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The research presented in this dissertation is guided by the question of how to improve the General Equilibrium Ecological Model (GEEM) as a realistic population model, and how to incorporate GEEM in a dynamic resource management model.

The first part of this dissertation (Chapter 2) extends GEEM from an 8 to a 13-species marine system with multiple predator-prey relations, and provides simulations of the ecosystem dynamics under various influences, especially human activities. Functional and numerical responses in GEEM as a population model are also derived and discussed.

The second part of the dissertation (Chapter 3 and 4) addresses the application of GEEM in economic models, including deriving a reduced form of GEEM (R-GEEM) so that the variables from GEEM can be easily integrated with the economic model, and applying R-GEEM to dynamic optimization problems with multiple species harvesting and endangered species protection plans.

**GENERAL EQUILIBRIUM ECOLOGICAL MODEL IN PRACTICAL USE**  
-- --AN ALTERNATIVE POPULATION DYNAMICS MODEL FOR INTERACTING  
SPECIES AND ITS APPLICATIONS IN RESOURCE ECONOMICS

by

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To my parents: Huazhi Gong (龚华志) and Shuangyuan Li (李双元). Your love  
and support made this possible.

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## Chapter 1

### INTRODUCTION

In the past two decades, human and nature interaction has been an increasingly important topic in both ecology and economics. Ecologists are usually concerned about the health of the ecosystem with human intervention (a scientific problem) while economists focus more on economic goals subject to the human-nature interrelationship (a social problem). Not surprisingly, there are a number of articles in the literature that aim to shed light on this interdisciplinary research (Costanza, 2004).

An example of this joint effort of ecologists and economists is renewable resource management in which economists attempt to optimally exploit the resource given the resource renewal constraints and ecologists build population models incorporating the interactions between human and the ecosystem (de la Mare, 1996; Estes et al, 1998). While significant progress has been made in developing integrated ecological models, there is a gap between ecologists and economics on the issue of how much ecological information should be taken into an economic model. The most noticeable and perhaps most harmful difference is the way ecologists and economists treat the resource renewal mechanism.

For centuries ecologists have been trying to understand the complicated relationships in ecosystems and predict population dynamics. Whenever an ecologist mentions a particular species, she thinks about not only the population of that species but also the characteristics of its prey, predators, living environment, and maybe parasites or symbiosis. Surprisingly it is a different story for most resource economists. In trying to find a balance between economic development and resource protection, economists search for detailed economic data, build various economic

models, take advantage of advanced computational technology, and simulate the evaluated economies as accurately as possible. But not many economists go through the same procedure when it comes to the evaluation of the ecosystem reactions. Most of us are quite comfortable with the one-species logistic function, assuming that function also accounts for the unknown interrelationships within an ecosystem and the interaction between the ecosystem and human activities.

Though the single species logistic growth function is simple and convenient, it is questionable as an efficient and reliable model for species' dynamics. One obvious shortcoming of the logistic growth function is that it does not consider the interactions among species that comprise ecosystems. Besides, the logistic growth function cannot incorporate either resource competition or substitutions of prey, both of which are important for the dynamics of any ecosystem.

Single-species management also creates problems for economic solutions. For example, in a single-fish dynamic management problem, economic optimality eradicates the stock whenever the maximum per capita growth rate is less than the discount rate and the price for the last fish is greater than the cost for harvesting it (MRAG Americas 2000).

Because resource exploitations usually operate within a complex array of species interactions, scientists increasingly recommend multi-species approaches to resource management. Basically, current multi-species resource management research focuses on two aspects. One is to capture the interactions between the ecosystems and the economies related to or contained in them (Lynne et al, 1981; Ellis and Fisher, 1986; Crocker and Tschirhart, 1993; Barbier and Strand, 1998; Barbier, 2003). For example, Settle and Shogren (2002) apply an economic system-ecosystem model to a

specific problem and compare the integrated model with the model in which two systems are separate.

The other strand of research, the direction I am following in this dissertation, is to address the interrelationships within an ecosystem and incorporate this information in economic models (Clark, 1990; Milton and Shogren, 1995; Tschirhart, 2000). A recent example is the GEEM (General Equilibrium Ecosystem Model) approach Finnoff and Tschirhart (2003) proposed. They employ this new integrated ecological/economic model to track both ecological relations and human influence on the ecosystem. Although they did not discuss the application of GEEM in multispecies management, GEEM offers a stock assessment method set in a food web context and provides an important step toward developing a method that recognizes resource exploitation as a component of ecosystem dynamics. In my dissertation, I will use GEEM as the basic ecological model. For those readers who are not familiar with the GEEM, an introduction to this model is provided in Chapter 2.

