Modeling Top-Down and Bottom-Up Effects on Estuarine Food Webs

1 Introduction

Estuaries and other coastal ecosystems represent interfaces between terrestrial and marine worlds, and an important role they play is in the assimilation of nutrients such as nitrogen (N) and phosphorus (P) that enter the water from the land. Growth of plankton for example, preyed upon by benthic filter feeders like oysters, or the growth of sea grasses grazed upon by larger aquatic animals are portions of some of the chains by which nutrients are taken into estuarine ecosystems (Jackson et al., 2001). These ecosystems typically are comprised of multiple trophic levels, any or all of which may be affected by environmental changes. The goal of the current study is to look at the relative importance these disturbances, grouped very broadly into *bottom-up* (meaning changes to nutrient inputs) and *top-down* (meaning changes to the relative presence of upper trophic levels due, for example, to changes in harvesting rates) perturbations may have across different aquatic ecosystems.

1.1 Top-down versus bottom-up impacts on ecosystems

Urban development in areas surrounding coastal ecosystems has been accompanied by changes in ecosystem structure. A commonly reported estuarine malady is an increase in the frequency and severity of seasonal hypoxic and anoxic conditions, associated with increased levels of algae and phytoplankton in the system (Jackson et al., 2001; Brawley et al., 2000). These events are often explained as being caused proximately by increased anthropogenic contributions to estuarine nutrient loads and have triggered significant effort into the modeling of nutrient inputs to estuaries from groundwater, point and non-point source runoff into estuarine feeders. The goal of such work is to determine estimates of critical nutrient load, or loading targets to guide agricultural and land-use policy (Brawley et al., 2000; Cerco et al., 1995). However, it is important to recognize that increased runoff and nutrient input is not the only anthropogenic influence on coastal ecosystems. Habitat destruction and fishing practices have affected the ability of macrofauna, like the oysters, to exert control over the structure of their ecosystems. The oyster reefs of the Chesapeake Bay were once capable of filtering the entire water column in only a few days, and it is only since exhaustive dredging of the bay led to the collapse of the oyster fishery that hypoxia and anoxia begin to be observed (Jackson et al., 2001). Jackson et al. discuss this and other correlations of ecosystem decline with destructive fishing practices, making it clear that comprehensive attempts to curb hypoxic and anoxic events via policy should consider the potential for both bottom-up and top-down effects to be significant in a target system.

1.2 Generality and models as management tools

Whether looking at top-down or bottom-up control, or both, a difficulty in modeling all estuarine systems is that the term "estuary" in itself is a fairly loose categorization of bodies where freshwater and marine systems meet. Estuaries may differ greatly in, among other factors, the structure of their biological communities, the distribution of nutrient and chemical inputs, and their basic physical structure (NRC), which in turn affects another important factor in estuarine heterogeneity - hydrodynamics. Both the volumes of river and tidal flow into the estuary, and the way that they flow into and out of the estuary, will affect the degree of mixing and the salinity gradient, an important characteristic of a freshwater-marine interface (NRC). Mixing characteristics of flows entering an estuary determine the dilution of nutrients entering with the flow, and flow levels in and out of the estuary, in concert with mixing, control the residence time.

In short, estuaries can be nearly as different as they are similar, presenting a difficult problem in ecosystem management. Management tools must be somewhat general in order to be useful over a wide enough range, but must also describe systems well enough to give meaningful results. In the case of estuaries, this has proven to be a difficult balance to achieve. Sophisticated three-dimensional hydrodynamic models have captured many of the flow and salinity characteristics of specific estuaries (Chau et al., 2001; Cugier et al., 2002), but the calibration and use of these models is resource intensive. In contrast, simple mechanistic box models that explain well some important processes in estuarine ecosystems have been around for decades (Kremer et al., 1982), but lack the spatially explicit resolution needed to make judgments. An open question in estuarine ecosystem modeling then, is "how general can the model be before it is no longer meaningful?" This question frames the second objective of the current investigation.

1.3 Immediate Project Goals

Estuarine modeling is at this time a rich and well-developed field but there does not yet exist significant work analyzing the relative importance of both bottom-up and top-down anthropogenic influences on ecosystem conditions. The long-term goal of the current study is to contribute to this work by comparing these effects across several ecosystems.

The immediate deliverable within the time constraints of the course project is a modeling framework linking nutrient input, anthropogenic harvesting and habitat-destructive effects to planktonic and macrobiotic growth in the ecosystem. This simple module will form the ecosystem component of larger, spatially explicit simulations that examine entire ecosystems. Within the reduced scope of the course project, the questions framing the overall study collapse then, to "can top-down and bottom-up effects be observed in physical subcomponents of an estuarine ecosystem?" The first target system for this study, and the system that is the scope of the course project, will be the Chesapeake Bay.

2 System Description

Already an extensively studied ecosystem, model results and historical data looking at estuary nutrient loading (Brawley et al., 2000; Cerco et al., 1995) and macrofauna (Miller, 2003) in the Chesapeake Bay exist as a backdrop against which to compare the results of this integrated study. In particular, Ulanowicz et al. have assembled box models of the mesohaline reach of the Chesapeake Bay that provide an excellent initial comparison for model results.

The Chesapeake Bay is a deep estuary, dominated by plankton growth and possessing a long residence time (NRC). A large share of phytoplankton production fuels zooplankton growth, which in turn are preyed upon by ctenophores and sea nettles, a seasonally-variant process peaking in summer, and by fishes such as the striped bass (Baird et al., 1989). Remaining phytoplankton may sink through the water column where it feeds several commercially important benthic macrofauna, namely oysters and blue crabs, which are thought to have significant roles in benthic community structure.

Seasonal variations in light and nutrient availability result in annual cycles of the ecosystem (Baird et al., 1989). While these should be incorporated into the simulation within the larger context of this study, for the purposes of this project only a single season (summer) is used for data input.

3 Method

GeiLoVe utilizes simple Lotka-Volterra dynamics, which allow for four different types of fluxes into, out of, or between model pools (Ulanowicz et al. 1992):

Flux Type	**Interpretation**	**Flux Term**
Fixed	Dependency on factors outside of model	dM1/dt = C
Donor Control	Flux not inhibited or promoted by recipient pool (i.e., decay)	dM1/dt = C*M2
Recipient Control	Flux not generally inhibited or promoted by donor pool (i.e., carbon fixation by phytoplankton)	dM1/dt = C*M1
Feeding Flux	Flux dependent on both donor and recipient (i.e., zooplankton grazing on phytoplankton)	dM1/dt = C*M1*M2

Table 1 – Lotka-Volterra Flux Descriptions

While simple in their treatment of food web interactions, Lotka-Volterra dynamics are simple to solve, as there exists only a single unknown coefficient for each new flux to the system. A single snapshot of the food web fluxes and average pool values over some interval is all that is required for input data.

GeiLoVe reads all pool and flux values from an input file (Appendix A) and calculates the model coefficients by simple algebra. A mass balance is then calculated for each pool to capture any mass imbalance in the input data. GeiLoVe then performs a simple forward time step of the form:

$$M_{t+1} = M_t + (dM/dt + E)*dt$$

where M is the vector of pool biomasses, dM/dt is the accumulation of biomass over the interval dt, and E is the vector of mass imbalances arising from the model input. Summing the mass contributions to each pool in the current interval based on the calculated Lotka-Volterra coefficients and the values M_t generates the vector dM/dt. The calculations required for this time-step are in no way computationally limiting, and there is no need to sacrifice ease-of-coding for more computational efficiency.

4 Model Input

GeiLoVe was applied to a set of season-average summer food web data for the mesohaline reach of the Chesapeake Bay (Appendix A). Dr. Robert Ulanowicz of the Chesapeake Biological Laboratory provided the raw data, as well as the software AGG.EXE used to aggregate the large number of pools into the 14 boxes used in this study. The boxes in the aggregated food web model are labeled as follows:

1 P – Phytoplankton
2 AB – Attached Bacteria
3 SB – Sediment Bacteria
4 BD – Benthic Diatoms
5 M – Microzooplankton
6 Z – Zooplankton
7 SF – Suspension Feeders
8 DF – Deposit Feeders

9 SFish – Suspension Feeding Fish
10 BFish – Benthic Fish
11 CFish – Carnivorous Fish
12 DON – Dissolved Nitrogen
13 SuspPON – Suspended Nitrogen
14 SedPON – Sediment Nitroge

These 14 boxes form a moderately complex food web from which a variety of aquatic species are harvested (Figure 1).

