is the wage rate and r the rental rate of capital. The regulator effectively determines aggregate effort in the fishery by their choice of TAC in (15) and the harvest function (16) under the assumption of harvests exhausting the TAC. L^t_i is then determined from the effort constant elasticity of substitution (CES) function directly. Thus, without capacity limitations there are two equations and two unknowns, K^t_i and L^t_i. With capacity limitations there is only one equation and one unknown, L^t_i, as $K^t_i = \overline{K}_i$ over all periods. In the absence of a capacity (or license) limitation program the cost minimization using (17) results in a capital labor ratio such that the marginal rate of technical substitution equals the input price ratio. Rents can arise in the fishery that accrue to the resource (the stock effect of the harvested species populations), but they may also exist given the rigidity of the TAC and further fishery regulations such as a capacity limitation program. Several authors have made the point that capacity limitation programs can allow some of the rent accruing to the resource to be captured by industry participants, but the magnitude of the rent capture depends on the relationship between regulated and unregulated inputs. Anderson (1985) demonstrated that a license limitation, modeled as a limit on the number of firms allowed to operate, can yield positive rent. Campbell and Lindner (1990) investigate the welfare consequences of input regulation. They find that a license limitation program can approximate a first-best solution in situations where unrestricted and restricted inputs cannot be easily substituted for one another or where restricted inputs account for a major component of the industry's total cost. Campbell (1991) empirically estimated the elasticity of substitution between restricted and unrestricted inputs for the Tasmanian rock lobster fishery and concluded that, in this case, a license limitation program results in significant rent capture. In the simulations rents that occur in the fishery are reflected through factor price markups and paid to primary factors employed in the fishery. The consequences on results of the elasticity of

substitution between restricted and unrestricted inputs are to be investigated through a sensitivity analysis over σ_i with and without a license limitation program.

II.c.2 Recreational fishing (written with Brad Gentner and Travis Warzinack) The treatment of recreational fishing is intended as a first step towards including a model of recreational demand in a CGE method. There are several challenges to confront. The prominent challenge we plan to incorporate is that people demand recreational experiences that are complex combinations of human and natural system inputs. People are able to substitute (to some extent) between human and natural inputs in the production of recreation. Early models of recreational demand (Bockstael and McConnell 1981) used a household production function model to represent this substitution where fishermen were able to improve their fishing experience by either spending more time fishing or by investing in a technology that improves the quality of fishing. Random utility models (RUMs) developed by Feenberg and Mills (1980) and Hanemann (1984) specified a given quality of a recreational option, but allowed free to choose between a suite of locations or activities. A major insight from the RUM literature was that substitution possibilities between locations and activities are important in determining welfare effects from changes in environmental quality.

There have been some recent notable advances that account for changes in the quality of a recreational option over time. Massey, Newbold and Gentner (2006) link a model of water quality with an ecological model of fish biomass production to measure the welfare consequences from changes in water quality. Considering both commercial and recreational angling of a single species, they estimated a per-angler catch function across sites. Catch functions were shown to depend on site characteristics such as fish biomass and water quality. The catch functions allowed a calculation of the probability anglers would choose to fish at each site. Changes in water quality at sites could then be valued though changes in angling, although the magnitude of the welfare change depended on the ability of anglers to substitute across alternative sites.

Abbott and Wilen (2009) consider the implementation of rights-based recreational fisheries management. They focus on the links between demand for recreation and the for hire recreational fishery under open access and rights-based management in a single species, dynamic framework. The authors demonstrate the multi-dimensional nature of the recreational goods provided. Catches are an important driver of demand for recreational trips, yet site characteristics, prices and angler preferences are also key in this demand.
Across the breadth of the previous literature there has been a clear emphasis on the substitution possibilities between environmental goods and ways to enjoy them, yet a literature where there is a endogenous composition of environmental goods and a set of endogenous relative prices of recreation and normal goods (i.e. in general equilibrium) for valuing nonmarket goods has been lacking. Instead, the environmental valuation literature has focused on partial equilibrium

analysis (e.g., chapters in Champ and Boyle, 2003). General equilibrium approaches to environmental valuation have typically been were limited to market effects of environmental changes. A few notable exceptions include Carbonne and Smith (2008) and Warziniack et al. (2011). Carbonne and Smith present a method for welfare analysis when environmental quality and consumption goods are nonseparable elements of consumer preferences. Their method relies on recent advances in calibration techniques for general equilibrium models (Rutherford, 2002; Sancho, 2009). Warziniack et al. (2011) extend the Carbonne and Smith framework to include nonmarket damages to the ecosystem and show large biases exist when general equilibrium externalities are ignored.

Here we outline two proposed methods to including a detailed representation of the recreational sector in the CGE. One employs a more standard model of recreational demand with a detailed use of available data, the other develops a detailed model of behavioral choice over multiple species.

IIc.2.i Recreation: Method 1 The first method employs a structural modeling for including the striped bass recreational sector. This approach will closely follow Massey, Newbold and Gentner (2006) and should be able to accommodate a wide range of changes in the ecology of the Chesapeake Bay. This approach has been demonstrated to work when the modeler is faced with many disparate data sets that describe stocks, water quality, recreational catch and recreational effort. The approach incorporates the full geographic scope of the Bay which is important for anadromous fish species such as the Alosids and striped bass that move into freshwater to spawn, spend a certain portion of their life in the Bay, and also move out of the Bay into the open ocean. The approach can be expanded relatively easily to incorporate a short time step on water quality monitoring and distinguishes between short and long-run stock impacts. With a given population level, this approach recognizes that there is a spatial relationship between abundance and water quality and that relationship depends on how a stock responds to changes in water quality and, in turn, that behavioral response impacts population density across a series of interconnected sites. In this relationship there are short-run impacts on the distribution of the stock and long-run impacts on overall abundance. That is, in the short run, fish will change sites and in the long run those fish will have less success breeding, impacting the overall stock size. To reflect these process in the GEEM model, the short run locational movements could be represented by differentiating predation locations as in Finnoff and Tschirhart (2011) or as an additional respiration cost in the variable respiration function. The long-run reproductive affects could be reflected through a modification of the efficiency of energy conversion in the population updating equation (10).

The dynamic model of the recreational fishery begins with abundance:

$$N_t = f_1(N_{t-1}, H_{t-1}, Q_{t-1})$$

where N_t is stock abundance in time t, H_{t-1} is total harvest, commercial and recreational, in the previous period and Q_{t-1} is water quality conditions in the previous period. Recreational catch per trip is then represented by:

$$C_{it} = f_2(Z_i, N_t, Q_t)$$

where catch is a function of abundance (N_t), angler skill and other characteristics of the individual angler (Z_i), and water quality (Q_t). Total catch for the recreational sector is therefore a function of the individual demand for trips in time period t expressed by:

$$R_{it} = f_3(X_{it}, Z_i, C_t, Q_t)$$

where this demand is a function of travel costs (X_{it}), characteristics of the individual angler (Z_i), catch rates per trip (C_t) and water quality (Q_t).

Following this structural modeling path, total harvest for striped bass would be:

$$H_{15t} = \sum_i C_{it} R_{it} + HC_{15}$$

where HC_{15} is total commercial harvest. In this model, average catch rate and aggregate trip demand determine harvest which changes abundance. In the next period, the change in abundance changes average trip catch which impacts trip demand.

Estimating trip demand begins with estimating expected catch per trip. Catch data is reported as non-negative integers suggesting the use of a count data model such as the Poisson or the negative binomial regression model. From this model we obtain the average catch per trip:

$$E[C_i] = exp\left(Z_i\delta + Q_i\eta + \theta ln\tilde{N}_i\right)$$

where δ, η, θ are parameters to be estimated, Z is a vector of angler characteristics, Q is a vector of water quality measures and A is an index of fish abundance. Maryland Department of Natural Resources (MD DNR) monitors water quality at a number of stations across the Chesapeake Bay and each of these stations measures temperature, salinity and secci depth.[8] Massey et al. (2006) use those parameters to estimate DO, and use DO as the water quality measure. MD DNR also collects self-reported angler catch data that includes area fished that can be matched with these water quality monitoring stations.[9] Finally, researchers have their choice of abundance measures. MD DNR produces an index of juvenile abundance from a seine survey[10] and Virginia (VA) also produces a juvenile index from a seine survey.[11] MD DNR also produces an index of spawning sized adults from their spring spawning stock survey. Finally, the US Fish and Wildlife Service (USFWS) conducts the Atlantic coast-wide cooperative striped bass tagging program. Trip

[8] http://mddnr.chesapeakebay.net/eyesonthebay/index.cfm
[9] http://www.dnr.state.md.us/fisheries/survey/index.asp
[10] http://dnr.maryland.gov/fisheries/juvindex/
[11] http://www.vims.edu/research/departments/fisheries/programs/juvenile_striped_bass/index.php

demand can be estimated using a random utility model using either revealed data from the MRFSS survey on actual trip choices or using hypothetical choices made by anglers using a stated preference choice experiment (SPCE) type survey. NMFS has been conducting SPCE type surveys for federally managed species in the region, but has not conducted one that contains striped bass because striped bass is a species managed by the Atlantic State Marine Fisheries Commission (ASMFC)[12].The trip demand model of choice is the mixed logit model regardless of whether the data is revealed or SPCE data. Anglers are assumed to select the trip that maximizes utility:

$$U_{ikt} = S_{ik}\,\varphi_i + \varepsilon_{ikt}$$

where S is a vector of individual and site characteristics. φ_i is a unique vector of coefficients that vary normally across individuals, are uncorrelated with one another and are constant across choices. Angler i is assumed to make a series of choices y_i over a series of choice occasions t =1,2,….T given preferences described by φ_i. The errors are assumed to be identically and independently distributed using an extreme value distribution giving rise to the logit probability and the following simulated probability of taking a trip:

$$SP(y_i|\Psi) = \frac{1}{D}\sum_{d=1}^{D}\left[\prod_t \frac{exp(S_{ikt}\Phi_i^d)}{\sum_j exp(S_{ij}\Phi_i^d)}\right]$$

where Ψ contains the means and variances of φ_i distributions, D is the number of draws, Φ_i^d is drawn from the estimated distributon of φ_i. The results allow the estimation of welfare impacts of changes in trip attribute via:

$$W_i = \frac{1}{D}\sum_{d=1}^{D}\left[\frac{ln\sum_{k=1}^{K}exp(S_{ik}\Phi_i^d) - ln\sum_{k=1}^{K}exp(S_{ik}^*\Phi_i^d)}{\phi_{TC}}\right]$$

which is the difference in expected maximum utility per choice occasion, the asterisk denoting the utility level after the change in trip attributes. ϕ_{TC} is the parameter on travel cost from the model estimated above. K in this case indexes the fishing sites included in the analysis. From the combination of these models a change in water quality changes survivorship which changes recruitment. The change in recruitment changes catch rates impacting the demand for trips. The change in trips changes recreational and total harvest. The change in total harvest feeds back into abundance in the next period.

Total welfare can be derived from the equation:

$$\text{Total welfare} = W * A^{sb} * O$$

---

[12] NMFS has conducted an SPCE survey that contains summer flounder, scup and black sea bass. While the survey should have contained striped bass as a substitute, the survey did include "take a striped bass or bluefish trip" as the opt out choice.

where A^{sb} is the total number of striped bass anglers (unknown), W is welfare per trip from above and O is the number of choice occasions per year per angler. A^{sb} can be determined using the following identity:

$$T \equiv A^{sb} * O * p$$

Where T is the total number of trips taken for striped bass in a period and p is the average probability of taking a trip on a given choice occasion. That is, p is the total number of striped bass trips during a period divided by the total number of days in that period. The total number of directed striped bass trips can be estimated readily from the MRFSS data as either only those trips that said they were targeting striped bass when interviewed after taking the trip and/or all trips that caught striped bass. This measure also interacts with the harvest model. Total trip demand can also be used to estimate total expenditures and expenditure changes resulting from any change in trip attributes. Expenditures drive the inputs into the CGE portion of this model. Trip expenditures can be estimated using a 2010 NMFS survey of angler expenditures and those expenditures can be estimated specific to striped bass trips.

Recreation: Method 1 Discussion

Currently the biggest hurdle for implementing the recreational model is the lack of an existing SPCE survey for striped bass. NMFS has been implementing many of these surveys lately, but striped bass is not a federally managed species. It is currently managed by the Atlantic States Marine Fisheries Commission and, as a result, NMFS is reluctant to spend economic data-collection funds on this species. It may be possible to estimate this model with the standard, site choice RUM model, but that would require significant extensions and combining the MRFSS data with the MD DNR striped bass survey data to make the model spatially explicit. Currently the MRFSS survey does not collect onwater fishing location. So a site choice model built using just the MRFSS data could only include the fishing access point as the fishing site. While this would pose another problem for species substitution as the revealed preference site choice RUM does not include substitutes, there are no other striped bass substitutes included in this CGE model as it is currently proposed. Other substitutes would include bluefish, speckled trout, Spanish mackerel and spot/croaker/white perch (bottomfish). At the end of the day, focusing only on the intensive margin using the revealed preference tool will underestimate the effort change of increased quality as speckled trout fishermen might be attracted to striped bass fishing and overestimate the effort change from decreased quality as more anglers leave to fish for other species. Similarly for welfare estimates as welfare estimates tend to be overstated when substitutes are not included.