While GEEM contributes to both population ecology and resource economics as an innovative biomass-based ecosystem model and a new resource management model, the success of integrating the GEEM with an economic model in application is not so obvious. There are at least two questions to be answered: how to improve the accuracy of the predictions of the ecosystem model in isolation and how well variables from one model can be effectively incorporated in the other.

## **1.1 The Research Proposed**

The research presented in this dissertation is guided by the question of how to improve the GEEM as a realistic population model, and how to incorporate GEEM in a dynamic resource management model. The first part of this dissertation is concerned

with extending GEEM to multiple predators and prey and applying the extended model to a 13-species marine system. The second part of the dissertation addresses the application of GEEM in economic models, including deriving a reduced form of GEEM so that the variables from GEEM can be easily integrated with the economic model.

My research contributes to the existing ecological economics literature in four ways. First, I extend the GEEM to include multiple predator-prey relationships. In the ecosystem I inspect there are 13 species, several of which have multiple predators or multiple prey. Second, I use time series techniques to reduce the nonlinear GEEM to a linear population dynamics model, which is consistent with the general model for interacting species proposed by previous research (Williams et al, 2002). Third, I introduce multiple-species harvestings into the traditional fishery model by using harvestings as control variables and including the interactions in the ecosystem as constraints. Fourth, I also include endangered species protection plans as constraints in the dynamic optimization model, which provides a new way to optimize the social welfare that includes both fishery benefits and ecological values of species.

## **1.2 The Dissertation Structure**

The structure of my dissertation is as following:

**Chapter 1** provides the introduction and the literature review that gives an overview of previous research-- the facts, the arguments, the positions taken, and proposes the research objects that are completed in this dissertation.

**Chapter 2** extends GEEM to a 13-species marine system with several multiple predator-prey relations, and provides simulations of the ecosystem dynamics under various influences, especially human activities. The simulation results in chapter 2 will be used in subsequent chapters. Functional and numerical responses in GEEM as a population model are also derived and discussed in this chapter. Appendices 1-9 report the parameter calibration table and GEEM simulations under various conditions.

**Chapter 3** focuses on using vector autoregression (VAR) to derive a linear dynamic population model for interactive species, the reduced form of GEEM, or R-GEEM in this paper. The stability of the R-GEEM is discussed and the resemblance of GEEM and R-GEEM are tested using three methods: mathematical, graphic, and statistical. Appendices 10-15 describe the R-GEEM structure, simulations, and the tests for the similarity.

**Chapter 4** applies R-GEEM to the dynamic optimization problem with multiple species harvesting and endangered species protection plans. This chapter provides application examples of the GEEM in resource management and jointly with chapter 3 completes the answer to the second question raised in chapter 1 on the integrating of GEEM with an economics model in application: how does one effectively incorporate variables in one model into the other? Appendices 16-21 present more details developed in this chapter.

**Chapter 5** summarizes the main contributions made by this dissertation and concludes the thesis by suggesting some directions for further research.

## Chapter 2

### THE GENERAL EQUILIBRIUM ECOLOGICAL MODEL WITH MULTIPLE PREDATORS AND PREY

This chapter attempts to answer one of two issues raised in Chapter 1 on the success of integrating the GEEM (Finnoff and Tschirhart, 2003) with an economic model in application: the accuracy of GEEM prediction. To improve GEEM as an ecosystem population model, I extend the GEEM to include multiple predators and prey, apply the extended GEEM to a 13-species marine system in the Eastern Bering Sea (EBS), explore 22 predator and prey dynamics, and simulate the ecosystem under various perturbations.

The layout of this chapter is as follows: section 2.1 is the introduction explaining why I focus on multiple interactions and why I choose the EBS ecosystem. Section 2.2 presents the ecological characteristics and interrelationships of 13 species in the food-web and is followed by section 2.3 which shows the underlying mechanism of GEEM in detail as well as introduce multiple predators and prey into the model. The data collection and the parameter calibration are illustrated in section 2.4. The GEEM simulations under various conditions, the stability of ecosystem, the functional responses and numerical responses of predators are discussed in section 2.5. The last section, section 2.6, concludes this chapter and proposes several extensions for future research.