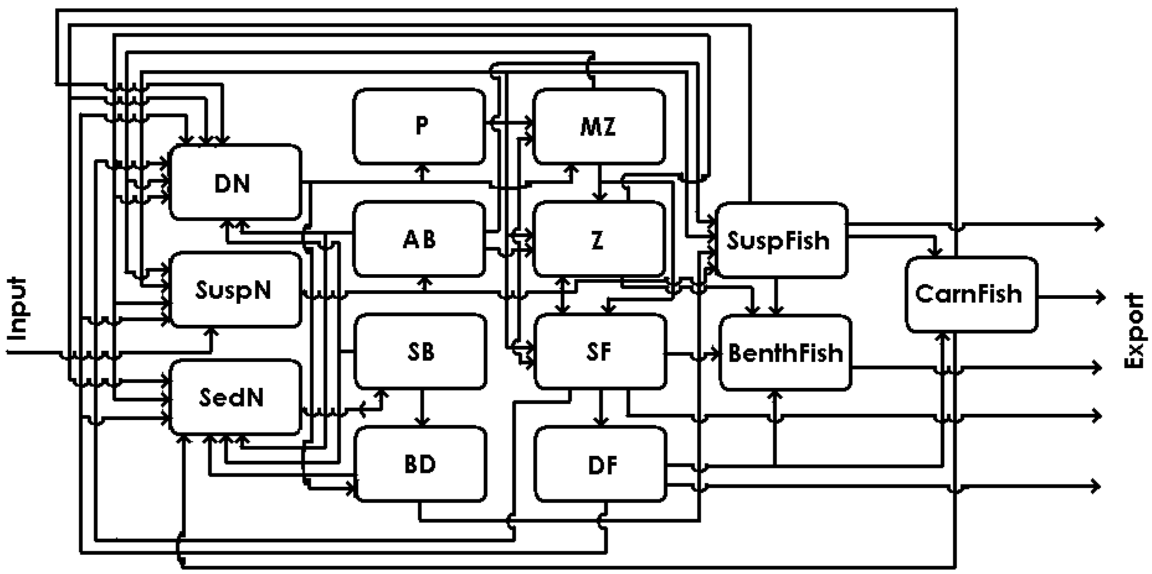

Figure 1 – Aggregated Food Web for the Chesapeake Bay (Biomass Nitrogen Basis) (Respiration fluxes not shown)

5 Results and Discussion

5.1 Implicit Mass Balance Check

As a first check of the model, a non-perturbed system should remain at steady state for any length of time t. The constant mass profiles over the period of about 5000 days, generated in MATLAB from the model outputs, show this to be true (Figure 2).

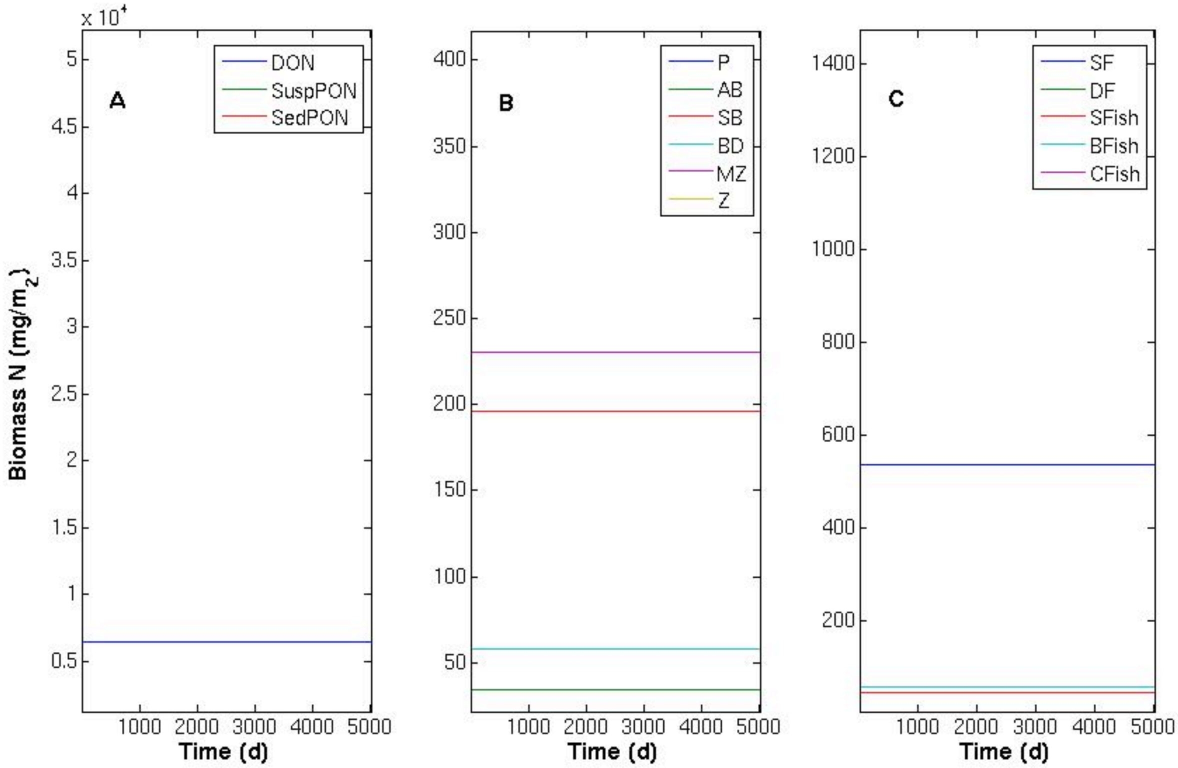

Figure 2 – Unperturbed Model Results. A) Nutrients B) Flora/Microfauna C) Macrofauna

Stepping through the model in this way serves to check that mass is being conserved in the model, beyond the error allowed in the input data.

5.2 Perturbation 1 – Nutrient Input

The input data for the summer season has a single fixed input to box 13 (Suspended Nitrogen), and as a first test of GeiLoVe's performance this input was manipulated to 110% of the original input value (Figure 3).

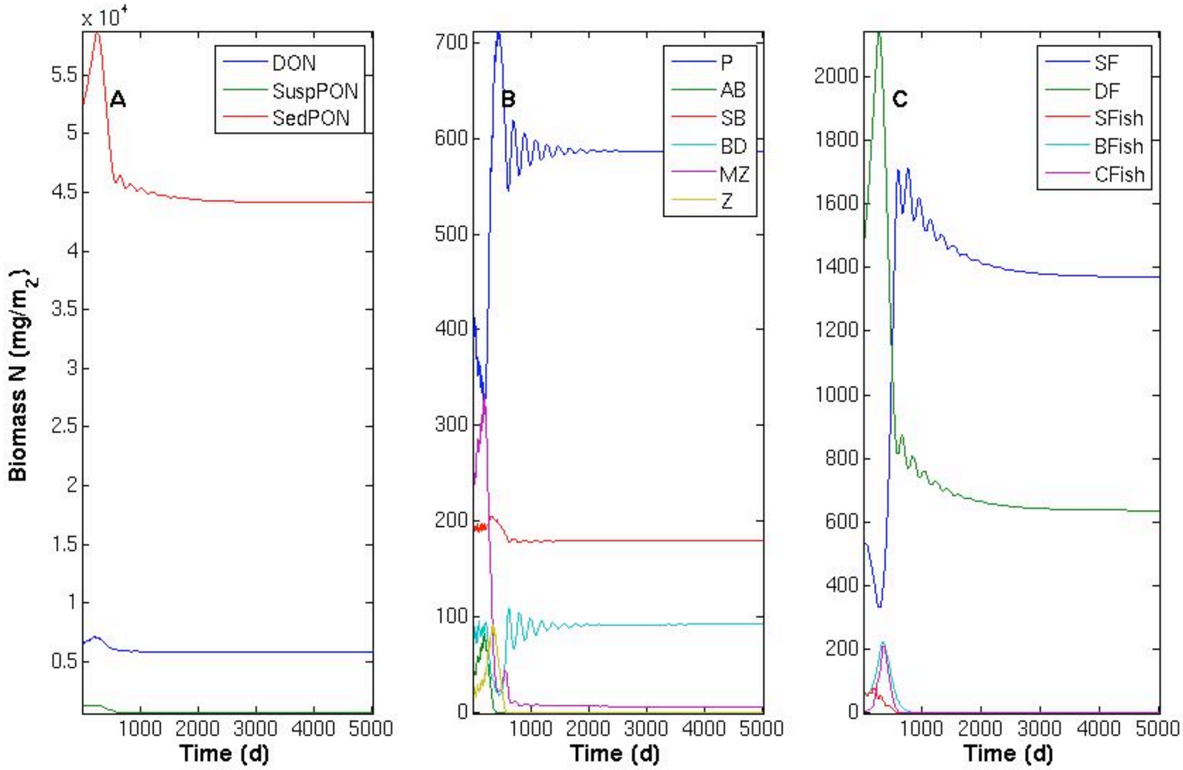

Figure 3 – Bottom-Perturbed Model Results. A) Nutrients B) Flora/Microfauna C) Macrofauna

The most striking result of this manipulation is that a number of food web members, such as the zooplankton and all fish species, have gone extinct within 1000 days in the run. Without needing to compare explicitly to experimental data, it is fairly clear that this is a specious result, an artifact of the simplicity with which the food web is modeled and the lack of the myriad negative feedback processes that in a real food web might serve to dampen the effect of perturbances on the system.