Recreation: Method 1 Extensions

A recent work by Gentner, Steinback and Lee (2012) includes a bioeconomic model of the scup fishery. [13] This model uses an age/size structured model of the stock linked to a RUM model constructed using an SPCE survey. This model also includes an extension that would allow the examination of bag and size limit policies. The authors simulated angler expected catch as in the above using the MRFSS catch data. They then randomly assign the maximum number of striped bass to each trip and used the MRFSS data to generate the probability distribution of expected catch using trips that targeted or caught scup. Given the expected catch, each fish is assigned a size based on the distribution of size at age, biomass age structure and historical selectivity of anglers. The length of this assigned fish is then compared to the minimum size limit and if it is large enough, it is retained. This process continues in the model until the bag limit is reached or the expected catch is reached.

Anglers choose a trip based on this expected catch with the probability that the trip is chosen taken from the RUM. If the trip is chosen, actual catch is then simulated using the same process as described above for expected catch. Welfare is calculated using this actual catch. Using a similar simulation, the striped bass model also could include the ability to examine bag and size limit regulations.

IIc.2.ii Recreation: Method 2 A second proposed method incorporates a behavioral model of anglers who are able to substitute across multiple fish species. This method is developed more fully in Warziniack and Finnoff (2013). Consider an angler who maximizes utility by catching several species of fish and by consuming other goods. Following the household production literature, the problem is modelled as if the household engages in schizophrenic interactions with nature (given by the GEEM), with fishing behavior occurring in three steps: 1) The angler maximizes utility by choosing between fishing f and other goods y, 2) The angler minimizes the cost of providing f by choosing which species to target, and 3) Catches are produced by combining effort and biomass. The model is developed from the perspective of a representative instant in time, although time notation is supressed in this section. Each of the three steps is considered in turn.

Step One: Maximize utility by choosing between fishing and other consumption goods

Let p_f be the price of the fishing experience, p_y be the aggregate price of other goods (all other good aggregated into a single composite good in this section), and I be an exogenous level of income. The budget constrained utility maximization problem is

$$Max\ U(f,y) \quad s.t.\ I - p_f f - p_y y = 0.$$

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[13] Gentner, B., S. Steinback, and M. Lee. 2012. Scup Allocation Analysis. Contract ending report for the Mid-Atlantic Fisheries Management Council. Currently undergoing peer review and not publicly available.

Assume $U_f, U_y > 0$, $U_{ff}, U_{yy} < 0$, and $U_{f,y} \geq 0$. Defining λ as the marginal utility of income, the necessary conditions for a maximum are:

$$U_f = \lambda p_f$$

$$U_y = \lambda p_y \qquad (18)$$

$$I = p_f f + p_y y$$

The first order conditions implicitly define demand functions for $f = f(p_f, p_y, I)$ and $y = y(p_f, p_y, I)$.

Step Two: Minimize the cost of fishing by choosing which fish to target

The level of fishing experience depends on the amount of fish caught throughout the year, which we assume is a choice variable. Let s index the set of fish species and S the vector of fish caught in the Bay throughout the year. The regulated species of interest are Eastern oyster (species *4*), blue crab (species *8*), blueback herring and alewife (species *11*), American shad (species *12*), and striped bass (species *15*), so $s \in S = \{4, 8, 11, 12, 15\}$. The demand for catches of each species s is given by the vector $x = [x_4, x_8, x_{11}, x_{12}, x_{15}]$ and the unit cost to the individual (or willingness to pay) of catching species s is given by p_s. The level of f is defined by $f = f(x), f'(x) > 0, f''(x) < 0, f_{x_s,x_t} \geq 0$. The cost minimization problem that characterizes optimal production of f is

$$Min \sum_s p_s x_s \quad s.t. \ f = f(x)$$

The necessary conditions for an interior solution are

$$p_s = \mu \frac{\partial f}{\partial x_s} \ \forall \ s \in RS \qquad (19)$$

$$f = f(x)$$

where μ is the Lagrange multiplier that measure the value of another unit of f. The solution to the cost minimization problem yields demand for catches $x_s = x_s(p, f) \ \forall \ s \in S$ and cost function $C(f, p) = \sum_s p_s x_s(p, f)$. $f(x)$ is assumed to be homogenous of degree one, so the cost function is also homogenous of degree one in f. If we define the unit cost of fishing to be $c_f(p)$:

$$C(f, p) = f c_f(p) = f p_f \qquad (20)$$

Conditions (18)-(20) define the optimal demand for catches of each species given the unit cost of catching each species.

Step Three: Production

The supply of catches, q_s, is determined by a combination of effort directed towards each species e_s, and the species density N_s (given by the GEEM) such that $q_s = q_s(N_s, e_s)$, where $\frac{\partial q_s}{\partial N_s} > 0, \frac{\partial q_s}{\partial e_s} > 0$, and $\frac{\partial^2 q_s}{\partial e_s N_s} > 0$. For given density at an instant in time N^t_s and catch q_s, effort is chosen optimally by minimizing costs,

$$Min \ w_e e_s \ s.t. \ q_s = q_s(N_s, e_s), N_s = N^t_s$$

where w_e is the unit cost of effort. Defining the Lagrange multiplier for the catch constraint as μ_{qs}, and the multiplier for density as μ_{Ns}, the Lagranigian is:

$$L = w_e e_s + \mu_{qs}(q_s - q_s(N_s, e_s)) + \mu_{bs}(N_s - N^t_s)$$

and the first order conditions are

$$w_e = \mu_{qs}\frac{\partial q_s}{\partial e_s}$$

$$\mu_{bs} = \mu_{qs}\frac{\partial q_s}{\partial N_s} \tag{21}$$

$$q_s = q_s(N_s, e_s)$$

$$N_s = N^t_s$$

The first order conditions implicitly define the demand for effort $e_s(w_e, N^t_s)$ and the marginal (shadow) value of biomass $\mu_{bs}(w_e, N^t_s)$, from which the marginal value of catches μ_{qs} can be determined.

Equilibrium conditions

The three steps of the problem are brought together in the equilibrium conditions. These conditions require $x_s = q_s$, which determines the willingness to pay for catches, $p_s = \mu_{qs}$. Furthermore, we know that in principle $p_s q_s = \mu_{bs} N^t_s + w_e e_s$. The price of effort is the same for all species, thus

$$w_e = p_s \frac{\partial q_s}{\partial e_s} = p_t \frac{\partial q_t}{\partial e_t} \ \forall \ s, t \ \in S$$

Note $\frac{\partial q_s}{\partial e_s}$ is the catch rate for species s for a given level of biomass. A key insight of this analysis is that catch rates and marginal willingness to pay are equilibrium concepts – jointly determined by the relative biomass of each species. Combining the above with the individual's first order conditions defines the allocation and catch rates in equilibrium.

$$\frac{p_s}{p_t} = \frac{\partial q_t/\partial e_t}{\partial q_s/\partial e_s} = \frac{\partial f/\partial x_s}{\partial f/\partial x_t} \quad \forall \, s,t \, \in S \tag{22}$$

Recreation method 2: Discussion

The model can be implemented using benchmark catch rates and levels of effort determined in prior work. Value of time spent recreating and benchmark willingness to pay for catches can be transferred from the valuation literature, allowing the model to be calibrated (see Warziniack and Finnoff, 2013 as an illustration).

II.c.3 Nutrient waste disposal   Nitrogen, phosphorus, and sediment enter the Bay primarily through runoff and drainage into the watershed. There are both point and non-point sources of this nutrient pollution. Point sources include municipal water treatment facilities, and industrial discharge facilities, storm water and sewer overflows, and animal feeding operations. Nonpoint sources include agriculture, atmospheric deposition, erosion, non-regulated storm water runoff, and tidal re-suspension.

However, nutrient loading in the Bay is not constant over time. The CGE is capable of simulating the impacts of variations in the flows of nutrients, for example from nitrogen and phosphorus flows. Finnoff and Tschirhart (2011) demonstrate how stochastic nutrient loads can be incorporated into a linked CGE-GEEM model for the Neuse River estuary in North Carolina. In that study nutrient flows were taken to be random variables distributed normally with known mean and standard deviation. Policies to reduce nutrient flows such as the Total Maximum Daily Load (TMDL) lower the mean.

There are several steps to including nutrient loading in a linked CGE-GEEM model as proposed in this document. The first is to model the nutrient generating activity. In Finnoff and Tschirhart (2011) the agricultural sector was modeled as generating the nutrient flows as a byproduct of production. Thus the nutrient flow at a given time, P_t was given by the amount of agricultural production in that time period, $Q_{A,t}$, or $P_t = pol_A Q_{A,t}$ (where pol_A is a positive constant reflecting the nutrient loading caused by agriculture in time t). The second step is to reflect how the nutrient loading affects the ecosystem. In Finnoff and Tschirhart (2011) nutrient loading caused detrimental phytoplankton blooms which increased sediment oxygen demand (SOD). Increased

SOD causes levels of dissolved oxygen (DO) in the water column to fall, with negative physiological impacts on harvestable species and their prey. Reductions in DO have been shown to stress species, Borsuk *et al.* (2002).

This methodology can be included in the GEEM through assuming the stress from low DO implies that an individual of the stressed species loses additional respiration energy for any biomass it demands (modifying the equation for variable respiration as given in Equation (1)). The methodology increases the variable respiration for a given biomass demand, where the increase is a result of the nutrient loading. While the standard bioeconomic model would establish harvestable species populations as a function of nitrogen loading, GEEM allows a more detailed picture of how the loads work their way through the trophic structure of the model.

III Economic structure of the CGE

The regional economy of Chesapeake Bay watershed consists of households and producing sectors and government, linked to each other and the rest of the world through commodity and factor markets. It is important to note that watershed boundaries may not coincide with government jurisdictions. Trade in and out of a watershed may include trade between counties within the same state. Definition of the economic region in the CGE must take this into consideration.

The CGE model developed in Ballard *et al.* (1985) and applied in the OECD GREEN model (Burniaux et al, 1991) by Seung and Kraybill (1999) and by Seung et al. (2000) may be most appropriate CGE for linking with GEEM. While most CGE's assume perfect foresight on the part of all agents, the recursive dynamics of Ballard's methods are consistent with those in GEEM. The approach used by Ballard *et al.* may be termed "myopically dynamic", as it consists of a sequence of static optimizations and resulting equilibria connected through the evolution of factor stocks. This parallels the ecological static optimizations and short-run static equilibria resulting in evolution of ecosystem population stocks.

Sectors that can be be included in the model are those that represent connections between the regional economy and the GEEM of the Bay. These sectors include commercial fishing, recreation, animal feeding operations, other agricultural operations, water treatment facilities and miscellaneous goods. Fish harvesting can be incorporated as described in Section II.c.i. Recreational fisheries can be incorporated into the framework as described in Section II.c.ii. Animal feeding operations and agricultural operations can be separated for their roles in nutrient loading in the Bay. Miscellaneous goods are a catch all for the residual private industries in the Chesapeake economic region.

In a Ballard type model, profit maximizing, price-taking firms employ capital and labor to produce their outputs in a continuous, nonreversible, and bounded process. Outputs from each

producing sector may be used as intermediate goods in production by other sectors, sold in regional markets and exported out of the watershed to domestic or foreign markets. Production within a watershed is differentiated from aggregate imports following Armington (1969). Capital and labor are homogeneous, perfectly mobile within the watershed, and defined as service units per period. Firms in each sector employ factors of production and intermediate goods to produce their output, which is sold in watershed markets and exported out of the watershed to either domestic markets or foreign markets. Firms smoothly substitute over primary factors through CES functions, but employ intermediates in fixed proportions through Leonteif functions.

Households are differentiated by their income category and demand of composites of goods produced in the watershed. Household demands are derived from CES functions over aggregated goods, where the price consumers face are indices of aggregate import and domestic prices, with domestic and foreign import prices taken exogenously. Imperfect substitution possibilities are given by the nested CES functions. Substitution possibilities in demand between foreign and domestic imports are also governed by CES functions. Household incomes are derived through a two-stage process. Households are endowed with varying amounts of labor and capital. These factors are exchanged in factor markets, and through production generate value added. Value added expenditures first flow to the factor "institutions", and are then redistributed to households. Total factor payments to households from value added are net of factor taxes, depreciation allowances, rents attributable to the factor (which are distributed to households from corporations through enterprise income), and labor payments out-of-watershed.

Government behavior typically enters into CGE models in two layers: a federal level and a state/local level. While state and local governments across counties in the watershed are obviously distinct, standard practice is to aggregate this level and focus on region level policies. This practice allows a good inspection of regionally relevant policies and issues, but makes the assumption that all levels of government act in the same way following the policy. Given this assumption, government entities operate according to a balanced budget, produce and consume goods. Government revenues are from taxes (indirect business taxes, primary factor taxes, and income taxes all taken fixed as proportions of output), sales of governmentally produced commodities, and government borrowing and transfers. These revenues are then redistributed in lump-sum both to consumers and producers.

The assumption that all levels of government act in the same way following the policy, that is, they act in unison, would need to be examined in more detail. Differentiating policy making (taxation and redistribution for example) by states in the watershed would require a significant expansion of the model, to one that represented each state explicitly. If policies by the states towards the Bay are significantly different, then this could be a worthwhile goal. However, if federal policies require the states to consider policies towards the Bay that are, for the most part, uniform across states, the aggregation outlined here may perform well enough for considerable

insights. Of course, these insights would have to be taken with an understanding of the limitations of the aggregation, namely that the individual states are not explicitly dissaggregated.