#### 2.1 Introduction

As a new population model built by economists using traditional economics tools, not surprisingly GEEM leaves much space for extensions. Possible extensions

include, but are not limited to, more realistic food-webs to incorporate multiple predator and prey, individual-based models to handle individual differences within one species, improved data collection for better parameter calibration, etc. Among all those possible improvements, I choose to deal with the issue of multiple predators and prey first because multiple prey traits and multiple predators are “keys to understanding complex community dynamics” (Dewitt and Langerhans, 2003.) “Multiple interactions” is also a key phrase for my effort to improve GEEM and incorporate it in economic problems in this dissertation.

In Chapter 2, GEEM is extended to include multiple predators and prey and applied to a 13-species marine ecosystem in the Eastern Bering Sea area (Figure 1). There are several reasons why I choose this particular ecosystem. First, although there are only 13 species in the model, this interlocking network includes four trophic levels. Phytoplankton and kelp, which perform the necessary process of photosynthesis, occupy the first trophic level, plants. Herbivores such as zooplankton and sea urchins are at the second level. Fish and most marine mammals are carnivores which belong to the third. The highest trophic level is the top carnivore, the killer whale. As a result of the feeding interactions between species on these four levels, clear paths of energy flow can be explored and a variety of interactions, beneficial or detrimental, on the same trophic level or different levels, are available for GEEM analysis.

Second, the ecosystem contains several multiple predator-prey interactions. For example, both pollock and herring are prey to northern fur seal that in turn is one of seven prey species to the top predator, killer whale. Notice that in order to track the interactions among species in the ecosystem, I hold all other relevant conditions constant, such as weather, ocean currents, and any other species that are connected to one or more of the 13 species in the real marine system but not in the food-web in

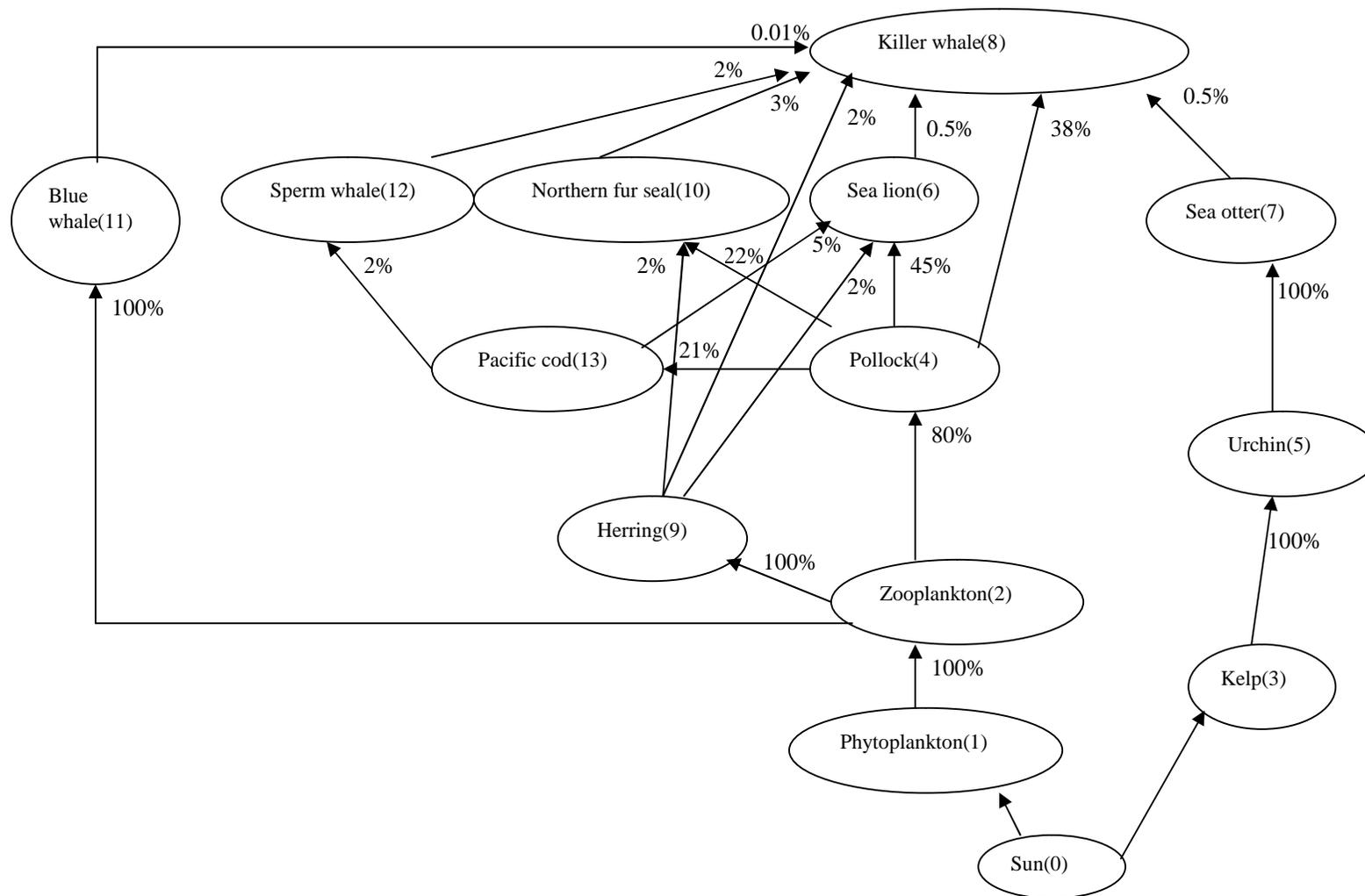
Figure 1. For instance, in the Gulf of Alaska, Pacific cod's major diets include capelin, pollock (21%), pandalids, miscellaneous fish, euphausiids, and crabs (Yang, 2004). Since only pollock are in the food-web, I consider only the biomass flow from pollock, which is  $160 \text{ kg unit}^{-1} \text{ y}^{-1}$ . The number on the energy arrow indicates the percentage of the prey in the diet composition of the predator. For more information, please refer to the calibration table in Appendix 3.