A rudimentary attempt at recreating some of these stabilizing bounds might be to assume that a given perturbation in any parameter should not move any state variable beyond a certain fraction F of its initial value. Such an approach compromises conservation of mass, but at least allows stocks whose prey pools would otherwise have speciously dropped to 0, a chance to respond to these dynamic changes. As a test, the same run was repeated with F = 0.2; that is, no state variable may drop below 80% of its initial value given the perturbation of 10% in the input nutrient flow (Figure 3).

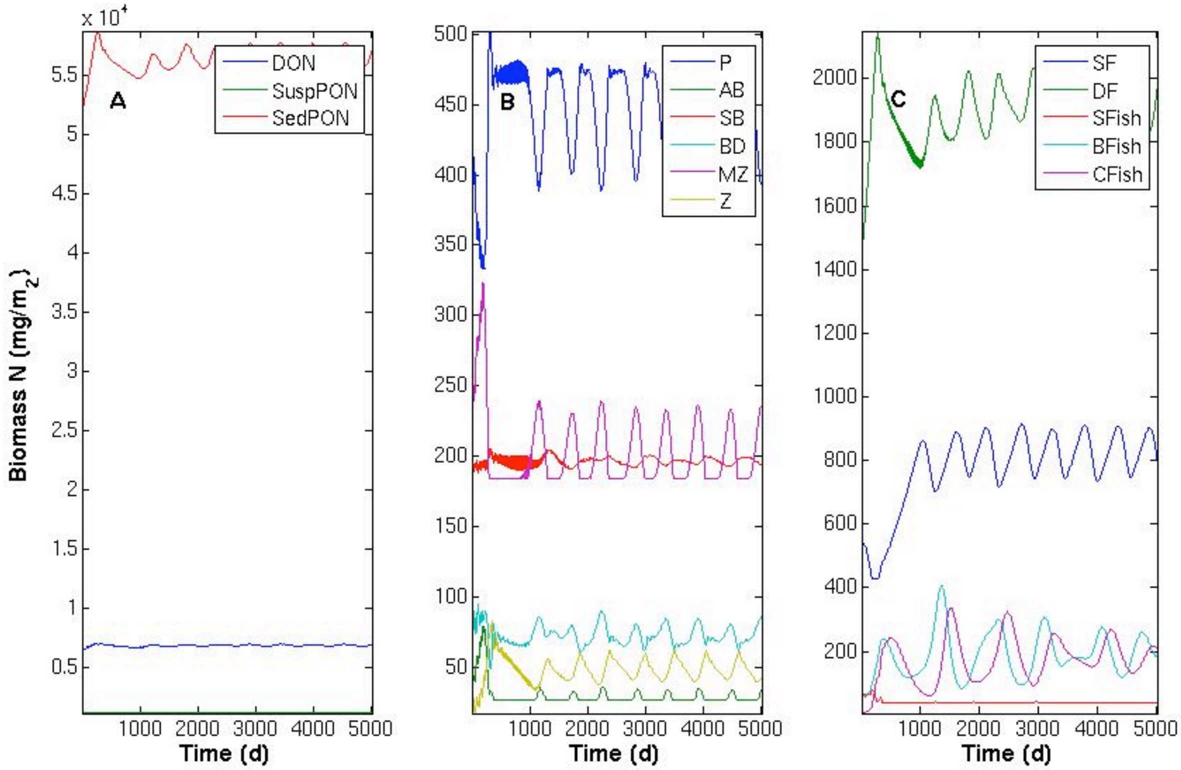

Figure 4 – Bounded Bottom-Perturbed Model Results. A) Nutrients B) Flora/Microfauna C) Macrofauna

The effect of these bounds is immediately obvious. While some species, such as the attached bacteria and suspension-feeding fish, still tend as much toward extinction as possible, others have rebounded (Figure 4). At least two cyclic patterns can be seen. One includes the zooplankton, the sediment feeders, deposit feeders, and others, and exhibits three peaks between day 1000 and the end of the model run. The second pattern is the predator-prey lag relationship seen between the carnivorous fish and the benthic fish. This cycle exhibits a distinctly different period than that observed in the first pattern.

5.3 Perturbation 2 – Carnivorous Fish

Looking now to effects from the top down, the parameter for harvest (export) of carnivorous fish was dropped to 99% of its original value with all other parameters retaining their original values (Figure 5).

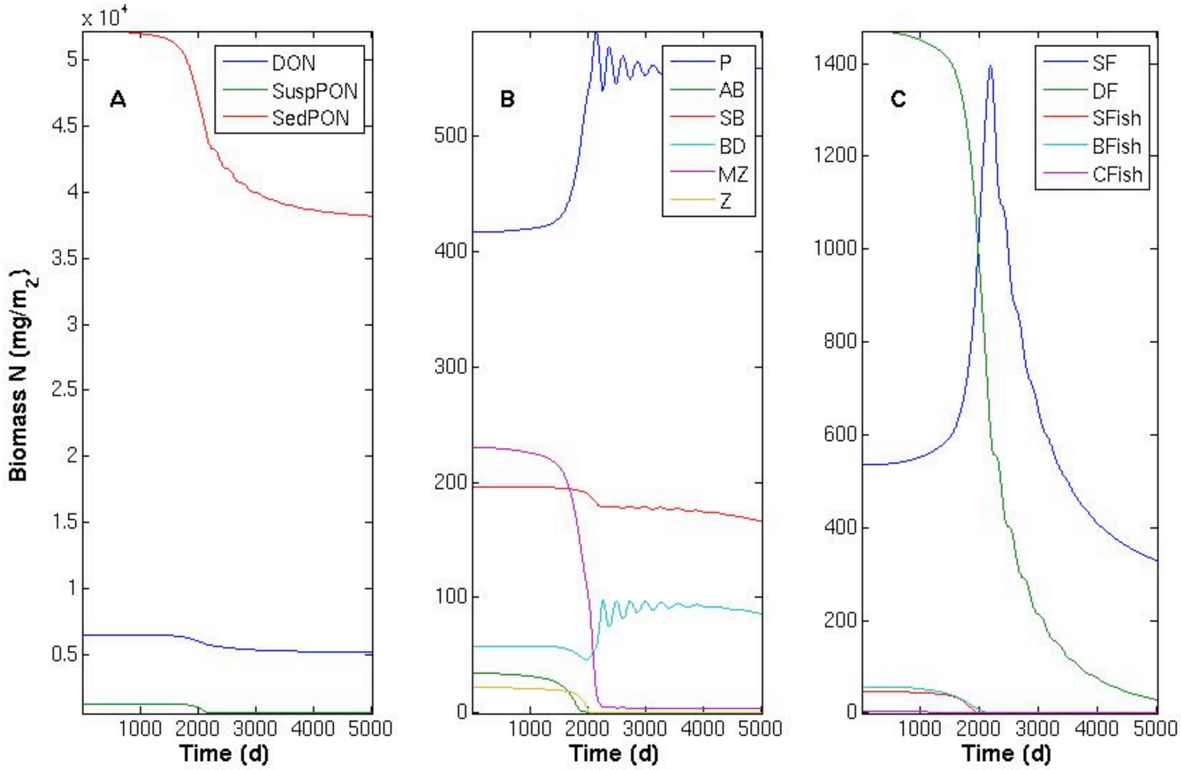

Figure 5 – Top-Perturbed Model Results. A) Nutrients B) Flora/Microfauna C) Macrofauna

Since intuitively, a decrease in fish harvests (i.e., a decrease in human impact) should restore stability to the food web, the mass extinctions that follow may seem surprising. Again, the limitations of the simple dynamics used in the model are exposed. A check was performed using the same bounding assumption as before with F = 0.2 to see the effect on the food web (Figure 6). However, in this case the application of bounds did little to preserve food web dynamics, and the system appears to be headed toward an invariant steady state beyond 2600 days of the model run. Noting that the carnivorous fish pool is small (on the order of 4mg/m2) compared with lower trophic levels such as phytoplankton (on the order of 400mg/m2), it is perhaps not appropriate to use it as a perturbation variable in the noisy context of the Lotka-Volterra dynamics.