In the short-run (for example, each year) model equilibrium conditions require domestic goods prices to adjust until total demand balances total supply, and all firms earn zero economic profits. Factor prices also adjust until supply of factors equals demand. The model is closed by (1) assuming factor endowments are given; (2) by specifying a fixed percentage of factor payments go to the rest of the world; (3) by allowing net government borrowing to adjust to maintain the government balanced budget; and (4) assuming import prices are constant.

In the long-run (as years go by) capital stock dynamics at the regional level are generally thought to be driven by investment (Seung and Kraybill, 1999). While regional investment adds to the capital stock over time, regional investment expenditures are myopic and given by fixed proportions of regional production. Labor stock dynamics, however, are not endogenous to the model and are taken to grow at an exogenous rate. This rate is usually assumed to be the rate of capital stock growth in the benchmark (Ballard) following balanced growth assumptions. But, as the specifics of these processes at the regional level have not been resolved and remain under debate, scenarios with growing factor stocks are to be contrasted against scenarios with factor stocks held constant.

The welfare effect of policy scenarios can be measured by the equivalent variation, the amount an individual is willing to pay to avoid an inferior outcome. Each scenario's welfare change can be calculated by household and for the watershed as a whole.

III.a   Chesapeake Bay Social Accounting Matrix (SAM)

Building the CGE model requires constructing a Social Accounting Matrix (SAM) for the watershed. The basic data for the watershed SAM can be taken from IMPLAN county-level data. Though deficient in many areas, IMPLAN data is the industry standard; it is more comprehensive than any other source and provides a decent building block on which to add. IMPLAN data is available at the county level. However, given the large numbers of counties from each state it may be more appropriate to purchase IMPLAN data for each of the six states (including the District of Columbia).

IMPLAN has 509 economic sectors. It differentiates households according to income class, the federal government's interactions with the economy from that of states and local governments, and between foreign and domestic trade into and out of regions. The sectors identified above are commercial fishing, recreation, animal feeding operations, other agricultural operations, water treatment facilities and miscellaneous goods. Table II.6 shows a portion of the mapping from IMPLAN sectors to these five sectors..

In addition to the mapping of IMPLAN data to sectors in the model, significant alterations to some sectors in the IMPLAN data must be made. Externally gathered data could be employed to better specify the commercial fishing sectors as shown in Finnoff and Tschirhart (2008).

Table II.6 Industries and IMPLAN sectors

Description	IMPLAN Accounts
Commercial Fishing	16 ! Fishing
Recreation	17 ! Hunting and trapping 477 ! Bowling centers 475 ! Museums historical sites zoos and parks 478 ! Other amusement gambling and recreation industry
Animal feeding operations	11 ! Cattle ranching and farming 12 ! Poultry and egg production 13 ! Animal production except cattle and poultry
Other Agriculture	1 ! Oilseed farming 2 ! Grain farming 3 ! Vegetable and melon farming 4 ! Tree nut farming 5 ! Fruit farming 6 ! Greenhouse and nursery production 7 ! Tobacco farming 8 ! Cotton farming 9 ! Sugarcane and sugar beet farming 10 ! All other crop farming
Water-Sewage and Other Systems	32 ! Water sewage and other systems
Employee Compensation	5001 !Employee Compensation
Capital Income	6001 ! Proprietary Income 7001 ! Other Property Income
Miscellaneous	15 ! Forest nurseries forest products and timber trac 18 ! Agriculture and forestry support activities 33 ! New residential 1-unit structures nonfarm 34 ! New multifamily housing structures nonfarm 35 ! New residential additions and alterations nonfarm 36 ! New farm housing units and additions and alteratio 37 ! Manufacturing and industrial buildings 38 ! Commercial and institutional buildings 39 ! Highway street bridge and tunnel construction 40 ! Water sewer and pipeline construction 41 ! Other new construction 42 ! Maintenance and repair of farm and nonfarm residen 43 ! Maintenance and repair of nonresidential buildings 44 ! Maintenance and repair of highways streets bridg 45 ! Other maintenance and repair construction 19 ! Oil and gas extraction 20 ! Coal mining 21 ! Iron ore mining 22 ! Copper nickel lead and zinc mining 23 ! Gold silver and other metal ore mining 24 ! Stone mining and quarrying 25 ! Sand gravel clay and refractory mining 26 ! Other nonmetallic mineral mining 27 ! Drilling oil and gas wells 28 ! Support activities for oil and gas operations 29 ! Support activities for other mining 30 ! Power generation and supply 31 ! Natural gas distribution 48 ! Flour milling 49 ! Rice milling 50 ! Malt manufacturing 51 ! Wet corn milling 52 ! Soybean processing 53 ! Other oilseed processing

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  480  ! Other accommodations
  481  ! Food services and drinking places
  482  ! Car washes
  483  ! Automotive repair and maintenance  except car wash
  484  ! Electronic equipment repair and maintenance
  485  ! Commercial machinery repair and maintenance
  486  ! Household goods repair and maintenance
  487  ! Personal care services
  488  ! Death care services
  489  ! Drycleaning and laundry services
  490  ! Other personal services
  491  ! Religious organizations
  492  ! Grantmaking and giving and social advocacy organiz
  493  ! Civic  social  professional and similar organizati
  495  ! Federal electric utilities
  498  ! State and local govt electric utilities
  499  ! Other State and local government enterprises
  501  ! Scrap
  502  ! Used and secondhand goods
  503  ! State & Local Education
  504  ! State & Local Non-Education
  505  ! Federal Military
  506  ! Federal Non-Military
  507  ! Rest of the world adjustment to final uses
  508  ! Inventory valuation adjustment
  509  ! Owner-occupied dwellings
  500  ! Noncomparable imports
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Adjustments will have to be made for recreation. To find the value of recreational fishing in the Chesapeake Bay watershed the sources used in the published literature can be followed, at a minimum using the data reported by NOAA Fisheries and Marine Recreational Fisheries Information Program (MRIP). Details on this data collection program can be found at http://www.st.nmfs.noaa.gov/st5/RecFishEcon.html. This data is far superior to USFWS data from 'U.S. Fish &Wildlife Service Survey of Fishing, Hunting, and Wildlife Associated Recreation' as the expenditure data is collected using trip intercepts. As a result, there is far more sample for each area, and expenditure estimates may be possible at the county level within the study region. Additionally, the data has been used through the years to estimate multiple site choice RUM models to estimate the value of access, catch and harvest, including models specifically for striped bass. For more detail see http://www.st.nmfs.noaa.gov/st5/RecFishEcon_pubs.html.

Additionally, NOAA Fisheries has recently conducted stated preference choice experiment surveys that include striped bass as a one of the target species. This recent data collection may allow the calculation of the elasticity of substitution needed for the EAL approach. It may also be necessary to improve the precision of the IMPLAN data across sectors. This typically requires the augmentation of the data with any industry specific data that has a higher degree of precision than the base IMPLAN data. NOAA Fisheries has two input/output models for fisheries that may be of some use. The model developed by Jim Kirkley that is used for Fisheries Economics of the U.S. contains 18 species by gear production functions that may be useful. Additionally, the Northeast Fisheries Science Center built a SAM that includes new sectors for every gear in the Northeast region by sug-region. Addtionally, NMFS just recently completed a cost and earnings survey for the for-hire fleet in this region that would allow the inclusion of that sector in the CGE model. The for-hire fishery is a very important economic driver in the Bay[14]

III.b   Modeling Details of a CGE

A specification of the CGE that follows standard methods as given by de Melo and Tarr (1992) is presented in brief here.

III.b.1 Producer Behavior   Firms from any sector a (a = all industries included) produce according to a two-level production function. The first level uses a Leontief combination of primary factor inputs, labor and capital, along with fixed intermediate inputs

$$Q_a = \min\left[VA_a(L_a, K_a), \frac{V_{1a}}{a_{1a}}, \frac{V_{2a}}{a_{2a}}, \ldots, \frac{V_{na}}{a_{na}} \right].$$

The gross output of sector a, is represented by Q_a. The CES value-added function is represented by VA_a. The required intermediate inputs are represented by V_{na}, and are fixed proportions of their output, a_{na}.

The firm's minimization problem for choosing factor inputs that comprise value added is

$$Min\ C_a = wL_a + rK_a \quad s.t. VA_a = \varepsilon_a\left[tva_{af}L_a^{-(\frac{\sigma_a-1}{\sigma_a})} + tva_{af}K_a^{-(\frac{\sigma_a-1}{\sigma_a})} \right]^{-(\frac{\sigma_a}{\sigma_a-1})}.$$

Firms choose labor (L) and capital (K) so that they minimize their costs where the unit costs of labor and capital are given by w and r. In a firm's minimization problem, ε_a is the efficiency parameter, tva_{af} is the share parameter for each factor, and σ_a is their elasticity of substitution.

The first-order conditions of the minimization problem define the labor and capital choices. The first-order conditions are:

$$0 = w - \lambda \, \varepsilon_a \left[\left[tva_{aL} L_a^{-\left(\frac{\sigma_a-1}{\sigma_a}\right)} + tva_{aK} K_a^{-\left(\frac{\sigma_a-1}{\sigma_a}\right)} \right]^{-\left(\frac{\sigma_a}{\sigma_a-1}\right)-1} tva_{aL} L_a^{-\left(\frac{\sigma_a-1}{\sigma_a}\right)-1} \right],$$

$$0 = r - \lambda \, \varepsilon_a \left[\left[tva_{aL} L_a^{-\left(\frac{\sigma_a-1}{\sigma_a}\right)} + tva_{aK} K_a^{-\left(\frac{\sigma_a-1}{\sigma_a}\right)} \right]^{-\left(\frac{\sigma_a}{\sigma_a-1}\right)-1} tva_{aK} K_a^{-\left(\frac{\sigma_a-1}{\sigma_a}\right)-1} \right].$$

Together these first-order conditions define the firm's optimal mix of labor and capital as given by the equality of the input price ratio to the marginal technical rate of substitution

$$\frac{w}{r} = \frac{tva_{aL} K_a^{\frac{\sigma_a-1}{\sigma_a}+1}}{tva_{aK} L_a^{\frac{\sigma_a-1}{\sigma_a}+1}}.$$

In the short-run (i.e. per year) labor and capital are taken as given, such that $\sum K_a = \bar{K}$ and $\sum L_a = \bar{L}$ although these endowments can change through time. Both factors are assumed to be perfectly mobile in the region and demands are homogenous of degree zero.

The firms' costs include primary costs and intermediate costs (net of indirect business taxes). Primary costs are those paid for factors of production, resulting from the cost minimization above. To find the primary cost function $PRIMC$ we substitute the factor demands in to the cost equation $(C_a = wL_a + rK_a)$

$$PRIMC(a) = \left(VA(a) \left(\sum_f \left(\frac{PF(f)}{tva(f,a)} \right)^{eta(a)} \right)^{\frac{1}{eta(a)}} \right),$$

where $eta_a = 1 - \sigma_a$. Intermediate costs are those for intermediate inputs, determined by the amount of required intermediate inputs and their cost

$$INTC(a) = \sum_c V(c,a) * PC(c).$$

Intermediate demands are *V(c,a)* and the price that the firms pay to the other sectors for those goods are *PC(c)*. By our use of a Leontief production function, these costs are separable so that total costs are

$$CTOT(a) = PRIMC(a) + INTC(a).$$

III.b.2 Household Behavior Households maximize their consumption over all the goods produced by sectors *a* based on a CES Utility function and constrained by their disposable income:

$$\max U_h = \sum_a \left[\alpha h_{ha}^{\frac{1}{\sigma_h}} HHX_{ah}^{\frac{\sigma_h - 1}{\sigma_h}} \right]^{\frac{\sigma_h}{\sigma_h - 1}} \quad s.t. \sum_a PC_a HHX_{ah} \leq HHID_h$$

HHX$_{ah}$ is a household's demand of sector *a,* and *PC$_a$* is the regional price for the final demanded commodity. The household's share parameters are represented by *αh$_{ha}$,* and are fixed. The household's elasticity of substitution parameter is represented by *σ$_h$*.