A third reason why I choose this area is because of its interactions with the human society. For instance, the Eastern Bering Sea supports the world's largest pollock fishery (Alaska Marine Information System, 2004). This ecosystem also contains endangered and keystone species, whose population declines have concerned both ecologists and tourism departments in recent years. I will model the interactions between the ecosystem and the economy both from the economist's and the ecologist's perspective.

Another reason for my choice is that researchers have been working on the ecosystem in this area for quite a long time, which means that there are better data available for parameter calibrations and simulation comparison. The last reason is that this model extends the 8-species marine ecosystem developed earlier by Finnoff and Tschirhart (2003). It will be interesting to see how the introduction of more species and multiple predators and prey affects the ecosystem stability and the converging path.

## **2.2 The Food-Web Representation**

Figure 1 represents the ecosystem I am going to simulate using GEEM. In ecological terms, it is an interactive system since the consuming population influences



**Figure 1:** The food web represented in my general equilibrium ecosystem model.

the rate of resource production and consumers interfere with each other's search for food.

In the ecosystem there are thirteen species, both from the Eastern Bering Sea (EBS) and the Alaska's Aleutian Islands (AI). Basically the ecosystem is an extension of the food-web in Finnoff and Tschirhart (2003), in which single predator-prey relationships among eight species (species 1- 8) are discussed and only one species (killer whale) has more than one prey species. To better represent the real Alaska marine system, I add five more species (species 9- 13) as well as multiple predators and prey interactions such that several species are preyed upon by several others, which may have several prey species. The selection of additional species and the design of the energy flow are based on previous ecology or zoology literature, such as Lowry et al. (1982), Perez and McAlister (1993), and Williams et al. (2004).

Note that some species in the food web actually are aggregates of various species. For example, various microscopic plants that live in the EBS and compete for light are aggregated into a single species called phytoplankton. They are the foundation of the marine food chain. Phytoplankton requires sunlight, water, and nutrients for growth. Because sunlight is most abundant at and near the sea surface, phytoplankton remains at or near the surface. As shown in the food web, zooplankton, which is another aggregate species, preys on phytoplankton. Larger fish then prey on zooplankton. Humans catch and consume some of these larger fish, which provides a link between the ecosystem and the economy. For example, in 2004 the inshore pollock catch in the Bering Sea was 637,970 metric tons (NOAA Catch Report, 2004) while the total U.S. domestic landing is 1,526,348 tons (NMFS Fishery Statistics Division, 2004).

In the Aleutian Islands (the right side of the food-web), the foundation of the food chain is the kelp forest that is an aggregate of various species of brown and red algae. A dependence upon light for photosynthesis restricts the kelp forest to clear shallow water and it is rarely much deeper than 40 m. Kelp is preyed on by the sea urchin that in turn is preyed on by the sea otter.