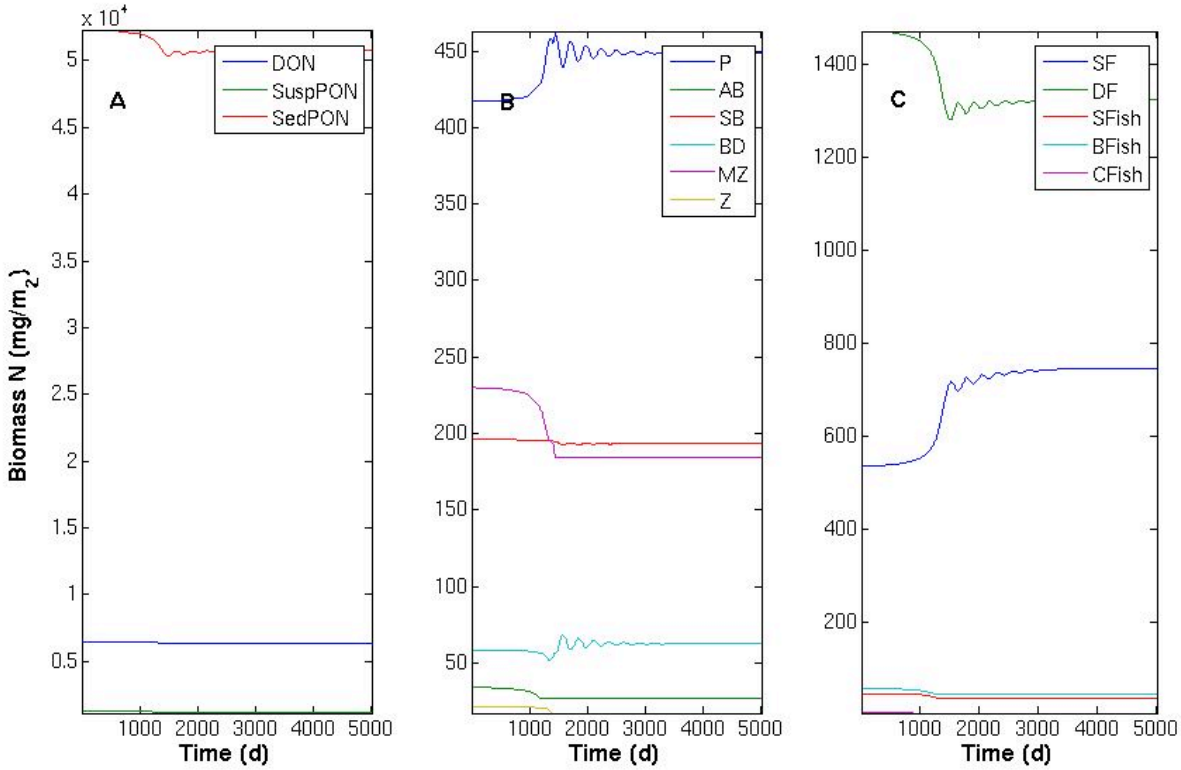

Figure 6 – Bounded Top-Perturbed Model Results. A) Nutrients B) Flora/Microfauna C) Macrofauna

5.4 Perturbation 3 – Deposit Feeders

There are other commercially important species in the Chesapeake Bay, such as crabs and oysters. These are included in the input to GeiLoVe as the deposit feeder and suspension feeder boxes, respectively. A manipulation of the deposit feeder harvest coefficient to 90% of its original value (with a bounding factor F = 0.2) yields an interesting dynamic solution (Figure 7), and so the deposit feeder pool is the first target for a response surface analysis.

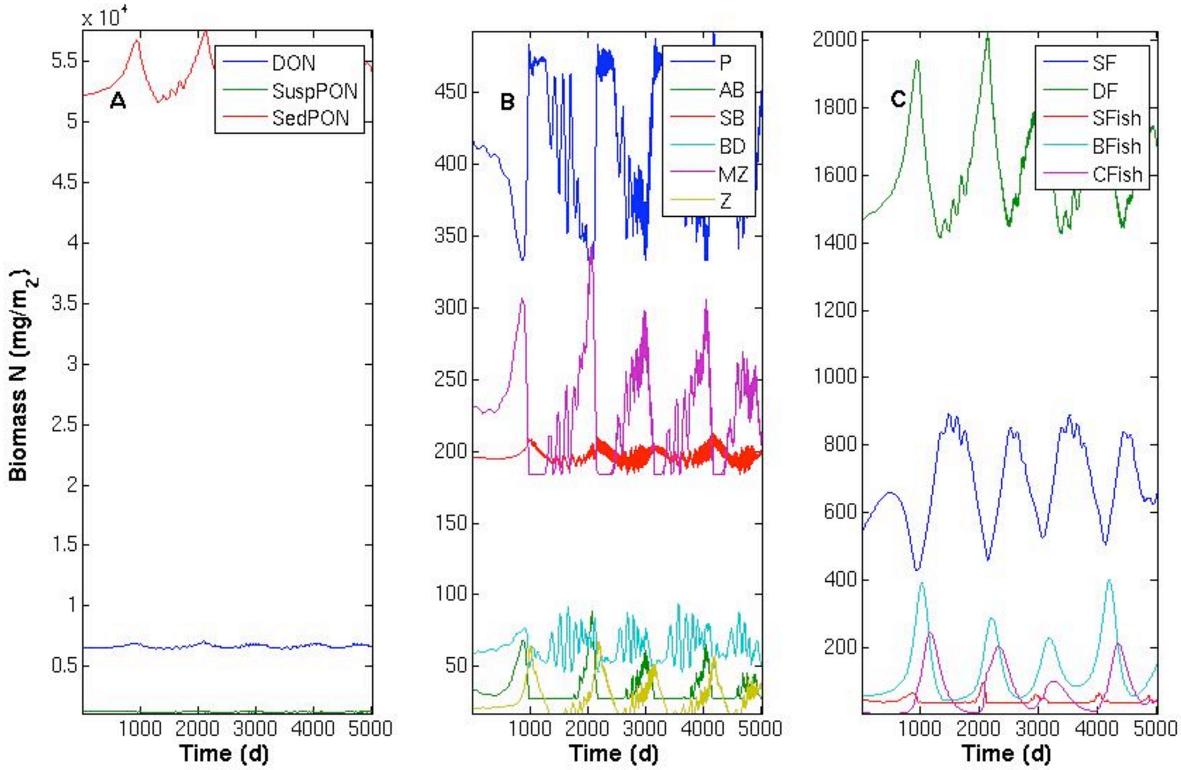

Figure 7 – Bounded Top-Perturbed Model Results. A) Nutrients B) Flora/Microfauna C) Macrofauna