Household incomes (*HHI$_h$*) are derived through a two-stage process. Households are endowed with varying amounts of labor and capital. These factors are exchanged in factor markets, and through the production process generate value added. Total value added expenditures flow first to the factor "institutions", and then redistributed to households.   Not all value added expenditures are paid to households as certain portions account for federal, state and local factor taxes, or are retained as corporate profits and capital consumption allowances (mainly for capital not labor and includes payments to corporations, gross private fixed investment, or inventory sale deletions), or are payments to the rest of the world (including corporate gifts of individuals, insurance payments and an artifact of rounding for labor in the IMPLAN data). Labor payments to households are then found as the net of total value added payments for labor net of these adjustments. Capital payments to households are found in the same fashion. Households also derive incomes from other sources including interest income, enterprise income and Federal and State and Local government transfers. Household income is then defined

$$HHI(h) = \underbrace{\sum_f \theta_f(h,f) * FACPMT(f)}_{HH\ Share\ of\ PACPMT} + \underbrace{\sum_g HTRNS(h,g)}_{Gov't\ transfer} + \underbrace{HINTINCo(h)}_{Interest\ Income}$$

$$+ \underbrace{\sum_t HEXINCo(h.t).}_{Outside\ Income}$$

When maximizing their utility, households' disposable income constrains their choices. Part of a household's income is allocated towards domestic and foreign savings, and federal and state government

$$HHID(h) = HHI(h) * \left[\left(1 - \underbrace{\sum_g htr(g,h)}_{HH\ Tax\ Rate}\right) - \underbrace{mps(h)}_{Savings\ Rate} - \underbrace{\sum_t mpsf(t,h)}_{Savings\ Rate\ Foriegn}\right].$$

The household's demands are determined by solving the first order conditions of utility maximization problem. In this economy households do not differentiate between domestic and foreign goods. The household's resulting demands are

$$HHX(c,h) = \frac{HHID(h)}{PC(c)^{\sigma h} * (\alpha h * \sum_c (PC(c)^{(1-\sigma h)} * \alpha h^{(\sigma h-1)}))^{\frac{1}{(1-\sigma h)}}}.$$

III.b.3 Trade: Product Differentiation in Production   Product differentiation is introduced to the supply side (for all sectors) through the use of constant elasticity of transformation (CET) functions following De Melo and Tarr (1992). Industry output for all sectors is allocated to regional consumption, XD_a, or export (in aggregate to foreign and domestic markets), XE_a, through a constrained maximization of industry revenues given regional prices PD_a and export prices PM_a, subject to a CET function with substitution possibilities governed by elasticities of transformation. The CET function and resultant first order conditions determine the mix of goods allocated for regional consumption and exports

$$X_a = AT_a \left[\sum_t (cetf_{at} XE_{at})^{\rho t_a} + cetd_a XD_a^{\rho t_a}\right]^{\frac{1}{\rho t_a}},$$

$$XD_a = \frac{cetd_a}{\sum_t cetf_{at}} \left(\frac{PM_a}{PD_a}\right).$$

The optimization allows for substitution between production for regional and export markets, driven by the relative prices of regional goods and exports, and the magnitude of substitution possibilities given by the elasticity of transformation $\sigma t_a = 1/(\rho t_a - 1)$. The distribution parameters are $ceft_{at}$ and $cetd_a$ and AT_a is the efficiency parameter. Exports for domestic or foreign markets are differentiated by another CET function and associated first order condition.

III.b.4 Trade: Product Differentiation in Consumption Regional demand is comprised of household, investment, (regional) intermediate, and government demands. Regional consumers demand a composite of regionally produced goods and imports (from both domestic and foreign sources), where the differentiation is assumed to occur in perfectly

competitive international markets. The blend of regional and imported goods is found through households minimizing their costs of meeting their composite commodity demands, given relative prices and substitution possibilities (from CES functions). The resulting first order conditions determine the mix of imports to regional production. The same technique is employed for differentiating between foreign and domestic imports.

This product differentiation in aggregate demand for all sectors Q_i is achieved through the use of the "Armington assumption" (Armington 1969). Regional consumers demand a composite of regionally produced goods QD_i and imports QM_i, (from both domestic and foreign sources) where the differentiation is assumed to occur in perfectly competitive markets. The blend of regional and imported goods is found through households minimizing the costs to them of meeting their composite commodity demands, given regional PD_i and import prices PM_i, prices and substitution possibilities (from CES functions with elasticity of substitution σ_i^C). The CES functions and resulting first order conditions determine the mix of imports and regional production

$$Q_a = AC_a \left[armd_a QD_a^{\rho c_c} + \sum_t armf_{tc} QIMP_{tc}^{\rho c_c} \right]^{\frac{1}{\rho c_c}},$$

$$QIMP_a = \frac{armd_a}{\sum_t armf_{tc}} \left(\frac{PD_a}{PM_a} \right)^{\sigma c_c},$$

where $armd_a$ and $armf_{tc}$ are the distribution parameters and AC_a is the efficiency parameter. The same technique is employed for differentiating between foreign and domestic imports. The remaining components of demand, investment I_i and intermediate demands V_{ac}, are modeled as fixed proportions of output. Demand prices of all goods are indices of import and regional prices, with import prices taken exogenously (following the "small" country assumption).

III.b.5 Government Federal, state and local governments operate under balanced budgets, produce and consume goods, and tax trade related activity. Government revenues are from taxes, sales of governmentally produced commodities, and government borrowing and transfers. These revenues are redistributed in lump sum to both consumers and producers to maintain a balanced budget.

Tax revenues are from indirect business taxes, primary factor taxes, and income taxes. Taxes are taken as fixed proportions of output. Indirect business taxes include sales and excise taxes, and other regionally specific taxes paid through day-to-day operations of industry (not including net income taxes). Profits are taxed similarly, found as a fixed proportion of rents to the factors of production. Factors are taxed according to the value of their employment. Labor, or payroll taxes, are determined from industry payments to labor while capital taxes are found in the same fashion.

The final sources of tax revenues are from household income taxes. Households are taxed on their gross incomes at differing rates, according to their income group. Government revenues are further supplemented through sales of government commodities, government interest received and amounts that the government borrows.

Expenditures by the government are on government demand for commodities, transfers to households, and transfers to producers. A balanced budget is maintained through a balance of total revenues and expenditures.

III.b.6 Equilibrium The economy is assumed to operate under equilibrium. In addition to the government operating under a balanced budget, the households also balance their budgets among savings and consumption, and the firms operate under a zero profit condition. The firm and household optimization problems yield the equilibrium conditions above. The final equations needed to ensure equilibrium are that profits equal zero and aggregate supply equals aggregate demand. Profits equal the difference between total costs and total revenues:

$$PD(a)DY(a) - CTOT(a) = 0.$$

Supply and demand equate at the regional level so that:

$$Q(c) = X(c).$$

III.b.7 Welfare Measures The welfare impacts of alternative scenarios can be evaluated in terms of modified Hicksian equivalent variation measures similar to those developed in Ballard *et al*. Each policy change leads to changes across prices and income in relation to a benchmark of business as usual. Equivalent variation calculates how much income a consumer would give up or accept to forgo a price change. The welfare measure is the difference between expenditure functions

$$EV = \underbrace{e(\mathbf{p}^o, u^n)}_{original\ price} - \underbrace{e(\mathbf{p}^n, u^n)}_{new\ price}.$$

Equivalent variation considers differences in expenditures. The first term represents the expenditures to achieve the new level of welfare at the original price, and the second term is level of expenditures necessary to achieve the new level of welfare at the new price.

IV) Connection to a Recent EPA Report

In section II.c.3 on nutrient waste disposal, a discussion was presented about introducing stochastic nutrient loads into a linked CGE-GEEM model. The point would be to mimic current nutrient loading practices and then determine how changes in the loading would alter the structure of the ecosystem, and alter the prices and quantities of goods and of welfare in the economy.

Another use of a linked CGE-GEEM would be to examine alternative strategies for restoring the Bay as outlined in U.S. EPA (2012). In that work, alternative pollution control projects are evaluated for their cost and effectiveness at meeting TMDL standards. Projects are divided into gray and green where the former are conventional projects such as waste-water treatment plants or upgrading septic systems, and the latter are projects that work directly with the ecosystems such as wetland restoration and reforestation. Gray projects would be incorporated into the CGE, while green projects would also be incorporated into the CGE, but in addition be incorporated into GEEM.

A wetland restoration project, for example, would require capital and labor inputs that might be transferred from the production of other goods. Simultaneously it would yield greater habitat and reduced pollution levels in GEEM; therefore, how the restoration would impact all species populations could be quantified. This in turn would change recreational and commercial harvesting opportunities, with concomitant flows of labor and capital into harvesting.

The inclusion of ecosystem services in the EPA report is considered a unique feature of the framework. The key questions addressed in the report are:
> "(1) what mix of pollution-control projects provides the least costly way to achieve water quality goals in an impaired watershed and
> (2) how does the consideration of bonus ecosystem services affect the desired mix of projects?" (p. ES-1)

The changes in ecosystem services brought about by pollution-control projects can be part of the CGE-GEEM, thereby broadening the assessment of these changes. Basically, the EPA report uses a partial equilibrium framework to assess alternative projects, and this can be expanded to a general equilibrium framework in the CGE-GEEM.

The GEEM presented in section I would need to be extended to include more species in order to incorporate the EPA work. Carbon sequestration and duck hunting, for examples, are two ecosystem services enumerated in the report. This may necessitate adding waterfowl to the GEEM food web in addition to plants such as submerged aquatic vegetation as a waterfowl food source. A method along the lines of the EPA report can be used to measure ecosystem carbon content.

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Appendix A. GEEM Calibration Table Notes

NA – not applicable or not needed. Weight is wet weight (WW). Mummichogs were used for littoral forage fish. Bay area is A = 10000 km^2 (Christensen 2009).

[a] Individuals are aggregated into population units and the units are divided by Bay surface area to yield population units per square kilometer. Bay area used is A = 10000 km^2 (Christensen 2009).

[b] The 1950 biomass estimate is 27 t/km^2 (1000 kg/t) = 27000 kg/ km^2 (Christensen et al. 2009). At 435.6 kg/unit this yields 61.98 units km^{-2}.

[c] 1950 biomass estimate 6.239 t/km^2 (1000 kg/t) = 6239 kg/ km^2 (Christensen et al. 2009). From EPA zooplankton SOP, 10% DW:WW conversion (Doohan 1973 in EPA zoop SOP) and average rotifer/nauplii dry weight 0.25 µg/ind (Theilacker and Kimball 1984), 0.25 µg DW (µg WW/.1 µg DW)(kg/1x10^9 µg) = 2.5 x 10^{-9} kg/ind. The microzoop population is then (6239 kg/km^2)/(2.5 x 10^{-9} kg/ind) = 2.4956 x 10^{12} ind/km^2. Let one unit be 1 x 10^{12} ind.

[d] 1950 biomass estimate 10.3 t/km^2 (p. 92), or 10300 kg/km^2 (Christensen et al. 2009). Using log W = 0.86475L (Heinle 1966) average dry weight of *A. tonsa* (dominant mesozoop species in Bay) is 10 ug. Using 15%DW:WW conversion (Jorgensen 1979 from Christiansen and Pauly Trophic Models of Aquatic Ecosystems book p. 227) wet weight of an individual (10 ug DW/1 ind)(1 ug WW/.15 ug DW) = 66.67 ug WW or 6.667 x10^{-8} kg/ind. Using estimated biomass (10300 kg/km^2)(6.667 x10^{-8} kg/ind) = 154942242887 ind/km^2. If 1 unit = 1 x 10^9 ind. then 154.942 units.

[e] 1950 biomass 20400 kg/km^2 (Christensen et al. 2009, p 56) and weight from Rothschild (1994) for an 88 mm ind. of 0.0995 kg → 205025 ind/km^2 Let one unit be 1000 ind.

[f] 1950 biomass of softshell 6923 kg/km^2 and hardshell 2626 kg/km^2, and average wet weight of softshell 0.051 kg and hardshell 0.0912 (Hammen 1978) 6923 kg/km^2/0.051 kg/ind + 2626 kg/km^2/0.0912 = 162185 ind/km^2.

[h] 1950 biomass of in/epi fauna 66675 kg/km^2 (Christensen et al. 2009).   Groups used: grass shrimp, mysids, polychaetes. Average weight of grass shrimp: 0.14 g, mysid: 0.0135 g, polychaete: 0.00003 g. Taking an average = 0.00005118 kg/ind. (66675 kg/km^2)(ind/0.00005118 kg) = 1302754982 ind/km^2. 1 unit = 1 x 10^8 individuals.

[i] 1950 biomass 4000 kg/km^2 (Christensen et al. 2009) and weight from Olmi and Bishop (1983) for an 137 mm ind. of 0.17 kg → 23529 ind/km^2 Let one unit be 1000 ind.

[j] 1950 biomass 33000 kg/km^2 (Christensen et al. 2009) at 0.315 kg/individual yields 104762 ind km^2 ≈ 105 units km^2.

[k] 5.21 t km^{-2} (Christensen 2009). Therefore, (5.21 t/ km^2)(1000 kg/ t)(unit /199.2 kg) = 26.15 units/km^2.

[l] 1950 biomass estimate for alewife/herring, 5986 kg/km^2 (Christensen et al. 2009). From fishbase.org, average length alewife = 30 cm and average length herring = 27.5 cm. Using the length/weight relationship, ln W(g) = ln a + b*ln L(cm), where ln a = -5.420 and b = 3.235 for alewife (Stewart and Binkowski 1985) , average weight of an alewife = 0.26583. Similarly for herring: ln a = -4.702 and b = 2.904 (Dept of int species profile), and average weight = 0.13733. Averaging the masses of both species, (0.26583 + .13733)/2 = 0.20158 kg/ind. Population is then (5986 kg/km^2)(ind/0.20158 kg) = 29695.41 ind/ km^2. A unit = 100 individuals, then 296.96 unit/ km^2.

[m] 1950 biomass estimate 0.4 t km^{-2} (Christensen et al. 2009). Thus (0.4 t/km^2)(1000 kg/t)(ind./1.422 kg)(unit/100 ind) = 2.813 units/km^2.