In the food-web there are also marine mammals that prey on larger fish. Marine mammals are thought to be important to the tourism industry, such as offering whale watching on a cruise ship and ecotourism to the region. Tourism or other entertainment industries provide alternative ways to link the ecosystem and the economy other than through commercial fishing. A third link between the ecosystem and the economy is that some marine mammals are endangered and subject to recovery plans. For example, the number of Steller sea lions in the western stock declined by 75% between 1976 and 1990 (National Marine Mammal Laboratory, 2005). In the 1990s, the decline continued for the western stock in Alaska, which was declared endangered by the National Marine Fisheries Service under the Endangered Species Act.

The top predator in the ecosystem is the killer whale, which preys on large fish, whales, and small marine mammals. As we will see later in the paper, GEEM predicts that the killer whale illustrates a very interesting predation pattern by switching prey when the populations of its prey change, which is consistent with what researchers have observed (Hatfield et al, 1998; Springer et al., 2003). For instance, Springer et al. (2003) suggests that overexploitation of large whales forced killer whales to prey switch from baleen whales to pinnipeds and sea otters, resulting in population declines for these smaller marine mammals. Later in this chapter I shall discuss how the GEEM predicts the killer whale's prey switching pattern when large fish, which are

preyed upon by the killer whale as well as by marine mammals, are harvested constantly by humans.

### 2.3 The General Equilibrium Ecological Model (GEEM)

Devised by Finnoff and Tschirhart (2003) and applied to an Alaskan marine ecosystem, the general equilibrium ecosystem model (GEEM) is a mass-balanced population model based on energy flows between species and individual plant and animal optimization. In this section, I extend GEEM to include multiple predators and prey and apply it to the 13-species ecosystem represented in Figure 1.

#### 2.3.1 The Net Energy Objective Functions

Following Finnoff and Tschirhart (2003), in a GEEM model, we assume that individual plants and animals are maximizing their net energy. A member of species  $i$  that preys on organisms in species  $j$  and is preyed on by members of species  $k$  chooses  $x_{i,j}$  to maximize

$$R_i = \sum_j [e_j - e_{i,j}]x_{i,j} - \sum_k e_i[1 + t_i e_{k,i}]y_{i,k} - f^i(x_{i,j_1}, x_{i,j_2}, \dots) - \beta_i \quad (1)$$

where  $R_i$  is in power units (Watts or kilocalories/time);  $e_j$  is the energy embodied in a unit of biomass (in kilocalories/kilogram) from a member of species  $j$ ;  $e_{i,j}$  is the energy price;  $x_{i,j}$  is the biomass (in kilograms/time) transferred from the member of species  $j$  to the member of species  $i$ ;  $t_i$  is a tax on the individual because it loses energy above what it loses owing to being captured;  $e_{k,i}$  is the energy the predator  $k$  use in capture attempts;  $y_{i,k}$  the biomass supplied by  $i$  to  $k$ , is a function of the summation of all  $x_{i,j}$ ;  $f^i$  is the variable respiration function in terms of all  $x_{i,j}$ ;  $\beta_i$  is the basal metabolism.

The first term on the RHS of (1) is the inflow of energy from prey species to the representative individual of species  $i$ ; the second term is the outflow of energy to animals of species  $k$  that prey on  $i$ , while the term in the brackets is the energy the individual uses in attempts to avoid being preyed upon; the third term is the part of respiration which depends on energy intake; the fourth term is basal metabolism which is independent of energy intake. The metabolism terms follow Gurney and Nisbet (1998).

For the biomass supply by species  $i$  to species  $j$ ,  $y_{i,k}$ , I assume that

$$y_{i,k} = d_{i,k} \left( \sum_j x_{i,j} \right)^5 \quad (2)$$

where  $d_{i,k}$  is the predator parameter that will be calibrated; the function form follows Tschirhart (2000).

The variable metabolism function  $f^i(x_{i,j_1}, x_{i,j_2}, \dots)$  takes the quadratic form (Tschirhart, 2000). Mathematically,

$$f^i(x_{i,j_1}, x_{i,j_2}, \dots) = .5r_i (x_{i,j_1}^2 + x_{i,j_2}^2 + \dots + x_{i,j_1}x_{i,j_2} + \dots) \quad (3)$$

where  $r_i$  is the metabolism parameter that will be calibrated later. A complete list of the net energy equations for all 13 species is showed in Appendix 1.