5.5 Response Surface 1 – Deposit Feeders and Nutrient Input

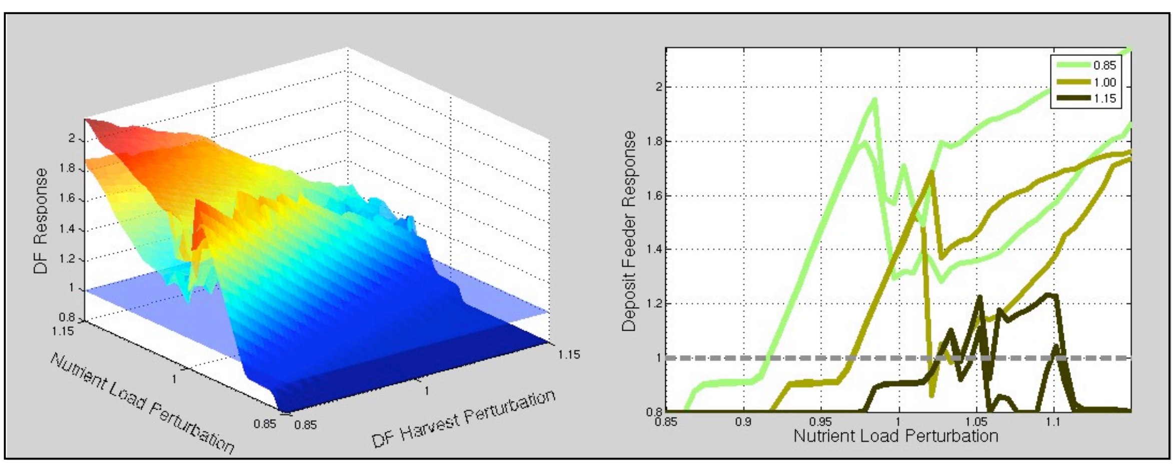

Figure 8 – Deposit Feeder Response to Nitrogen load and DF Perturbation A) Surface B) Slices at several DF Perturbation levels

The harvest coefficient for deposit feeders was varied from 85% to 115% of its original value, and that for the nutrient load was varied from 85% to 115% of its original value to generate a multivariate response surface (Figure 8 A and B). Since in many cases the food web settled into stable periodic dynamics rather than a steady state, both the minimum and maximum observed in the last 25% of the run were plotted in order to more fully represent the state of the system. In general, the periodic dynamics occurred when nutrient loading was high, whereas the system reached a stable steady state when nutrient loading was kept low (Figure 8 B). Since the results in 5.1 to 5.4 indicated that a stable steady state was linked to an extinction of many of the food webs, it should be noted that this may be true for many (or all) of the steady state cases shown in the response surface.

The response surface reveals that when nutrient loading is high and harvests are low, the deposit feeder stock is quite high (Figure 8 A). In contrast, when harvests are high and nutrient loading is low, the stock is low. These results have intuitive appeal. The shape of the response surface is also important, in that it has a significant slope along both axes of perturbation. Taken together, these results suggest that in the case of deposit feeders, perturbations to nutrient load as well as harvests can act as independent control knobs on the simulation, with their effects being discernable within the simple model framework.

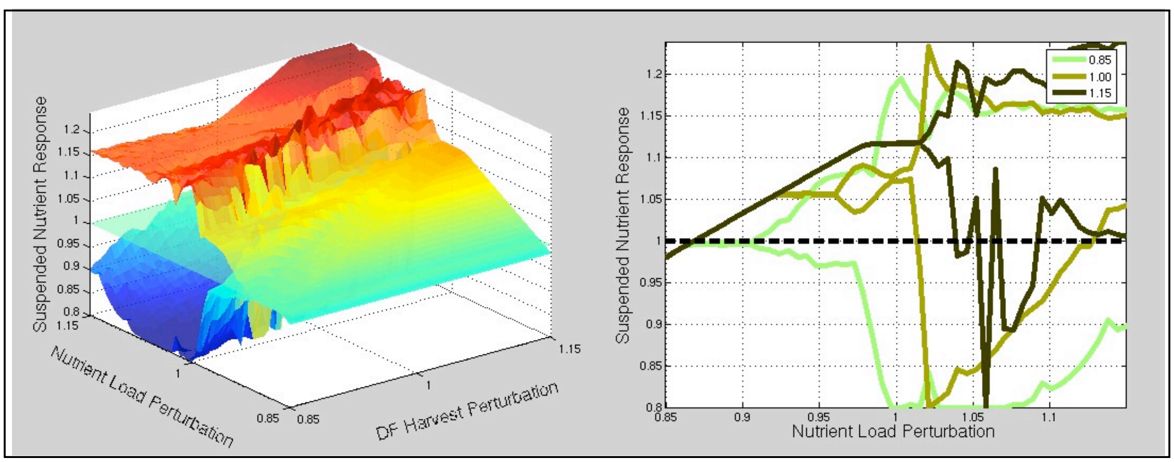

Figure 9 – Suspended Nitrogen Response to Nitrogen load and DF Perturbation A) Surface B) Slices at several DF Perturbation levels

The response of the suspended nitrogen pool to the same set of perturbations was also generated (Figure 9 A and B). It is clear that when harvests of deposit feeders are high, the level of nutrient in the system is also high (Figure 9 B), supporting the intuitive notion that upper trophic levels have a strong influence on the ability of the food web to take up nutrients.

5.6 Response Surface 2 – Suspension Feeders and Nutrient Input

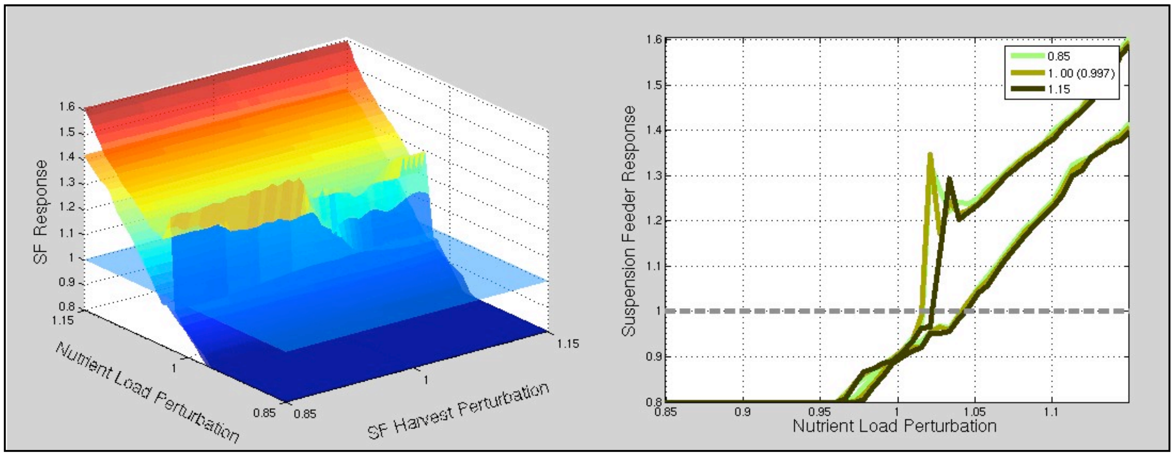

Figure 10 – Suspension Feeder Response to Nitrogen load and SF Perturbation A) Surface B) Slices at several SF Perturbation levels

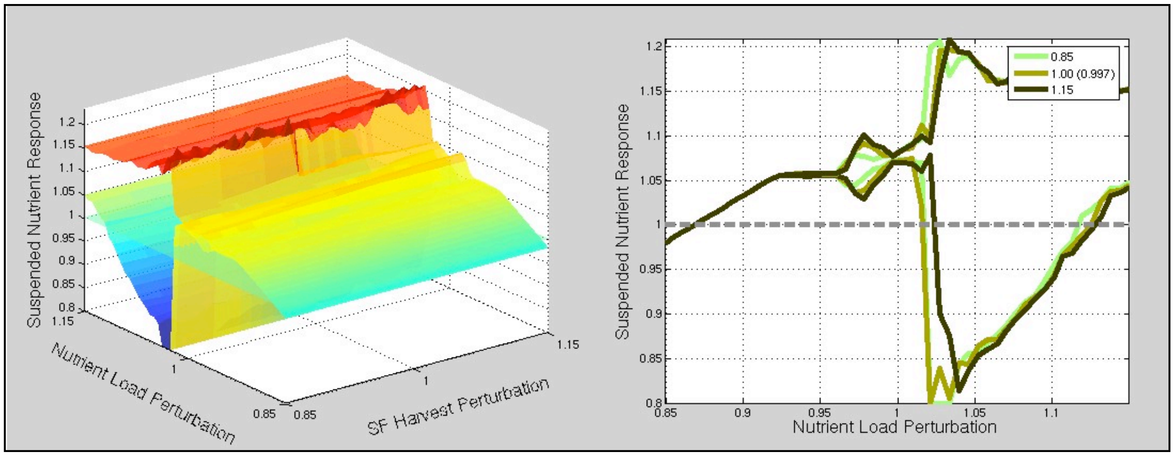

Figure 11 – Suspended Nitrogen Response to Nitrogen load and SF Perturbation A) Surface B) Slices at several SF Perturbation levels

In the same way as for the deposit feeders, a set of response curves showing the responses of suspension feeders (Figure 10 A and B) and suspended nitrogen (Figure 11 A and B) to perturbations in suspension feeder harvest and nitrogen loading were developed.