[n] 1950 biomass estimate 3400 kg/km^2 (Christensen et al. 2009). From fishbase.org, average anchovy length is 59mm. Using the length/weight relationship, ln W(kg) = ln a + b*ln L(cm), where ln a

= -4.76779 and b = 2.82589 (Anchovy species profile) the average weight of a 59 mm anchovy is 0.0017236 kg. (3400 kg/km^2)(ind/.0017236 kg) = 1972615 ind/km^2.

[o] A weighted average of phytoplankton species' body weights (4.35615x10^{-10} kg., Petipa et al. 1970, Table 1). Hence, (4.35615x10^{-10} kg/ind) (10^{12} ind/unit) = 435.615 kg/unit.

[p] 1950 Q/B estimate 350 y^{-1} (Christensen et al. 2009). (350 y^{-1}) (2500 kg/unit micro) = 875000 kg unit^{-1} y^{-1} for microzoo consumption of phytoplankton.

[q] 1950 Q/B estimate 83.333 y^{-1} (Christensen et al. 2009). (83.333 y^{-1})(66.67 kg/unit meso)(72% diet is micro) = 4000 kg unit^{-1} y^{-1} for meso consumption of microzoo. Similarly, for phytoplankton prey at 28% of diet yields 1556.63 kg unit^{-1} y^{-1} of phytoplankton.

[r] Assuming prey biomass consumed is 2 times predator biomass which is 20400 kg/km^2 (Christensen 2009), we get (40800 kg/km^2 y)(km^2/205.025 units) = 199.00 kg/unit y. Assuming 90% of predation is on phytoplankton (Christensen 2009) yields (179.10 kg/ unit y) of phytoplankton consumed. Similar for the other two prey.

[t] 1950 Q/B estimate softshell: 2.25 year^{-1}, hardshell 5.1 y^{-1} Weighted average (82*2.25 + 18*5.1)/100 = 2.763 y^{-1}. Diet item = microzoo: (58.974 kg/unit meso)(2.763/y)(9% diet) = 14.7 kg unit^{-1} y^{-1}. Diet item = phyto: (58.974 kg/unit meso)(2.763/y)(57.5% diet) = 93.7 kg unit^{-1} y^{-1}. Diet item = detritus: (58.974 kg/unit meso)(2.763/y)(13% diet) = 21.2 kg unit^{-1} y^{-1}.

[v] 1950 Q/B estimate for in/epi fauna: 5 y^{-1}. Diet item = microzoo: (B for in/epi from note h - 66675 kg/km^2) (5/y)(km^2/13.0275 units) *8% diet = 2047.21 kg unit^{-1} y^{-1}. Diet item = in/epi fauna: (in/epi B from note h - 66675 kg/km^2) (5/y)(km^2/13.0275 units)*2% diet = 511.80 kg unit^{-1} y^{-1}. Diet item = phyto: (in/epi B from note h - 66675 kg/km^2) (5/y)(km^2/13.0275 units)*40% diet = 10236.04 kg unit^{-1} y^{-1}. Diet item = detritus: (in/epi B from note h - 66675 kg/km^2) (5/y)(km^2/13.0275 units)*20% diet = 5118.02 kg unit^{-1} y^{-1}.

[x] Assuming prey biomass consumed is 4.0 and 12.057 times predator biomass (8000 kg/km^2 (Christensen 2009)) for adults and juveniles, respectively, and since there is no age structuring, we use an approximate average of 8.0 times to obtain (32000 kg/km^2 y)(km^2/235.29 units) ≈ 136.00 kg/unit y). Assuming 15% of predation is on clams (Christensen 2009) yields (20.40 kg/ unit y) of clams consumed. Similar for other prey.

[y] 1950 Q/B estimate for menhaden: 7.8 year^{-1}. Diet item = phyto: (315 kg/unit micro)(7.8/year)*100% diet = 2457 kg unit^{-1} year^{-1}.

[z] Using mummichogs for all littoral forage fish, then prey biomass is 4.0 times predator biomass which is 5209 kg/km^2 (Christensen 2009), we get (20836 kg/km^2 y)(km^2/26.15 units) = 796.8 kg/unit y). Assuming 4% of predation is on mesozooplankton (Christensen 2009) yields (31.87 kg/ unit y) of mesozoo consumed. Similar for other prey: In/Epi Fauna is 60% for 478.08; detritus is 28% for 223.10.

[aa] 1950 Q/B estimate for alewife: 8.62 y^{-1}, herring: 10.1 y^{-1}. Herring are more common in the Chesapeake so 10.1 is used. Diet item = phyto: (20.15 kg/unit micro)(10.1/y)*68% diet = 138.39 kg unit^{-1} y^{-1}. Diet item = both microzoo and mesozoo are 16% of diet: (20.15 kg/unit micro)(10.1/y)*16% diet = 32.56 kg unit^{-1} y^{-1} for each prey.

[ab] Prey biomass consumed is 3.5/y times predator biomass which is 400 kg/km^2 (Christensen 2009). However, 3.5 is considerably lower than the Q/B ratios for alewife, herring, menhaden and anchovy, and when it is used in the calibration negative net energy prices are obtained. Therefore, biomass consumed is assumed to be 5/y times predator biomass which yields (2000 kg/km^2 y)(km^2/2.831 units) = 706.46 kg/unit y). Assuming 13% of predation is on microzooplankton (Christensen 2009) yields (91.84 kg/ unit y) of microzooplankton consumed. Similar for other prey: mesozooplankton is 13% for 91.84; In/Epi fauna is 31% for 219.00; detritus is 10% for 70.65.

[ac] 1950 Q/B estimate for bay anchovy is 10.9 y^{-1} with 37% (56%, 7%) of the diet consisting of microzooplankton (mesozooplankton, in/epi fauna) (Christensen 2009). Diet items: microzoo: (17.236

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kg/unit)(10.9/y)*37% = 69.5 kg unit^{-1} y^{-1}; mesozoo: (17.236 kg/unit)(10.9/y)*56% = 105.2 kg unit^{-1} y^{-1}; in/epi fauna: (17.236 kg/unit micro)(10.9/y)*7% = 13.2 kg unit^{-1} y^{-1}.

[ad] Energy content and dry weight percentages varied across diatom species (Whyte 1989). Representative values of 4000 kcal/kg DW, and 30% dry weight content were used to obtain 1200 kcal/kg.

[ae] From Theilacker and Kimball (1984), caloric content of rotifer: 5.8 cal/mg . (5.8 cal/mg)(kcal/1000 cal)(1000 mg/g)(1000 g/kg)(.3 kg DW/kg WW) = 1740 kcal/kg WW. WW/DW conversion same as used in note ad.

[af] Using data for *Acartia tonsa* (dominant copepod species in Bay), caloric content of *A. tonsa* is 5664 kcal/kg AFDW (Laurence 1977, from EPA technical report). A 15% DW:WW conversion appears in Jorgensen (1979) (in Christensen and Pauly Trophic Models of Aquatic Ecosystems book p. 227), and approximately 30% conversion for shrimp appears in Power et al. (2002). Using an average yields (5664 kcal/kg AFDW)(.225 DW/WW) = 1274.4 kcal/kg WW.

[ag] Harris (2000) reports 2.967 cal/mg DW. Thus, (2.967 cal/mg DW) (kcal/1000cal) (1000000 mg/kg) (0.03755 DW/WW (Kremer 1979)) = 111.41 kcal/kg.

[ah] From Fig. 2 in Hartman, using 4000 J/g WW we get (4000 J/g)(.000239 kcal/J) (1000 g/kg) = 956 kcal/kg.

[ai] Chipps and Bennett (2002): mysid caloric content = (3.14 kJ/g WW)(0.239 kcal/kJ)(1000 g/kg) = 750.4 kcal/kg.
Welsh (1975); grass shrimp energy content = (4.6 kcal/g DW)(0.225 DW/WW)(1000 g/kg) = 1035 kcal/kg. DW/WW conversion an average for polychaetes from Davis (1993 p. 9). Polychaetes are a type of annelids which are used in Christensen (2009).

[aj] Hard and soft shell clams - Brey et al. (p. 272, 1988) for ash free dry weight (AFDW) energy content (22.79 J/mg AFDW ≈ 5447 kcal/kg AFDW) and Ricciardi and Bourget (p. 248, 1998) for dry/wet weight (WW) ratios. Only soft shell data available so used for both species. (5447 kcal/kg AFDW)(0.065 kg AFDW/kg WW ≈ 354 kcal/kg WW. Eastern oysters – same as clam except 0.027 AFDW/WW yields 147 kcal/kg WW. Blue crabs - Brey et al. (p. 272, 1988) for ash free dry weight (AFDW) energy content (22.74 J/mg AFDW ≈ 5435 kcal/kg AFDW) and Ricciardi and Bourget (p. 248, 1998) for DW/WW ratios. (5435 kcal/kg AFDW)(0.205 kg AFDW/kg WW) ≈ 1114 kcal/kg WW.

[ak] Insufficient data available in Hartman (1995) for forage fish; therefore, the value used for anchovy (see note ah) is used for forage fish.

[al] From Flath and Dana (2011) average caloric content of alewife is 5.653 kcal/g WW or 5653 kcal/kg WW.

[am] Approximate mean energy content for ocean and fresh water shad per mean weight in Connecticut is 10000 kj/1600 g (Leonard and McCormick 1999). Thus, (10000 kj/1600 g)(1000 g/kg)(0.238846 kcal/kj) ≈ 1492.8 kcal/kg.

[an] A rough rule of thumb is that 10% of the energy taken at one trophic level is passed on to the next trophic level (See, e.g., Pauly and Christensen 1995). Petipa et al. (1970) suggest a 20% transfer rule for ocean communities. Therefore, equate 20% of the light energy taken by phytoplankton to the energy taken from phytoplankton by micro- and meso-zooplankton, oysters,clams, in/epi, menhaden: (20%) N_1 $x_{0100} e_{01} = N_2 x_{0201} e_1 + N_3 x_{0301} e_1 + N_4 x_{0401} e_1 + N_5 x_{0501} e_1 + N_7 x_{0701} e_1 + N_9 x_{0901} e_1 + N_{11} x_{1101} e_1$ and solve to obtain $e_{01} = 930440.079$ kcal kg^{-1} yr^{-1}. (Note N_1 is from [b], x_{0100} from [o], N_2 from [c], x_{0201} from [p], e_1 is from [ad] and so forth.)

[ao] Not applicable because only plants photosynthesize.

[ap] Durbin et al. (1983) for dry/wet weight ratios and dry weight energy content.

[aq] An average of respiration as a percent of body weight over multiple phytoplankton species yields 6% (Petipa et al. 1970, Table 2). Incoming phytoplankton energy is $e_{01} x_{10} = (24355.9)(435.6)$, and 6% of this is 636565.8 kcal y^{-1}.

[ar] Using anesthetized respiration of rotifer 4.17×10^{-4} µlO$_2$/ind h^{-1} (Epp 1984), $(4.17 \times 10^{-4}$ µl O$_2$/ind h$^{-1})(288$ h)(ml/1000 µl)(4.83 cal/ml O$_2$)(kcal/1000 cal)$(1 \times 10^{12}$ ind/unit) = 580063.68 kcal/unit y^{-1}. This is the respiration for a unit over 288 h (12 d), but since 12 days is the lifetime of the unit, it is respiration for the unit for one year.

[as] Using respiration of *A. clausi* (same Acartia zoop family) (Mayzand 1973) 66.96 µlO$_2$/mg DW d^{-1} converting to mg and years (66.96 µl O$_2$/mg d^{-1})(ml O$_2$/1000 µl (365 d/y) = 24.2202 ml O$_2$/mg y^{-1}. Converting to kcal, (24.2202 ml O$_2$/mg y^{-1})(0.00483 kcal/ml O$_2$) = 0.118047 kcal/mg y^{-1}. Finally, converting to WW and ind, (0.118047 kcal/mg y^{-1}) (0.15 DW/WW) (0.06676 mg/ind)(1000000000 ind/unit) = 1181021.1 kcal/unit y^{-1}.

[at] From Dame (1972) convert 99 g WW per oyster to 15.246 g DW with ln DW = -1.687 + 0.96 ln WW ((1) p 244). Use O$_2$ µl h^{-1} = 372 DW$^{0.71}$ (p 246) to obtain 2.57385 ml h^{-1}. Convert using 4.83 cal ml^{-1} O$_2$ (p 245) to obtain (2.57385 ml h^{-1})(4.83 cal ml^{-1})(kcal/1000cal)(8760 h/y) ≈ 108.972 kcal y^{-1}. No distinction is made in Dame between RMB and active metabolic rate. Therefore we arbitrarily assign 50% of this respiration to RMB. On a per unit basis this yields (0.5)(108.97165 kcal/y ind)(1000 ind/unit) = 54485.825 kcal/y unit.