To better understand the above equations which are core equations in GEEM, I will explain the net energy objective function for pollock in detail. As seen in Figure 1, pollock prey on zooplankton and are preyed on by sea lion, Pacific cod, and Northern fur seal. So the net energy objective function for pollock is

$$R_4 = (e_2 - e_{4,2})x_{4,2} - r_4 x_{4,2}^2 - d_{4,6}e_4(1 + t_4 e_{6,4})x_{4,2}^5 - d_{4,10}e_4(1 + t_4 e_{10,4})x_{4,2}^5 - d_{4,13}e_4(1 + t_4 e_{13,4})x_{4,2}^5 - d_{4,8}e_4(1 + t_4 e_{8,4})x_{4,2}^5 - b_4 \quad (4)$$

The first term on the right side of the above equation is the inflow of energy from zooplankton to pollock; the second, third, and fourth terms are the outflow of

energy to sea lion, Northern fur seal and Pacific cod, respectively. The fifth term is the part of respiration which depends on how much the pollock prey on zooplankton, and the last term is the basal metabolism.

### 2.3.2 Short-Run Equilibrium

In a short-run equilibrium, each individual in the ecosystem chooses optimal intake energy to maximize its net energy. In mathematical terms, each individual choose  $x_{i,j}$  to maximize its respective net energy objective functions (see Appendix 1). Each function is associated with one or more first-order conditions, depending on how many different prey the species feeds on. In this ecosystem, there are 22 predator-prey pairs in the food-web, which yields 22 first-order conditions. In the short run, the value of  $R_i$  can be positive, zero, or negative, which as shown later, will correspond to increasing, constant, and decreasing populations respectively.

Besides all first-order conditions, there are another set of equations to be met during a short-run equilibrium. Similar to an economy, there should be no excess demand or supply of any species biomass or energy. The supply-demand equilibrium condition of each pair of predator and prey is constructed by equating the sum of all the predator demands with the sum of all the prey supplies. Thus, the equilibrium equation for animals can be written as:

$$N_k x_{k,i} = N_i y_{i,k} = N_i d_{i,k} \left( \sum_j x_{i,j} \right)^5 \quad (5)$$

where  $N_k$  is the predator's population and  $N_i$  is the prey's population.

For example, the equilibrium condition between sea lion and its predator, killer whale, can be written as:

$$N_8 x_{8,6} = N_6 d_{6,8} (x_{6,4} + x_{6,9} + x_{6,13})^5 \quad (6)$$

The left side of (6) is the total killer whale demand for sea lion, and the right side is the total supply of sea lion to killer whale, which depends on how much sea lion feeds on its prey, including pollock, Pacific herring, and Pacific cod.

For plants in the ecosystem, namely kelp and phytoplankton, the equation is similar to equation (5) except that the supply depends on the physical space the plants occupy (Tschirhart, 2002). A complete list of the supply-demand equations is reported in Appendix 2. Simultaneously solving the above 22 first-order conditions and 22 supply-demand equations, we get a set of 22 energy prices and 22 biomass demands for the short-run equilibrium.

### 2.3.3 Population Updating and Long-Run Equilibrium

Unlike the short-run equilibrium in which positive, zero, or negative net energy is possible, a long-run equilibrium or a steady state implies that the populations adjust annually until all species have zero net energy and constant populations. Following Finnoff and Tschirhart (2003), the population updating equation for species  $i$  is

$$N_i^{t+1} = N_i^t + N_i^t \left[ p + \frac{(1-p)^{s_i}}{s_i} \right] \left[ \frac{R_i(\bar{N}^t) + V_i}{\hat{V}_i} - 1 \right] \quad (7)$$

where  $p = \frac{d_{i,j} x_{i,k}^5}{w_i}$  is the predation rate and equals to zero for the top predator, killer whale;  $\bar{N}^t$  is a vector of the populations of all 13 species in period  $t$ ;  $s_i$  is the lifespan of a representative species;  $\hat{V}_i$  is the steady-state variable respiration;  $V_i$  is the non-steady-state variable respiration.

An example of the updating equation is that for the top predator, the killer whale:

$$N_8^{t+1} = N_8^t + N_8^t \left[ \frac{1}{s_8} \left[ \frac{R_8(\bar{N}^t) + V_8}{\hat{V}_8} - 1 \right] \right] \quad (8)$$

For more details and the derivation of the equations, please refer to Finnoff and Tschirhart (2003). A complete list of updating equations for all species is available upon request.

## 2.4 Data Collection and Parameters Calibration

A common procedure to select parameter values in a general equilibrium model is “calibration” (Mansur and Whalley, 1984). Typically, researchers use only one year’s data or an average observation for the calibration (Shoven and Whalley, 1992). In this paper, most benchmark data are from the year of 1980 with a few exceptions. For details, please refer to the notes attached to the calibration table in Appendix 3.