The suspension feeder stock responded to perturbations in nitrogen load in a very similar way to that of the deposit feeders, and the suspended nitrogen response was similar to that in the previous case. However, both pools appeared relatively insensitive to changes in suspension feeder harvest over the range of analysis.

5.7 A Note on the Response Surface – Lack of Unperturbed Points

Since it is expected that when the relative perturbations for both variables are 1, the stock response is also 1, it may seem surprising that this point does not appear on any of the response surfaces. The reason for this is that the due to grid spacing (a total of 50 grid points over the range 0.85 to 1.15), the point shown as 1.00 is actually 0.997. Noting that the system is further constrained by the bounding factor F = 0.2, which in many cases pulls the pool values away from their unconstrained state, it is not surprising that pool values for systems even close to the unperturbed state will be very different.

5.8 Comparison against other Studies

Ulanowicz et al. (1992) used a set of analogously derived data using a carbon basis to look at the effect of oyster harvest on the same mesohaline reach of the Chesapeake Bay. Their study also made use of Lotka-Volterra dynamics; in fact, much of the method applied in the current study used this Ulanowicz study as a basis.

The Ulanowicz study used a 13-box model of the system, one of which modeled oyster biomass. They derived the Lotka-Volterra coefficients defining the food web model in the same way as defined in this paper, and then proceeded to decrease the coefficient defining oyster export from the system in increments of 1%, allowing the system to solve to a steady state at each step.

One key difference in methodology is that they used an iterative Newton zero-finding approach to find the time-invariant solution (i.e., dM/dt = 0), and used that solution as the steady state value. It is clear that such an approach would not have solved satisfactorily in most of the cases in the current study – periodic dynamics are not time-invariant and thus there is no zero to be found. The forward time-step method applied in the current study is more appropriate to this type of behavior.

The Ulanowicz study also observed what was regarded as specious extinction of a pool, though not to the extent observed in the current work. The major finding of the modeling study was that a XX% reduction in oyster harvest (as a proportion of the standing stock) led to an overall higher catch volume. This is consistent with the findings of this study that low harvests of deposit feeders, and to a lesser extent harvests of suspension feeders (oysters) led to overall higher stocks (Figures 7 and 9).

6 Current Conclusions

Lotka-Volterra dynamics alone are not sufficient to reproduce the food web dynamics of the Chesapeake Bay, although it seems that an augmentation of these simple dynamics may help. One possibility would be to allow the Lotka-Volterra flux coefficients to vary as functions of the biomass pools they connect to. As prey grow scarce, they become harder for predators to find, which in the Lotka-Volterra framework can be interpreted as a decrease in the value of the coefficient for a feeding flux. This semi-mechanistic approach may help to dampen the wild oscillations in the current system that contribute to extinctions of upper trophic levels, and should be a target of future work.

While the current model was unable to adequately simulate effects of perturbations to exports of the top trophic levels in the food web, a two-factor response surface showed clear and distinct responses to perturbations in nitrogen input and deposit feeder export. Specifically, deposit feeder stocks were high under conditions of high nutrient load and low harvest, and low under conditions of low loading and high harvest. Additionally, high harvest of the deposit feeders led to high levels of suspended nutrients.

Without reproducing similar response curves for other pairs of perturbed variables in the system, these results are at best anecdotal. However, they satisfy intuitive expectations for the system and suggest the potential for application of this method to other systems.

In its current form, the food web model generated with Lotka-Volterra dynamics in GeiLoVe is not stable enough to reproduce the dynamics resulting from perturbations to flux parameters. Even small perturbations can cause some pools, particularly in the upper trophic levels, to go to extinction. However, artificial bounding of pool values in some cases allowed the system to rebound and produce interesting dynamics. If this effect could be reproduced in a more mechanistic way by augmenting the basic Lotka-Volterra dynamics, the resultant model might be sufficient to study top-down and bottom-up effects on the Chesapeake Bay and other relevant coastal ecosystems.

7 Acknowledgements

I gratefully acknowledge Dr. Robert Ulanowicz for providing the raw data used in this study, the software necessary for its preparation, and for invaluable technical assistance in setting up and interpreting the model.

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Appendix B – Formatted Input File

The first two lines in the following file indicate the number of pools and fluxes, respectively. These are followed by the list of pool variable names. There then follow five groups of inputs, each with up to five entries. The meaning of these inputs is as follows:

Column 1	Meaning	Column 2	Column 3	Column 4	Column 5
0	Pool Initial Values	Pool Number	Pool Value	Blank	Blank
1	Inputs	Fixed? (1/0)	Pool	Value	Blank
2	Exports	Fixed? (1/0)	Pool	Value	Blank
3	Respiration	Fixed? (1/0)	Pool	Value	Blank
4	Inter-pool Fluxes	Feeding? (1/0)	From Pool	To Pool	Value

```
14  0  0  0  0
62  0  0  0  0
Phytoplankton
AttachedBacteria
SedimentBacteria
BenthicDiatoms
Microzooplankton
Zooplankton
SuspensionFeeders
DepositFeeders
SuspensionFish
BenthicFish
CarnivorousFish
DON
SuspPON
SedPON
0  1   4.17E+02  0  0
0  2   3.40E+01  0  0
0  3   1.96E+02  0  0
0  4   5.81E+01  0  0
0  5   2.30E+02  0  0
0  6   2.16E+01  0  0
0  7   5.36E+02  0  0
0  8   1.47E+03  0  0
0  9   4.65E+01  0  0
0  10  5.68E+01  0  0
0  11  5.14E+00  0  0
0  12  6.51E+03  0  0
0  13  1.25E+03  0  0
0  14  5.22E+04  0  0
1  1   12  1.81E+04  0
2  0   1   1.05E+04  0
2  0   6   6.34E+02  0
2  0   7   3.96E+02  0
2  0   8   1.73E+02  0
2  0   9   1.76E+01  0
2  0   10  2.65E+01  0
2  0   11  1.75E+00  0
2  0   13  3.74E+03  0
2  0   14  2.34E+03  0
3  0   3   2.39E+02  0
4  1   1   5   2.73E+03
4  1   1   6   9.14E+02
4  1   1   7   8.45E+02
4  1   1   9   1.91E+01
4  0   1   13  4.50E+03
4  1   2   5   7.08E+01
4  1   2   6   6.44E+00
4  1   2   7   1.75E+01
4  1   2   9   1.84E+00
4  0   2   12  1.06E+03
4  0   2   14  1.45E+03
4  1   3   8   9.92E+03
4  0   3   12  9.11E+03
```

4	0	3	14	1.69E+04
4	1	4	8	8.86E+02
4	0	4	14	3.39E+03
4	1	5	6	7.52E+02
4	1	5	7	1.05E+02
4	0	5	12	4.22E+03
4	0	5	13	1.28E+04
4	1	6	9	1.60E+02
4	0	6	12	3.69E+02
4	0	6	13	6.62E+02
4	0	6	14	8.00E+01
4	1	7	8	1.07E+02
4	1	7	10	8.37E-01
4	0	7	12	3.39E+02
4	0	7	14	6.81E+02
4	1	8	10	1.18E+02
4	1	8	11	2.94E-01
4	0	8	12	3.27E+03
4	0	8	14	7.35E+03
4	1	9	10	3.59E+00
4	1	9	11	1.33E+01
4	0	9	12	9.22E+01
4	0	9	14	7.62E+01
4	1	10	11	1.00E+00
4	0	10	12	7.09E+01
4	0	10	14	2.42E+01
4	0	11	12	9.84E+00
4	0	11	14	2.93E+00
4	1	12	1	1.95E+04
4	1	12	4	4.27E+03
4	1	12	5	1.28E+04
4	1	13	2	2.60E+03
4	1	13	5	2.25E+03
4	1	13	6	2.32E+02
4	1	13	7	5.55E+02
4	1	13	9	2.24E+01
4	0	13	14	8.56E+03
4	1	14	3	3.62E+04