[au] From Hammen (1978), softshell clam, *Mya arenaria,* respiration is 4.11 µmol O$_2$/g h^{-1} and hardshell clam, *Mercenaria mercenaria,* respiration is 2.68 µmol O$_2$/g h^{-1}. For softshell (4.11 µmol O$_2$/g h^{-1}) (mol/1000000 µmol)(16 g O$_2$/mol O$_2$)(3.38 kcal/g O$_2$)(8760 h/y)(51.9 g/ind)(1000 ind/unit) = 101053.18 kcal/unit y^{-1}; for hardshell (2.68 µmol O$_2$/g h^{-1}) (mol/1000000 µmol)(16 g O$_2$/mol O$_2$)(3.38 kcal/g O$_2$)(8760 h/y)(91.6 g/ind)(1000 ind/unit) = 116297.68 kcal/unit y^{-1}. A weighted average of the entire clam population (82% biomass softshell) yields (116297.68 *18 + 101053.18 *82)/100 = 103797.19 kcal/unit y^{-1}. No distinction is made in Hammen between RMB and active metabolic rate. Therefore we arbitrarily assign 50% of this respiration to RMB. Finally, because only 75% of the clam diet is accounted for in the model based on Christensen (2009), the RMB is used is (103797.19 kcal/unit y^{-1}) (0.5)(0.75) = 38923.95 kcal/unit y^{-1}.

[aw] Groups used to determine resting metabolic rate: grass shrimp (Welsh 1975), mysid (Hiller-Adams 1983), amphipod (Manyin & Rowe 2006), polychaete (Kemp and Boynton 1981). Grass shrimp: (from Fig 9 - .0073 kcal/h g DW)(1000 g/kg)(0.175 DW/WW)(8760 h/y)(5120 kg/unit) = 57297408 kcal/unit y^{-1}. Mysid: (1.28 µmol O$_2$/g WW h^{-1})(mol/1000000 µmol)(16 g O$_2$/mol O$_2$)(3.38 kcal/g O$_2$)(8760 h/y)(0.0135 g/ind)(100000000 ind/unit) = 818624.1 kcal/unit y^{-1}. Amphipod: (250 uL O$_2$/g WW h^{-1})(mL O$_2$/1000 uL O$_2$)(4.83 cal/mL O$_2$)(1 kcal/1000 cal)(8760 h/y)(0.012 g WW/ind)(100000000 ind/unit) = 12775000 kcal/unit y^{-1}. Polychaete: (0.15 g O$_2$/m^2 d^{-1})(m^2/1000 ind)(3.38 kcal/g O$_2$)(365 d/y))(100000000 ind/unit) = 18505500 kcal/unit y^{-1}. Averaging above = 22349133 kcal/unit y^{-1}. No distinction is made in in the above papers between RMB and active metabolic rate; therefore, we arbitrarily assign 45% of this respiration to RMB. Finally, because only 70% of the in/epi diet is accounted for in the model based on Christensen (2009),the RMB is multiplied by 0.7 to yield 7039976.90.

[ax] 49.6 µmol O$_2$/kg min extraction on average (Booth et al. 1982, p. 113. Also for conversion of O$_2$ to cal use use 3.38 cal/mg O$_2$ (Elliott and Davison 1975). Then (0.0000496 mol O$_2$/kg min)(16 g/mol) (3.38kcal/g O$_2$) ≈ 0.0026824 kcal/ kg min. Further, (0.0026824 kcal/ kg min)(60 min/h)(8760 h/y) ≈ 1409.853 kcal/kg y. Thus (1409.853 kcal/kg y)(17 kg/unit) = 23967.51 kcal/unit y). Finally, the RMB is multiplied by 0.65 because only 65% of the crab diet is accounted for in the model based on Christensen (2009): (23967.51 kcal/unit y)(0.65) ≈ 15578.883 kcal/unit y.

[ay] 0.1 mg O$_2$/g WW h (Durbin and Durbin 1983). (0.1 mg O$_2$/g WW h)(g O$_2$/1000 mg O$_2$)(1000g WW/kg WW)(3.38 kcal/g O$_2$)(8760h/yr)(.315 kg/ind)(1000 ind/unit) = 932677 kcal/unit y^{-1}.

[az] Mummichogs - 1.4520 mg O_2/g DW h (Valiela 1977). Thus (1.4520 mg O_2/g h)(g/1000 mg)(1000g/kg) = 1.4520 g O_2/kg h. From Elliott and Davison (1975) use 3.38 cal/mg O_2. Then (1.4520 g O_2/kg h) (3.38 kcal/g O_2) (8760 h/y) = 42992.206 kcal/ kg y. Finally, (42992.206 kcal/kg y)(1.992 kg/unit) ≈ 85650.43 kcal/unit y. The RMB is multiplied by 0.92 because only 92% of the forage fish diet is accounted for in the model based on Christensen (2009): (85650.43 kcal/unit y)(0.92) ≈ 78798 kcal/unit y.

[ba] Alewives and herring are very similar and we use data from alewives for both species. From Stewart and Binkowski (1986) the resting (standard) metabolic rate for alewives can be determined using ln R (mL O_2/kg h^{-1}) = 4.894 - 0.215lnW(g) + 0.0548T(deg C). Using average Bay temperature of 18 degrees C and average alewife/herring weight (note bn) of 20.15 g, R = 107.765 mL O_2/kg h^{-1}. (107.765 mL O_2/kg h^{-1}) (8760 h/y)(4.83 cal/mL O_2)(kcal/1000 cal)(.2015 kg/ind)(100 ind/unit) = 91876.42 kcal/unit y^{-1}.

[bb] 3.6 mmol O_2/kg h oxygen extraction in cold water (18° C) (Leonard et al. 1999, P. 291). Thus (0.0036 mol O_2/kg h)(16 g/mol) = 0.0576 g O_2/kg h. Next (0.0576 g O_2/kg h) (3.38 kcal/g O_2) (8760 h/y)(142.2 kg/unit) ≈ 242517.39 kcal/unit y. The RMB is multiplied by 0.67 because only 67% of the shad diet is accounted for in the model based on Christensen (2009): (282936.96 kcal/unit y)(0.67) ≈ 162486.65 kcal/unit y.

[bc] Resting metabolic rate is 0.15 mg O_2/g h (Boggs, Tble. 5, 1991). Thus, (0.15 mg O_2/g h) (g/1000 mg) (3.38 kcal/ g O_2) (1000 g/kg) (8760 h/y) (0.001724 kg/ind) (10000 ind/unit) = 76568. kcal/unit y.

[bd] Phytoplankton are plants, therefore weight is given by x_{10}. For longevity, most species' individuals in the food web are assumed to reproduce once per year. But phytoplankton can reproduce every few days and zooplankton that can reproduce every few weeks, and both may have lifespans less than one year. To adjust for the rapid turnover of the planktons, their weights in the population update equations are multiplied by 365 to put them on a daily basis, and the longevity term is redefined to be the number of times the individual reproduces over the life divided by longevity. For phytoplankton we use 8 day reproduction cycle and 80 day longevity (0.219 y) (Petipa 1970).

[be] Using the average weight of an individual microzooplanter, 2.5 x10^{-9} kg, (2.5 x10^{-9} kg/ind)(1 x10^{12} ind/unit) = 2500 kg/unit. From Allan (1976), a reproduction cycle of a rotifer at 20 deg C is 12 days (0.0329 y). We use 132 days for longevity. See note bd.

[bf] Using the average weight of an individual mesozooplanter, 6.667 x10^{-8} kg, (6.667 x10^{-8} kg /ind)(1 x10^{9} ind/unit) = 66.67 kg/1 unit mesozooplankton. From Allan (1976), a reproduction cycle of a copepod is 50 days, 50 (0 .137 y). We use 500 days for longevity. See note bd.

[bg] Weight from Rothschild (1994) for an 88 mm ind. of 0.0995 kg. One unit is 1000 ind. Age is from Powell and Cummings (1985).

[bh] Average weight of softshell clam: 51.9g, average weight of hardshell clam 91.2g (Hammen 1978). Taking a weighted average of the weights (softshell clams make up 82% of clam biomass) (.0519*82 + .0912*18)/100 = .059 kg/ind. 1 unit = 1000 individuals, so 59.947 kg/unit. From Hawker and Connell (1985), the maximum age of softshell clam is 8 years.

[bj] Average weight of in/epi fauna (see note h) 0.0000512 kg/1 ind * 100000000 ind/unit = 5120 kg/unit. For species with short longevity (less than 3 years for model purposes) and rapid turnover, the updating is adjusted. See note bd. For longevity, the polychaeta *Hediste diversicolor* is used. They reproduce one or more times annually: the reproduction cycle used is 0.5 y and longevity used is 3 y which is the higher end observed (Scaps 2002).

[bk] Average carapace widths in South Carolina were 137 mm (males) and 151 mm (females) (Tagatz, 1965). Converting widths to weight using formulas ln weight = -3.2047 + 2.5510 ln width (males) and ln weight = -2.3783 + 2.1083 ln width (females) (Olmi and Bishop 1983, p. 576) and averaging the sexes gives (175+165)/2 = 170g. Maximum age for Chesapeake blue crabs 4 y, with most between 2-3 y (van Engel 1958).

[bl] Weight an average from 3-4 year olds in early 1950s (Vaughan, 2010, p.110) is .315 kg. (.315 kg/1 ind)(1000 ind/1 unit) = 315 kg/unit; max age 8-10 yr (Rogers and van den Avyle 1989).

[bm] An average weight over 1-3 year old mummichogs is 12.95 g DW. (Table 2, Valiela 1977). (12.95 g DW) (WW/.065 DW) (kg/1000g) = 0.1992 kg WW. One unit = 1000 individuals and 1 unit is 199.2 kg. Valiela (1977) shows age classes up to three years.

[bn] Average weight of alewife = 0.266 kg (using fishbase.org average length and length/weight relationship from Stewart and Binkowski 1985), average weight herring = .137 kg (fishbase.org average length and Dept of Int species profile for length/weight). Averaging the two masses (assuming equal density of alewife and herring, because only one biomass estimate was given in Ecopath), (.266 + .137)/2 = .2015 kg/ind. 1 unit = 100 ind, weight/unit = 20.15 kg/unit. From fishbase.org, http://fishbase.org/summary/Alosa-pseudoharengus.html, maximum age of alewife = 9 years. Maximum age herring = 8 years. http://fishbase.org/summary/Alosa-aestivalis.html

[bo] Weight from Chittenden (1976) is average of male and female samples from Delaware River (p. 152). Age from Kessler, S. 2011. "Alosa sapidissima" (On-line), Animal Diversity Web. http://animaldiversity.ummz.umich.edu/site/accounts/information/Alosa_sapidissima.html.

[bp] Average weight of anchovy is 0.0017236 kg/ind (fishbase.org for length, anchovy species profile for length/weight. This weight is consistent with Luo and Brandt (1993) for Bay anchovy.). 1 unit = 10000 ind, so weight/unit = 17.236 kg/unit. From Newberger and Haude (1995), average age of anchovy is 1 year.

[bq] In population units km^{-2}. Calculated from the short-run equilibrium (i.e., biomass clearing) conditions using benchmark values for populations, biomasses and biomass flows (i.e., demands) from the first two table columns.

[br] Calculated using the plant congestion conditions and assuming that at the benchmark values for populations, biomasses and biomass flows, the plants fully occupy the available water pace.

[bs] In kcal y^{-1}. Derived from calibration. The benchmark biomasses (plants) and biomass flows (animals) were used as parameters in the eight net energy objective functions set to zero and in the nine first-order conditions to derive values for the variable respiration terms, r_i, and the energy prices, e_{ij}. The derived energy prices are benchmark energy prices in the simulations.

[cf] 3.4 t km^{-2} (Christensen 2009). Therefore, (3.4 t/ km^2)(1000 kg/ t)(unit /50 kg) = 68 units/km^2 where one unit is 10000 individuals.

[ch] Respiration for 42.9 g of Ctenophores is approximately 25.3 cal d^{-1} (Fenenko, Tble 4, 2006). Thus, (25.3 cal/42.9 g d)(1000g/kg)(365 d/y)(kcal/1000 cal)(50 kg/unit) = 10762.82 kcal/unit y. No distinction is made in Fenenko between RMB and active metabolic rate, therefore we arbitrarily assign 75% of this respiration to RMB or 8072.12 kcal/ unit y.

[ci] An average weight from Figure 1 in Purcell (1988) shows approximately 0.005 kg/individual or 50 kg/unit. Life span ranges from months to one year (Ghabooli et al. 2011). For species with short longevity (less than 3 or more years for model purposes) and rapid turnover, the updating is adjusted. See note bd. Baker and Reeve (1974) report Mnemiopsis mccradyi reproduce as early as 17 d and can produce continually if food is available. The reproduction cycle used is 17 d and longevity used is 182.5 d.

[cj] 1950 biomass estimates for resident 2949 kg/km^2 and migratory/YOY 12.5 kg/km^2 (Christensen et al. 2009). From fishbase.org, the average length of striper = 120 cm and using the length/weight relationship ln W(kg) = ln a + b*ln L(cm), where ln a = -11.7959 and b = 3.1383 (NOAA fish length/weight relationship) the average weight of a 120 cm striper = 25.2464 kg. (2949 kg/km^2 + 12.5 kg/km^2)/(25.2464 kg/1 ind) = 117.304 ind/km^2.

[ck] An estimate of marine detritus energy content is 5.41 j/mg (Palavesam 2005). Thus, (5.41J/mg) (kJ/1000 J)(1000000 mg/kg) (kcal/4.184 kJ) ≈ 1293.02 kcal/kg.

[cl] Hartman and Brandt (1995) for dry/wet weight ratios and energy content to wet weight formula.