In the calibration, I assume that the year-of-record benchmark system is in a steady state (Finnoff and Tschirhart, 2002), which means that populations are constant, which in turn implies that the net energies are zero. Simultaneously solving 13 zero net energy equations, 22 first-order conditions, and 22 supply-demand equations, yields the values of 57 parameters in the system. Calibrated parameter values are reported in the calibration table in Appendix 3. All equations can be found in the GAMS codes, which are available upon request.

## 2.5 Simulated Ecosystem Dynamics

Once we calibrate the parameter values as in Section 4, we can use the GEEM to simulate the dynamics of the ecosystem. As discussed in Section 3, in each period, we solve 22 first-order conditions and 22 supply-demand equilibrium conditions simultaneously for 22 energy prices and 22 biomass demands. Then we substitute the optimum prices and demands into the net energy objective function (1) to obtain the

optimum net energy which is used in the updating equation (7) as the net energy in current period to yield the beginning population in the next period. The long-term ecosystem dynamics obtained as the above procedure is repeated over time.

In this section, I use GEEM simulations to address the following three issues: 1) the stability analysis and the converging path discussion of GEEM under assorted shocks; 2) functional and numerical components of predations in GEEM in response to the prey density change; 3) how the ecosystem responds to human activities (fishery), including the new steady state of the system and the prey switching behaviors of the sea lion and the killer whale.

### **2.5.1 The Stability Analysis and the Converging Paths**

To determine whether or not a given community is stable, the researcher needs to know all the intrinsic rates of population increase, all the species interaction terms, and the equations that describe the interactions. Usually, because we do not have this information, we cannot determine whether or not the system is stable. Nevertheless, the simulation graphs from GEEM when the ecosystem is affected by various exogenous perturbations shed light on the community stability<sup>1</sup> as well as the converging paths. By perturbations, I mean any element within or outside of the system that changes the population of one or more species and causes the ecosystem to deviate from the steady state. Possible perturbations include, but are not limited to, weather changes, ocean currents, seasonal oscillations, species behavior adjustments, human interventions, etc.

#### **2.5.1.1 GEEM Simulation under Random Shocks**

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<sup>1</sup> A mathematical stability analysis is presented in 3.4.2 after the reduced form of the GEEM (R-GEEM) is derived.

To simulate the ecosystem within a more realistic framework and test the stability, I add shocks to the system at a random frequency, then observe how the system responds to the shocks, including whether the system returns to the steady state and its converging paths from shocks of various scales. Figure 2 illustrates the GEEM dynamics under relatively small shocks with the standard deviation equal to 0.03.