Appendix C – Sample Adapted (and Abridged) Output File

All values in mg N / m^2

Time (Days)	Phytoplankton	Attached Bac.	Sediment Bac.	Benthic Diatoms	Microzooplank.	Zooplankton	Susp. Feeders	Deposit Feeders	Susp. Fish	Benthic Fish	Carn. Fish	Dissolved N	Suspended N	Sediment N
1.0000000e+00	4.1700000e+02	3.4000000e+01	1.9600000e+02	5.8100000e+01	2.3000000e+02	2.1600000e+01	5.3600000e+02	1.4700000e+03	4.6500000e+01	5.6800000e+01	5.1400000e+00	6.5100000e+03	1.2500000e+03	5.2200000e+04
1.1000000e+01	3.5958852e+02	5.7124584e+01	1.8970870e+02	8.3934816e+01	2.8263027e+02	3.0114829e+01	5.1187804e+02	1.6511493e+03	5.7697175e+01	6.3790713e+01	9.0677904e+00	6.7384732e+03	1.2772441e+03	5.3904748e+04
2.1000000e+01	3.4265833e+02	7.0333359e+01	1.9591730e+02	8.9403536e+01	3.3004461e+02	3.0900373e+01	4.2104375e+02	1.9275199e+03	7.8107492e+01	9.7848333e+01	3.1398686e+01	6.8682710e+03	1.2965796e+03	5.6517903e+04
3.1000000e+01	4.1141388e+02	5.4304287e+01	1.9740096e+02	7.3762061e+01	2.2314233e+02	6.6619128e+01	3.2694397e+02	2.1541723e+03	5.0567052e+01	1.7996020e+02	1.1081065e+02	7.0557221e+03	1.2476401e+03	5.8854703e+04
4.1000000e+01	6.1998660e+02	7.4980768e+00	2.0440049e+02	3.3416557e+01	6.5732934e+01	8.4469773e+01	4.4039413e+02	1.8506649e+03	3.2332678e+01	2.2533237e+02	2.1506901e+02	6.8499733e+03	1.1414851e+03	5.5934929e+04
5.1000000e+01	7.0457336e+02	4.0723418e-01	1.9885431e+02	1.6684974e+01	2.0875009e+01	6.0234921e+01	8.4554892e+02	1.3186004e+03	2.4042489e+01	1.5150362e+02	1.0723913e+02	6.2924852e+03	9.6365525e+02	5.0685278e+04
6.1000000e+01	6.5866670e+02	2.6525193e-01	1.9131583e+02	3.3755420e+01	3.6492868e+01	1.2226885e+01	1.5169252e+03	8.7446628e+02	6.8485550e+00	6.9634605e+01	2.3741852e+01	6.1029398e+03	8.2927626e+02	4.6375500e+04
7.1000000e+01	5.4152916e+02	1.6785489e-01	1.7692295e+02	1.1471872e+02	1.1700858e+01	3.0069770e-02	1.6348870e+03	8.5143854e+02	1.2835072e-01	2.6686593e+01	1.8683404e+00	5.9281986e+03	5.8884616e+02	4.6190963e+04
8.1000000e+01	6.2291831e+02	1.8189054e-01	1.8312774e+02	6.5353856e+01	1.0049967e+01	5.2647613e-02	1.6477609e+03	7.9790473e+02	-1.3083872e-01	1.0994946e+01	9.5700286e-02	5.9118850e+03	6.4313692e+02	4.5656559e+04
9.1000000e+01	5.5608060e+02	1.6191661e-01	1.7697570e+02	1.0920514e+02	6.2988383e+00	3.0541149e-02	1.6198456e+03	7.8720829e+02	-1.3962581e-01	4.1156310e+00	-1.9019627e-02	5.8808937e+03	5.6797009e+02	4.5546004e+04
1.0100000e+02	6.1049965e+02	1.7687228e-01	1.8109153e+02	7.3886560e+01	7.8047638e+00	4.5186404e-02	1.5624494e+03	7.6845591e+02	-1.4194392e-01	1.6667617e+00	-2.6026560e-02	5.8623058e+03	6.2480598e+02	4.5396456e+04
1.1100000e+02	5.6918108e+02	1.6576258e-01	1.7918636e+02	1.0227577e+02	6.4890526e+00	3.3208388e-02	1.5784637e+03	7.4074645e+02	-1.4103753e-01	6.8862767e-01	-2.6394498e-02	5.8599995e+03	5.8278140e+02	4.5096298e+04
1.2100000e+02	6.0245852e+02	1.7401974e-01	1.7974140e+02	8.1762529e+01	6.8405400e+00	4.1409447e-02	1.5033408e+03	7.4630247e+02	-1.4156072e-01	3.5314967e-01	-2.6409668e-02	5.8251092e+03	6.1425877e+02	4.5156613e+04
1.3100000e+02	5.7701731e+02	1.6895047e-01	1.7907527e+02	9.5785821e+01	6.5627261e+00	3.5432244e-02	1.5372094e+03	7.0892836e+02	-1.4149009e-01	2.2481154e-01	-2.6390024e-02	5.8351292e+03	5.9395921e+02	4.4805778e+04
1.4100000e+02	5.9418056e+02	1.7146079e-01	1.8022533e+02	8.7952939e+01	6.2546171e+00	3.8285437e-02	1.4644602e+03	7.2266676e+02	-1.4124146e-01	1.8235602e-01	-2.6391789e-02	5.8109573e+03	6.0439482e+02	4.4937267e+04
1.5100000e+02	5.8592165e+02	1.7125488e-01	1.7981320e+02	9.2319370e+01	6.5573393e+00	3.7471035e-02	1.4977339e+03	6.9107774e+02	-1.4169558e-01	1.6456628e-01	-2.6380975e-02	5.8132180e+03	6.0250481e+02	4.4613553e+04
1.6100000e+02	5.8778897e+02	1.7045052e-01	1.7920854e+02	9.1854895e+01	5.9746548e+00	3.6865830e-02	1.4420558e+03	7.0285936e+02	-1.4114829e-01	1.5847163e-01	-2.6382018e-02	5.7924271e+03	5.9981239e+02	4.4739022e+04
1.7100000e+02	5.8887829e+02	1.7226922e-01	1.7979101e+02	8.9996414e+01	6.4059170e+00	3.8150025e-02	1.4626010e+03	6.7769663e+02	-1.4172553e-01	1.5495450e-01	-2.6376146e-02	5.7976357e+03	6.0572184e+02	4.4498541e+04
1.8100000e+02	5.8495314e+02	1.6998335e-01	1.7966541e+02	9.4062631e+01	5.8519738e+00	3.6136334e-02	1.4272899e+03	6.8464517e+02	-1.4116529e-01	1.5289213e-01	-2.6375007e-02	5.7854193e+03	5.9761598e+02	4.4565583e+04
1.9100000e+02	5.9134089e+02	1.7266200e-01	1.8008317e+02	8.9806699e+01	6.2429517e+00	3.8455376e-02	1.4340227e+03	6.7022136e+02	-1.4166422e-01	1.5175346e-01	-2.6372485e-02	5.7837117e+03	6.0713809e+02	4.4418137e+04
2.0100000e+02	5.8436204e+02	1.7037399e-01	1.7948631e+02	9.4568573e+01	5.8376167e+00	3.6237528e-02	1.4171361e+03	6.7100747e+02	-1.4127013e-01	1.5022186e-01	-2.6370056e-02	5.7757413e+03	5.9861731e+02	4.4426228e+04
2.1100000e+02	5.9061030e+02	1.7251728e-01	1.7978152e+02	9.0266466e+01	6.0657393e+00	3.8129631e-02	1.4126467e+03	6.6384572e+02	-1.4156896e-01	1.4972116e-01	-2.6369431e-02	5.7728091e+03	6.0632714e+02	4.4359786e+04
2.2100000e+02	5.8485097e+02	1.7086388e-01	1.7962231e+02	9.4100131e+01	5.8448318e+00	3.6476615e-02	1.4078047e+03	6.5999837e+02	-1.4137184e-01	1.4846841e-01	-2.6366592e-02	5.7704940e+03	6.0009722e+02	4.4323777e+04
2.3100000e+02	5.8966370e+02	1.7213746e-01	1.7990759e+02	9.1359080e+01	5.9247608e+00	3.7664043e-02	1.3975873e+03	6.5832998e+02	-1.4147850e-01	1.4815073e-01	-2.6366688e-02	5.7663175e+03	6.0484180e+02	4.4307127e+04
2.4100000e+02	5.8637450e+02	1.7143657e-01	1.7980985e+02	9.3488465e+01	5.8597737e+00	3.6899421e-02	1.3988748e+03	6.5289448e+02	-1.4145017e-01	1.4722928e-01	-2.6364234e-02	5.7650879e+03	6.0207015e+02	4.4251891e+04
2.5100000e+02	5.8849668e+02	1.7187478e-01	1.7980487e+02	9.2352847e+01	5.8320206e+00	3.7315173e-02	1.3879315e+03	6.5352428e+02	-1.4142801e-01	1.4693111e-01	-2.6364354e-02	5.7605355e+03	6.0372874e+02	4.4258152e+04
2.6100000e+02	5.8734182e+02	1.7185119e-01	1.7977990e+02	9.2889959e+01	5.8530044e+00	3.7186549e-02	1.3904498e+03	6.4809011e+02	-1.4149092e-01	1.4632464e-01	-2.6362624e-02	5.7602066e+03	6.0343768e+02	4.4205331e+04
2.7100000e+02	5.8747970e+02	1.7170632e-01	1.7975243e+02	9.2993722e+01	5.7758377e+00	3.7055791e-02	1.3816995e+03	6.4885780e+02	-1.4141036e-01	1.4599674e-01	-2.6362436e-02	5.7570319e+03	6.0294565e+02	4.4214076e+04
2.8100000e+02	5.8795354e+02	1.7204357e-01	1.7984360e+02	9.2621651e+01	5.8282758e+00	3.7304872e-02	1.3829246e+03	6.4481333e+02	-1.4149690e-01	1.4563058e-01	-2.6361424e-02	5.7567471e+03	6.0406528e+02	4.4174577e+04
2.9100000e+02	5.8713145e+02	1.7169089e-01	1.7980269e+02	9.3333682e+01	5.7514912e+00	3.6972857e-02	1.3774750e+03	6.4497535e+02	-1.4141728e-01	1.4529539e-01	-2.6360943e-02	5.7545566e+03	6.0278643e+02	4.4176060e+04
3.0100000e+02	5.8819919e+02	1.7210802e-01	1.7986753e+02	9.2640535e+01	5.7972993e+00	3.7324987e-02	1.3768661e+03	6.4262044e+02	-1.4148616e-01	1.4508295e-01	-2.6360468e-02	5.7537045e+03	6.0425485e+02	4.4152650e+04
3.1100000e+02	5.8712241e+02	1.7178270e-01	1.7980587e+02	9.3390183e+01	5.7437486e+00	3.7001140e-02	1.3742877e+03	6.4195742e+02	-1.4143575e-01	1.4478038e-01	-2.6359854e-02	5.7523867e+03	6.0303208e+02	4.4146083e+04
3.2100000e+02	5.8806563e+02	1.7208672e-01	1.7984103e+02	9.2791946e+01	5.7660948e+00	3.7265329e-02	1.3723466e+03	6.4085621e+02	-1.4147073e-01	1.4464548e-01	-2.6359668e-02	5.7513599e+03	6.0412099e+02	4.4135540e+04
3.3100000e+02	5.8727032e+02	1.7189323e-01	1.7981532e+02	9.3304849e+01	5.7404396e+00	3.7058973e-02	1.3715443e+03	6.3967297e+02	-1.4145278e-01	1.4440215e-01	-2.6359078e-02	5.7507613e+03	6.0336722e+02	4.4124117e+04
3.4100000e+02	5.8783938e+02	1.7203640e-01	1.7983939e+02	9.2990479e+01	5.7411579e+00	3.7186192e-02	1.3691561e+03	6.3931815e+02	-1.4145831e-01	1.4429620e-01	-2.6358988e-02	5.7497703e+03	6.0389220e+02	4.4120860e+04
3.5100000e+02	5.8749223e+02	1.7198777e-01	1.7984139e+02	9.3210214e+01	5.7368854e+00	3.7118033e-02	1.3690939e+03	6.3807814e+02	-1.4146342e-01	1.4411998e-01	-2.6358526e-02	5.7494516e+03	6.0367336e+02	4.4108648e+04
3.6100000e+02	5.8766195e+02	1.7200567e-01	1.7984267e+02	9.3157059e+01	5.7250159e+00	3.7132241e-02	1.3669860e+03	6.3800727e+02	-1.4145270e-01	1.4402245e-01	-2.6358428e-02	5.7485766e+03	6.0374336e+02	4.4107970e+04
3.7100000e+02	5.8765091e+02	1.7205072e-01	1.7985032e+02	9.3152196e+01	5.7311187e+00	3.7156018e-02	1.3669739e+03	6.3699071e+02	-1.4146754e-01	1.4390488e-01	-2.6358121e-02	5.7483112e+03	6.0387562e+02	4.4097944e+04
3.8100000e+02	5.8754993e+02	1.7200170e-01	1.7983907e+02	9.3250909e+01	5.7158471e+00	3.7106310e-02	1.3654827e+03	6.3689650e+02	-1.4145278e-01					