[cm] From Brougher et al. (2005) the standard metabolic rate for striped bass is 68 mg $O_2/kg^{3/4}$ h^{-1}. Multiply respiration by the average weight of bass used, or (68 mg O_2/1 $kg^{3/4}$ h^{-1})(546 g/ind)$^{3/4}$= 43.19 mg $O_2/kg^{3/4}$ h^{-1}. Then (43.19 mg O_2/kg h^{-1}) (8760 hour/y) (g O_2/1000 mg O_2) (3.38 kcal/g O_2) (25.2464 kg/ind) (ind/unit) = 32285.20 kcal/unit y^{-1}. 79% of striped bass diet is included in the model, so 0.79* 32285.20 kcal/unit y^{-1} = 25505.31 kcal/ unit y^{-1}.

[cn] Average weight of striped bass is 25.2464 kg/ind (fishbase.org for length, NOAA length/weight for weight). 1 unit equals 1 ind, so weight/unit is 25.2464 kg/unit. From http://fishbase.org/summary/Morone-saxatilis.html, max reported age is 30 years.

[ct] Assuming prey biomass is 35.2 times predator biomass which is 3400 kg/km^2 (Christensen 2009), we get (119680 kg/km^2 y)(km^2/68 units) = 1760 kg/unit y). Assuming 33% (67%) of predation is on microzooplankton (mesozooplankton) (Christensen 2009) yields 586.67 (1173.33) kg/ unit y of microzooplankton (mesozooplankton) consumed.

[cu] 1950 Q/B estimate: resident: 4.41 year^{-1}, migratory 2.3 y^{-1}. Weighted average: (58*4.41 + 42*2.3)/100 = 3.5238 y^{-1}. Diet item = menhaden: (25.2464 kg/unit micro)(3.5238/y)*58% diet = 51.6 kg unit^{-1} y^{-1}. Diet item = alewife/herring: (25.2464 kg/unit micro)(3.5238/y)*11% diet = 9.8 kg unit^{-1} y^{-1}. Diet item = anchovy: (25.2464 kg/unit micro)(3.5238/y)*4% diet = 3.6 kg unit^{-1} y^{-1}. Diet item = littoral forage fish/suspension/in/epi fauna: (25.2464 kg/unit micro)(3.5238/y)*3% diet = 2.7 kg unit^{-1} y^{-1}.

[bc] Resting metabolic rate is 0.15 mg O_2/g h (Boggs, Tble. 5, 1991). Thus, (0.15 mg O_2/g h) (g/1000 mg) (3.38 kcal/ g O_2) (1000 g/kg) (8760 h/y) (0.001724 kg/ind) (10000 ind/unit) = 76568. kcal/unit y.

[ay] 0.1 mg O_2/g WW h (Durbin and Durbin 1983). (0.1 mg O_2/g WW h)(1 g O_2/1000 mg O_2)(1000g WW/kg WW)(3.38 kcal/1g O_2)(8760h/yr)(.315 kg/1 ind)(1000 ind/1 unit) = 932677 kcal/unit y^{-1}.

[ba] From Stewart and Binkowski (1986) the resting (standard) metabolic rate for alewives can be determined using ln R (mL O_2/kg h^{-1}) = 4.894 - 0.215lnW(g) + 0.0548T(deg C). Using average temperature of bay = 18 degrees C and average weight of alewife = 266 g, R = 107.765 mL O_2/kg h^{-1}. (107.765 mL O_2/kg h^{-1})(8760 h/1 year)(4.83 cal/1 mL O_2)(1 kcal/1000 cal)(.266 kg/1 ind)(100 ind/1 unit) = 121286 kcal/unit year^{-1}.

Appendix B. References for GEEM Calibration Table

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Appendix C – GEEM Equations

For the Chesapeake fifteen species food web the net energy objective functions are as follows:

Phytoplankton (indexed as 01):

$$R_{01} = (e_{00} - e_{0100})x_{0100} - r_{01}x_{0100} - 0.5\,r_{01}x_{0100}^2 - d_{0103}e_{01}(1 + t_{01}e_{0301})x_{0100}^{.5}$$

$$- d_{0104}e_{01}(1 + t_{01}e_{0401})x_{0100}^{.5} - d_{0105}e_{01}(1 + t_{01}e_{0501})x_{0100}^{.5}$$

$$-d_{0106}e_{01}(1 + t_{01}e_{0601})x_{0100}^{.5} - d_{0107}e_{01}(1 + t_{01}e_{0701})x_{0100}^{.5}$$

$$- d_{0109}e_{01}(1 + t_{01}e_{0901})x_{0100}^{.5} - \beta_{01} \tag{1-Ph}$$

Microzooplankton (indexed as 02):

$$R_{02} = (e_{01} - e_{0201})x_{0201} - r_{02}x_{0201} - 0.5\,r_{02}x_{0201}^2 - d_{0203}e_{02}(1 + t_{02}e_{0302})x_{0201}^{.5}$$

$$- d_{0204}e_{02}(1 + t_{02}e_{0402})x_{0201}^{.5} - d_{0205}e_{02}(1 + t_{02}e_{0502})x_{0201}^{.5} - d_{0212}e_{02}(1 + t_{02}e_{1202})x_{0201}^{.5}$$

$$- d_{0213}e_{02}(1 + t_{02}e_{1302})x_{0201}^{.5} - d_{0214}e_{02}(1 + t_{02}e_{1402})x_{0201}^{.5} - \beta_{02} \tag{1-Izo}$$

Mesozooplankton (indexed as 03):

$$R_{03} = (e_{01} - e_{0301})x_{0301} - (e_{02} - e_{0302})x_{0302} - r_{03}(x_{0301} + x_{0302})$$

$$-0.5r_{03}(x_{0301}^2 + x_{0302}^2 + x_{0301}x_{0302}) - d_{0310}(1 + t_{03}e_{1003})(x_{0301} + x_{0302})^{.5}$$

$$-d_{0312}(1 + t_{03}e_{1203})(x_{0301} + x_{0302})^{.5} - d_{0313}(1 + t_{03}e_{1303})(x_{0301} + x_{0302})^{.5}$$

$$-d_{0314}(1 + t_{03}e_{1403})(x_{0301} + x_{0302})^{.5} - \beta_{03} \tag{1-Ezo}$$

Oyster (indexed as 04):

$$R_{04} = (e_{01} - e_{0401})x_{0401} + (e_{02} - e_{0402})x_{0402} + (e_{99} - e_{0499})x_{0499}$$

$$-r_{04}(x_{0401} + x_{0402} + x_{0403}) - 0.5r_{04}(x_{0401}^2 + x_{0402}^2 + x_{0499}^2 + x_{0401}x_{0402} + x_{0401}x_{0499} + x_{0402}x_{0499}) - \beta_{04} \tag{1-Oy}$$

Clam (indexed as 05):

$$R_{05} = (e_{01} - e_{0501})x_{0501} + (e_{02} - e_{0502})x_{0502} + (e_{99} - e_{0599})x_{0599}$$

$$- r_{05}(x_{0501} + x_{0502} + x_{0599})$$

$$- 0.5r_{05}(x_{0501}^2 + x_{0502}^2 + x_{0599}^2 + x_{0501}x_{0502} + x_{0501}x_{0599} + x_{0502}x_{0599}) - d_{0508}(1 + t_{05}e_{0805})(x_{0501} + x_{0502} + x_{0599})^{0.5} - \beta_{05} \tag{1-Cl}$$

In/epi fauna (indexed as 07):

$$R_{07} = (e_{01} - e_{0701})x_{0701} + (e_{02} - e_{0702})x_{0702} + (e_{07} - e_{0707})x_{0707} + (e_{99} - e_{0799})x_{0799}$$

$$-r_{07}(x_{0701} + x_{0702} + x_{0707} + x_{0799}) - 0.5r_{07}(x_{0701}^2 + x_{0702}^2 + x_{0707}^2 + x_{0799}^2 +$$
$$x_{0701}x_{0702} + x_{0701}x_{0707} + x_{0701}x_{0799} + x_{0702}x_{0707} + x_{0702}x_{0799} + x_{0707}x_{0799})$$

$$-d_{0707}(1 + t_{07}e_{0707})(x_{0701} + x_{0702} + x_{0707} + x_{0799})^{0.5}$$

$$-d_{0708}(1 + t_{07}e_{0807})(x_{0701} + x_{0702} + x_{0707} + x_{0799})^{0.5} - d_{0710}(1 + t_{07}e_{1007})(x_{0701} +$$
$$x_{0702} + x_{0707} + x_{0799})^{0.5} - d_{0712}(1 + t_{07}e_{1207})(x_{0701} + x_{0702} + x_{0707} + x_{0799})^{0.5}$$

$$-d_{0713}(1 + t_{07}e_{1307})(x_{0701} + x_{0702} + x_{0707} + x_{0799})^{0.5} - d_{0715}(1 + t_{07}e_{1507})(x_{0701} +$$
$$x_{0702} + x_{0707} + x_{0799})^{0.5} - \beta_{07}$$

<div align="right">(1-Fau)</div>

Blue Crab (indexed as 08):

$$R_{08} = (e_{05} - e_{0805})x_{0805} + (e_{06} - e_{0806})x_{0806} + (e_{07} - e_{0807})x_{0807}$$

$$+(e_{99} - e_{0899})x_{0899} - r_{08}(x_{0805} + x_{0806} + x_{0807} + x_{0899})$$

$$-0.5r_{08}(x_{0805}^2 + x_{0806}^2 + x_{0807}^2 + x_{0899}^2 + x_{0805}x_{0806} + x_{0805}x_{0807} + x_{0805}x_{0899} +$$
$$x_{0806}x_{0807} + x_{0806}x_{0899} + x_{0807}x_{0899})$$

$$-d_{0815}(1 + t_{08}e_{1508})(x_{0805} + x_{0806} + x_{0807} + x_{0899})^{0.5} - \beta_{08} \qquad \text{(1-Cra)}$$

Menhaden (indexed as 09):

$$R_{09} = (e_{01} - e_{0901})x_{0901} - r_{09}x_{0901}^2 - d_{0915}(1 + t_{09}e_{1509})x_{0901}^{.5} - \beta_{09} \qquad \text{(1-Men)}$$

Littoral Forage Fish (indexed as 10):

$$R_{10} = (e_{03} - e_{1003})x_{1003} + (e_{07} - e_{1007})x_{1007} + (e_{99} - e_{1099})x_{1099}$$

$$-r_{10}(x_{1003} + x_{1007} + x_{1099})$$

$$-0.5r_{10}(x_{1003}^2 + x_{1007}^2 + x_{1099}^2 + x_{1003}x_{1007} + x_{1003}x_{1099} + x_{1007}x_{1099})$$

$$-d_{1015}(1 + t_{10}e_{1510})(x_{1003} + x_{1007} + x_{1099})^{0.5} - \beta_{10} \qquad \text{(1-Lit)}$$

Alewife/herring (indexed as 11):

$$R_{11} = (e_{01} - e_{1101})x_{1101} + (e_{02} - e_{1102})x_{1102} + (e_{03} - e_{1103})x_{1103} - r_{11}(x_{1101} + x_{1102} +$$
$$x_{1103})$$

$$-0.5r_{11}(x_{1101}^2 + x_{1102}^2 + x_{1103}^2 + x_{1101}x_{1102} + x_{1101}x_{1103} + x_{1102}x_{1103})$$

$$-d_{1115}(1 + t_{11}e_{1511})(x_{1101} + x_{1102} + x_{1103})^{.5} - \beta_{11} \qquad \text{(1-Ale)}$$

American Shad (indexed as 12):

$$R_{12} = (e_{02} - e_{1202})x_{1202} + (e_{03} - e_{1203})x_{1203} + (e_{07} - e_{1207})x_{1207} + (e_{99} - e_{1299})x_{1299}$$

$$-r_{12}(x_{1202} + x_{1203} + x_{1207} + x_{1299}) - 0.5r_{12}(x_{1202}^2 + x_{1203}^2 + x_{1207}^2 + x_{1299}^2 + x_{1202}x_{1203}$$

$$+x_{1202}x_{1207} + x_{1202}x_{1299} + x_{1203}x_{1207} + x_{1203}x_{1299} + x_{1207}x_{1299}) - \beta_{12} \qquad \text{(1-Am)}$$

Bay Anchovy (indexed as 13):

$$R_{13} = (e_{02} - e_{1302})x_{1302} + (e_{03} - e_{1303})x_{1303} + (e_{07} - e_{1307})x_{1307}$$

$$-r_{13}(x_{1302} + x_{1303} + x_{1307}) - 0.5r_{13}(x_{1302}^2 + x_{1303}^2 + x_{1307}^2 + x_{1302}x_{1303} + x_{1302}x_{1307} +$$
$$x_{1303}x_{1307}) - d_{1315}(1 + t_{13}e_{1513})(x_{1302} + x_{1303} + x_{1307})^{.5} - \beta_{13} \qquad \text{(1-Anch)}$$

Ctenophore (indexed as 14):

$$R_{14} = (e_{02} - e_{1402})x_{1402} + (e_{03} - e_{1403})x_{1403} + r_{14}(x_{1402} + x_{1403})$$

$$- 0.5r_{14}(x_{1402}^2 + x_{1403}^2 + x_{1402}x_{1403}) - \beta_{14} \qquad \text{(1-Cte)}$$

Striped Bass (indexed as 15):

$$R_{15} = (e_{06} - e_{1506})x_{1506} + (e_{07} - e_{1507})x_{1507} + (e_{09} - e_{1509})x_{1509} + (e_{10} - e_{1510})x_{1510}$$

$$+(e_{11} - e_{1511})x_{1511} + (e_{13} - e_{1513})x_{1513} - r_{15}(x_{1506} + x_{1507} + x_{1509} + x_{1510} + x_{1511} + x_{1513})$$

$$-0.5r_{15}(x_{1506}^2 + x_{1507}^2 + x_{1509}^2 + x_{1510}^2 + x_{1511}^2 + x_{1513}^2 + x_{1506}x_{1507} + x_{1506}x_{1509} + x_{1506}x_{1510} + x_{1506}x_{1511} + x_{1506}x_{1513} + x_{1507}x_{1509} + x_{1507}x_{1510} + x_{1507}x_{1511} + x_{1507}x_{1513} + x_{1509}x_{1510} + x_{1509}x_{1511} + x_{1509}x_{1513} + x_{1510}x_{1511} + x_{1510}x_{1513} + x_{1511}x_{1513}) - \beta_{15} \qquad \text{(1-Bas)}$$

The first-order conditions are simply the derivatives of the above net energy expressions with respect to the x terms. They can be found in the Mathematica file for GEEM.