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1.4381267e-01  -2.6357987e-02   5.7476725e+03   6.0369421e+02   4.4097082e+04
   3.9100000e+02   5.8770874e+02   1.7207782e-01   1.7985055e+02   9.3141579e+01   5.7234630e+00   3.7164996e-02   1.3652300e+03   6.3620334e+02  -1.4146691e-01
1.4373682e-01  -2.6357809e-02   5.7474136e+03   6.0395239e+02   4.4090338e+04
   4.0100000e+02   5.8751664e+02   1.7201604e-01   1.7984180e+02   9.3284609e+01   5.7111218e+00   3.7101953e-02   1.3643629e+03   6.3599352e+02  -1.4145570e-01
1.4365431e-01  -2.6357652e-02   5.7470145e+03   6.0371938e+02   4.4088341e+04
   4.1100000e+02   5.8770529e+02   1.7208188e-01   1.7985290e+02   9.3169521e+01   5.7157540e+00   3.7156605e-02   1.3638791e+03   6.3560147e+02  -1.4146430e-01
1.4360343e-01  -2.6357557e-02   5.7467387e+03   6.0395110e+02   4.4084535e+04
   4.2100000e+02   5.8754147e+02   1.7203963e-01   1.7984816e+02   9.3284471e+01   5.7086767e+00   3.7111071e-02   1.3634642e+03   6.3530911e+02  -1.4145914e-01
1.4353554e-01  -2.6357405e-02   5.7464966e+03   6.0378670e+02   4.4081667e+04
   4.3100000e+02   5.8767232e+02   1.7207782e-01   1.7985343e+02   9.3211940e+01   5.7093580e+00   3.7143168e-02   1.3628878e+03   6.3511921e+02  -1.4146187e-01
1.4349759e-01  -2.6357349e-02   5.7462202e+03   6.0392298e+02   4.4079820e+04
   4.4100000e+02   5.8758143e+02   1.7206257e-01   1.7985161e+02   9.3271584e+01   5.7068478e+00   3.7122890e-02   1.3627111e+03   6.3481046e+02  -1.4146172e-01
1.4344612e-01  -2.6357225e-02   5.7460688e+03   6.0385672e+02   4.4076787e+04
   4.5100000e+02   5.8763300e+02   1.7207377e-01   1.7985231e+02   9.3249303e+01   5.7047104e+00   3.7131180e-02   1.3621803e+03   6.3471613e+02  -1.4146055e-01
1.4341447e-01  -2.6357181e-02   5.7458324e+03   6.0389613e+02   4.4075890e+04
   4.6100000e+02   5.8761265e+02   1.7207861e-01   1.7985358e+02   9.3261191e+01   5.7048793e+00   3.7130709e-02   1.3620774e+03   6.3444938e+02  -1.4146295e-01
1.4337783e-01  -2.6357091e-02   5.7457274e+03   6.0390529e+02   4.4073285e+04
   4.7100000e+02   5.8760652e+02   1.7207326e-01   1.7985262e+02   9.3274244e+01   5.7017109e+00   3.7124016e-02   1.3616722e+03   6.3438087e+02  -1.4146032e-01
1.4335007e-01  -2.6357048e-02   5.7455487e+03   6.0388427e+02   4.4072635e+04
   4.8100000e+02   5.8762957e+02   1.7208727e-01   1.7985530e+02   9.3259737e+01   5.7027587e+00   3.7133582e-02   1.3615595e+03   6.3418599e+02  -1.4146312e-01
1.4332480e-01  -2.6356989e-02   5.7454587e+03   6.0392988e+02   4.4070731e+04
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