The 38 biomass balance conditions are as follows:

$$\tau_{01}BAYarea_{00} = N_{01}x_{0100} \qquad\qquad\qquad \text{- phytoplankton on sun}$$

$N_{02}x_{0201} = N_{01}d_{0102}x_{0100}^{.5}$ — microzooplankton on phytoplankton

$N_{03}x_{0301} = N_{01}d_{0103}x_{0100}^{.5}$ — mesozooplankton on phytoplankton

$N_{03}x_{0302} = N_{02}d_{0203}x_{0201}^{.5}$ — mesozooplankton on microzooplankton

$N_{04}x_{0401} = N_{01}d_{0104}x_{0100}^{.5}$ — oyster on phytoplankton

$N_{04}x_{0402} = N_{02}d_{0204}x_{0201}^{.5}$ — oyster on microzooplankton

$N_{04}x_{0499} = \tau_{04}detritus$ — oyster on detritus

$N_{05}x_{0501} = N_{01}d_{0105}x_{0100}^{.5}$ — clam on phytoplankton

$N_{05}x_{0502} = N_{02}d_{0205}x_{0201}^{.5}$ — clam on microzooplankton

$N_{05}x_{0599} = \tau_{05}detritus$ — clam on detritus

$N_{07}x_{0701} = N_{01}d_{0107}x_{0100}^{.5}$ — in/epi fauna on phytoplankton

$N_{07}x_{0702} = N_{02}d_{0207}x_{0201}^{.5}$ — in/epi fauna on microzooplankton

$N_{07}x_{0707} = N_{07}d_{0707}(x_{0701} + x_{0702} + x_{0707} + x_{0799})^{.5}$ — in/epi fauna on in/epi fauna

$N_{07}x_{0799} = \tau_{07}detritus$ — in/epi fauna on detritus

$N_{08}x_{0805} = N_{05}d_{0508}(x_{0501} + x_{0502} + x_{0599})^{.5}$ — blue crab on clam

$N_{08}x_{0807} = N_{07}d_{0708}(x_{0701} + x_{0702} + x_{0707} + x_{0799})^{.5}$ — blue crab on in/epi fauna

$N_{08}x_{0899} = \tau_{08}detritus$ — blue crab on detritus

$N_{09}x_{0901} = N_{01}d_{0109}x_{0100}^{.5}$ — menhaden on phytoplankton

$N_{10}x_{1003} = N_{03}d_{0310}(x_{0301} + x_{0302})^{.5}$ — littoral forage fish on mesozooplankton

$N_{10}x_{1007} = N_{07}d_{0710}(x_{0701} + x_{0702} + x_{0707} + x_{0799})^{.5}$ — littoral forage fish on in/epi fauna

$N_{10}x_{1099} = \tau_{10}detritus$ — littoral forage fish on detritus

$N_{11}x_{1101} = N_{01}d_{0111}x_{0100}^{.5}$ — alewife/herring on phytoplankton

$N_{11}x_{1102} = N_{02}d_{0211}x_{0201}^{.5}$ — alewife/herring on microzooplankton

$N_{11}x_{1103} = N_{03}d_{0311}(x_{0301} + x_{0302})^{.5}$ — alewife/herring on mesozooplankton

$$N_{12}x_{1202} = N_{02}d_{0212}x_{0201}^{.5}$$ - shad on microzooplankton

$$N_{12}x_{1203} = N_{03}d_{0312}(x_{0301} + x_{0302})^{.5}$$ - shad on mesozooplankton

$$N_{12}x_{1207} = N_{07}d_{0712}(x_{0701} + x_{0702} + x_{0707} + x_{0799})^{.5}$$ - shad on in/epi fauna

$$N_{12}x_{1299} = \tau_{12}detritus$$ - Shad on detritus

$$N_{13}x_{1302} = N_{02}d_{0213}x_{0201}^{.5}$$ - anchovy on microzooplankton

$$N_{13}x_{1303} = N_{03}d_{0313}(x_{0301} + x_{0302})^{.5}$$ - anchovy on mesozooplankton

$$N_{13}x_{1307} = N_{07}d_{0713}(x_{0701} + x_{0702} + x_{0707} + x_{0799})^{.5}$$ - anchovy on in/epi fauna

$$N_{14}x_{1402} = N_{02}d_{0214}x_{0201}^{.5}$$ - ctenophore on microzooplankton

$$N_{14}x_{1403} = N_{03}d_{0314}(x_{0301} + x_{0302})^{.5}$$ - ctenophore on mesozooplankton

$$N_{15}x_{1509} = N_{09}d_{0915}x_{0901}^{.5}$$ - striped bass on menhaden

$$N_{15}x_{1511} = N_{11}d_{1115}(x_{1101} + x_{1102} + x_{1103})^{.5}$$ - striped bass on alewife/herring

$$N_{15}x_{1513} = N_{13}d_{1315}(x_{1302} + x_{1303} + x_{1307})^{.5}$$ - striped bass on anchovy

$$N_{15}x_{1510} = N_{10}d_{1015}(x_{1003} + x_{1007} + x_{1009})^{.5}$$ - striped bass on littoral forage fish

$$N_{15}x_{1507} = N_{07}d_{0715}(x_{0701} + x_{0702} + x_{0707} + x_{0799})^{.5}$$ - striped bass on in/epi fauna

Appendix D – GEEM Negative Prices and Corner Solutions

In the general equilibrium calculations for each year, there are 76 variables: the x_{ij} terms from the 38 predator/prey relationships, and the e_{ij} energy cost terms also from the 38 predator/prey relationships. Negative values for these variables are ruled out, but we allow for the possibility that some of these variables could be zero at the optimum. Continuing with alewife/herring, in the calculations this species contributes six variables, x_{1101}, x_{1102}, x_{1103}, e_{1101}, e_{1102} and e_{1103}, to the 76. If the general equilibrium calculations yield a negative value for one of the energy prices, then that energy price is set to zero and a corner solution is obtained. Basically, a negative price implies that the demand and supply curves intersect at a negative price. The remedy is to set price to zero in which case the demand is less than supply.

Consider how this works for alewife/herring demand for phytoplankton. The Kuhn-Tucker conditions for an optimum are an extension of expressions (3) and (4) in the text:

$$\frac{\partial R_{11}}{\partial x_{1101}} = e_{01} - e_{1101} - r_{11} - 0.5r_{11}(2x_{1102} + x_{1101} + x_{1103})$$
$$- 0.5d_{1115}(1 + t_{11}e_{1511})(x_{1101} + x_{1102} + x_{1103})^{-.5} \leq 0$$

$$\frac{\partial R_{11}}{\partial x_{1101}}x_{1101} = 0 \qquad x_{1101} \geq 0 \tag{D-1}$$

$$N_{11}x_{1101} - N_{01}d_{0111}x_{0100}^{.5} \leq 0$$

$$e_{1101}[N_{11}x_{1101} - N_{01}d_{0111}x_{0100}^{.5}] = 0 \qquad e_{1101} \geq 0 \tag{D-2}$$

Conditions (D-1) and (D-2) characterize alewife/herring consumption of phytoplankton alewife /herring. For positive optimum consumption, $x_{1101} > 0$ and (D-1) yields a year-length version of the marginal value theorem (Charnov 1976):

$$e_{01} = e_{1101} + r_{11} + 0.5r_{11}(2x_{1102} + x_{1101} + x_{1103}) +$$
$$0.5d_{1115}(1 + t_{11}e_{1511})(x_{1101} + x_{1102} + x_{1103})^{-.5} \tag{D-3}$$

The left side is the benefit to the alewife/herring of consuming one more unit of phytoplankton biomass, and the right side is the cost comprised of the energy cost of locating, capturing and handling the unit of phytoplankton (first term), the respiration energy loss from the unit of phytoplankton (second and third terms), and the additional energy lost to striped bass predators from alewife/herring grazing on the unit of phytoplankton (fourth term). The fourth term captures the tradeoff between consuming and exposure to predators (Lima et al. 1985). Alternatively, if the alewife/herring benefit from consuming one unit of phytoplankton biomass

is less than the costs, (3) implies that $x_{1101} = 0$. In this way prey are "ranked" according to their profitability as in optimum foraging theory, and a prey that does not provide the predator with at least as much energy as it costs to attack and handle is avoided (Stephens and Krebs 1986).

Conditions (D-2) represent biomass balance where N_{01} and N_{11} are the phytoplankton and alewife/herring densities. The left side of the first inequality is the total alewife/herring demand for phytoplankton biomass and the right side is the total biomass the phytoplankton are willing to supply to alewife/herring at the current period's predation risk. The first-order conditions are actually special cases of (D-1) and (D-2); that is, regardless of negative energy prices, there are 38 sets of conditions like (D-1) and (D-2) for each period, and they allow a precise definition of competition:

Defn1 : If the solution to the general equilibrium yields $N_{11}x_{1101} - N_{01}d_{011}x_{0100}^{.5} < 0$ then $e_{1101} = 0$ and there is said to be no competition among alewife/herring for phytoplankton.

Defn2 : If $e_{1101} > 0$ then $N_{11}x_{1101} - N_{01}d_{0111}x_{0100}^{.5} = 0$ and there is said to be competition among alewife/herring for phytoplankton that is increasing in e_{1101}.

For Defn1, the density of alewife/herring is small relative to the density of phytoplankton, and the cost to alewife/herring to locate and consume phytoplankton is zero.[15] The interpretation is that there is predator saturation: phytoplankton are costless prey and alewife/herring are satiated in them.[16] Alewife/herring demand is less than what the phytoplankton are willing to supply given the low predation risk that phytoplankton are exposed to. The quantity of phytoplankton consumed under saturation is determined by the net energy gains from consumption balanced with the net energy losses to respiration and predation. There is no need to balance gains against searching and handling costs, because they are zero under saturation. If alewife/herring consumed only phytoplankton, then its consumption would not change as long as saturation holds. However, with more than one prey, its consumption of phytoplankton can change even if phytoplankton is costless, because consumption of phytoplankton also depends on the costs of other prey. This possibility can be shown in simulations.

For Defn2, the ratio of alewife/herring density to phytoplankton density is larger than in Defn1 and this places upward pressure on the alewife/herring energy cost until the cost to

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[15] The energy cost measures locating, capturing and handling prey and no matter how small the predator population, this cost may never be zero. The results would not change, however, if we define $e_{1101} = \varepsilon > 0$ as the predator cost when its density is very small, where ε is arbitrarily small.

[16] Eichner and Pethig (2003, 2006) also use endogenous predation prices as scarcity indicators. They develop theoretical models in which each species maximizes its biomass that depends on consumption of prey, losses to predators, and predation cost. Their price of capturing prey is either positive indicating the prey is scarce, or zero indicating the prey is abundant in which case the predator is satiated. Using a three species food chain, the authors identify eight regimes differentiated by whether the three prices are zero or positive. Population dynamics depend on optimum biomasses attained by the species, and species growth equations differ depending on satiation. This contrasts to Lotka-Volterra equations with population independent parameters.

alewife/herring to locate and consume phytoplankton becomes positive. Then by (D-2), alewife/herring demand equals phytoplankton supply, and increases in alewife/herring density or decreases in phytoplankton density will drive up the alewife/herring energy cost and depress its consumption of phytoplankton. Therefore, the energy cost, e_{1101}, is a measure of intraspecific competition. There are 38 energy costs in the model allowing us to track 38 intraspecific competitions simultaneously. Energy costs and saturation play a central role in species growth functions.

A solution to all 76 equations in a period yields the optimum biomass consumptions and the energy costs as functions of the densities and the system parameters:

$$\bar{x}(\overline{N}, \bar{e}, \bar{d}, \bar{r}, \bar{t}, \overline{\beta}) \quad \text{and} \quad \bar{e}_{ij}(\overline{N}, \bar{e}, \bar{d}, \bar{r}, \bar{t}, \overline{\beta}) \tag{D-4}$$

where the bar notation indicate vectors of the 38 biomasses, energy costs some of which may be zero, d and t terms, and 15 densities, r and β terms.