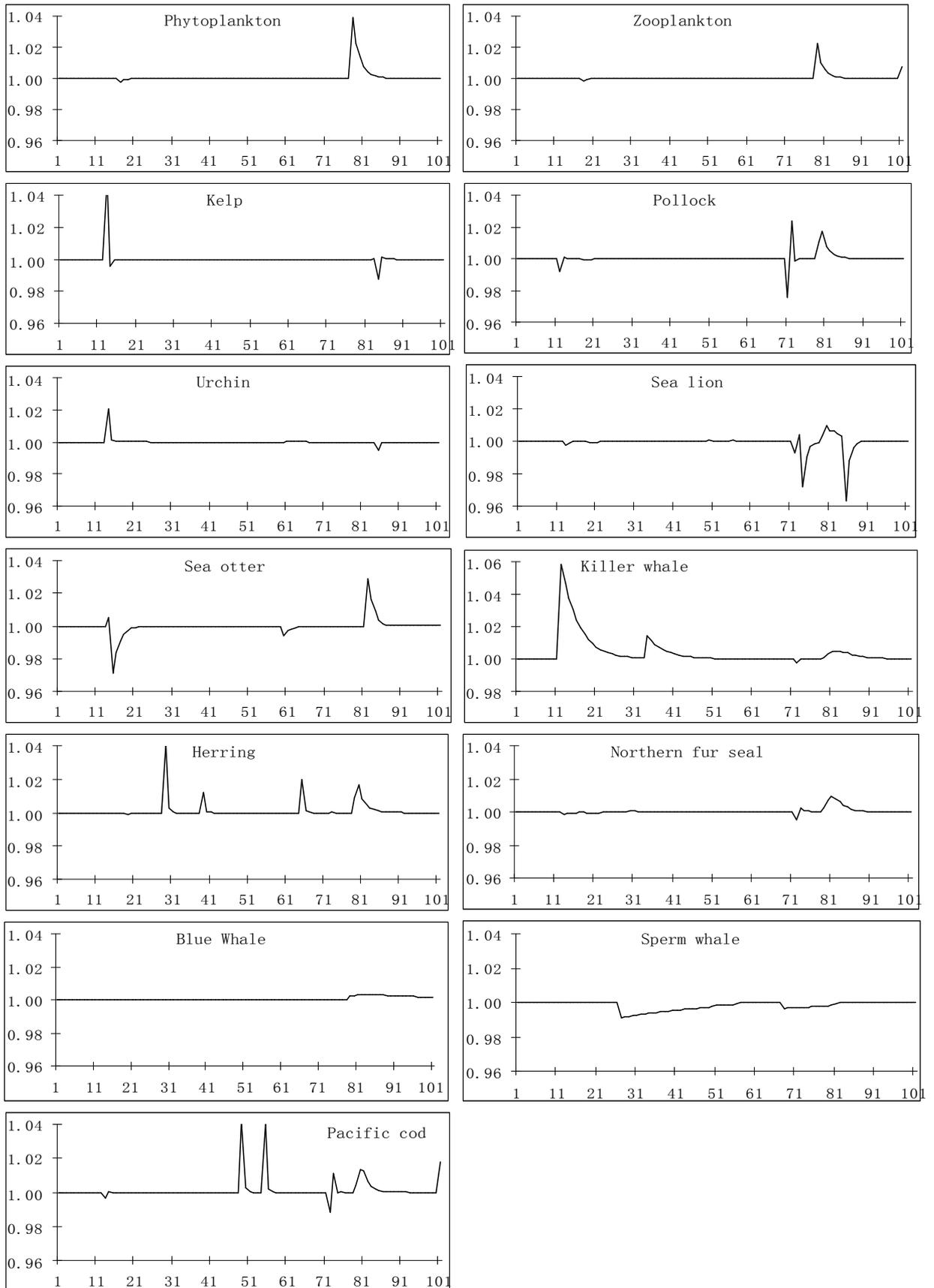
In Figure 2, as well as in most graphs in this paper, the horizontal axis is the time period (year) and the vertical axis indicates the population values in each period. The units used in the graph are not the same units used in Table 1. Instead, they are the percentages relative to their respective steady state values. For example, the steady state population of pollock is 6.16215. In time period  $t$ , the calculated pollock population from GEEM is 6.34. Then I divide 6.34 by 6.16215 and get 1.03, which is the population of pollock at time  $t$  in the graph in terms of percentage of the steady state value. The steady state values themselves are, of course, equal to one.

The dynamics in Figure 2 are simulated as follows: in each period, the computer randomly chooses one number for each species. The chosen numbers are uniformly distributed between 0 and 1. If a species' number in time period  $t$  is greater than 0.978, this species receives a percentage shock to its population. So in each period, the probability that at least one of 13 species is hit by a shock is about 0.25.<sup>2</sup> Shocks are normally distributed with a mean of 0 and a standard deviation of 0.03. Shocks are independent between species as well as periods. If a species is hit by a shock, its population is adjusted accordingly.

For instance, in time period  $t$ , a computer generates 13 numbers for 13 species. Only the number for the pollock is greater than 0.978. Then the computer generates

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<sup>2</sup> The probability of no shock added in a period is  $0.978^{13}$ . So the probability that at least one shock is added is  $1 - 0.978^{13} = 0.25$ .



**Figure 2: GEEM Simulations under Random Shocks**

another random number, -0.05, for the pollock, whose population is 1.02. Hit by the shock, the pollock population becomes  $1.02*(1-0.05) = 0.969$ . By substituting all populations including the pollock's adjusted population into GEEM as the new starting populations, solving for the optimal net energies which are then input to the updating equations, we get the populations in the next period. Repeating the same procedure in every period, we have the dynamics of the ecosystem under small shocks along the time path.

Formally

$$N_i^t = \begin{cases} \Omega(\bar{N}^{t-1}) & \text{if } V_i^t \leq 0.978 \\ \Omega(\bar{N}^{t-1})(1 + \varepsilon_i^t) & \text{if } V_i^t > 0.978 \end{cases} \quad (9)$$

where  $\bar{N}^{t-1}$  is the steady state population vector of species;  $\Omega$  is the population updating function through GEEM;  $\varepsilon_i^t \sim i.i.dN(0, 0.03)$ ;  $V_i^t \sim U(0,1)$ ;  $i = 1, 2, \dots, 13$ .

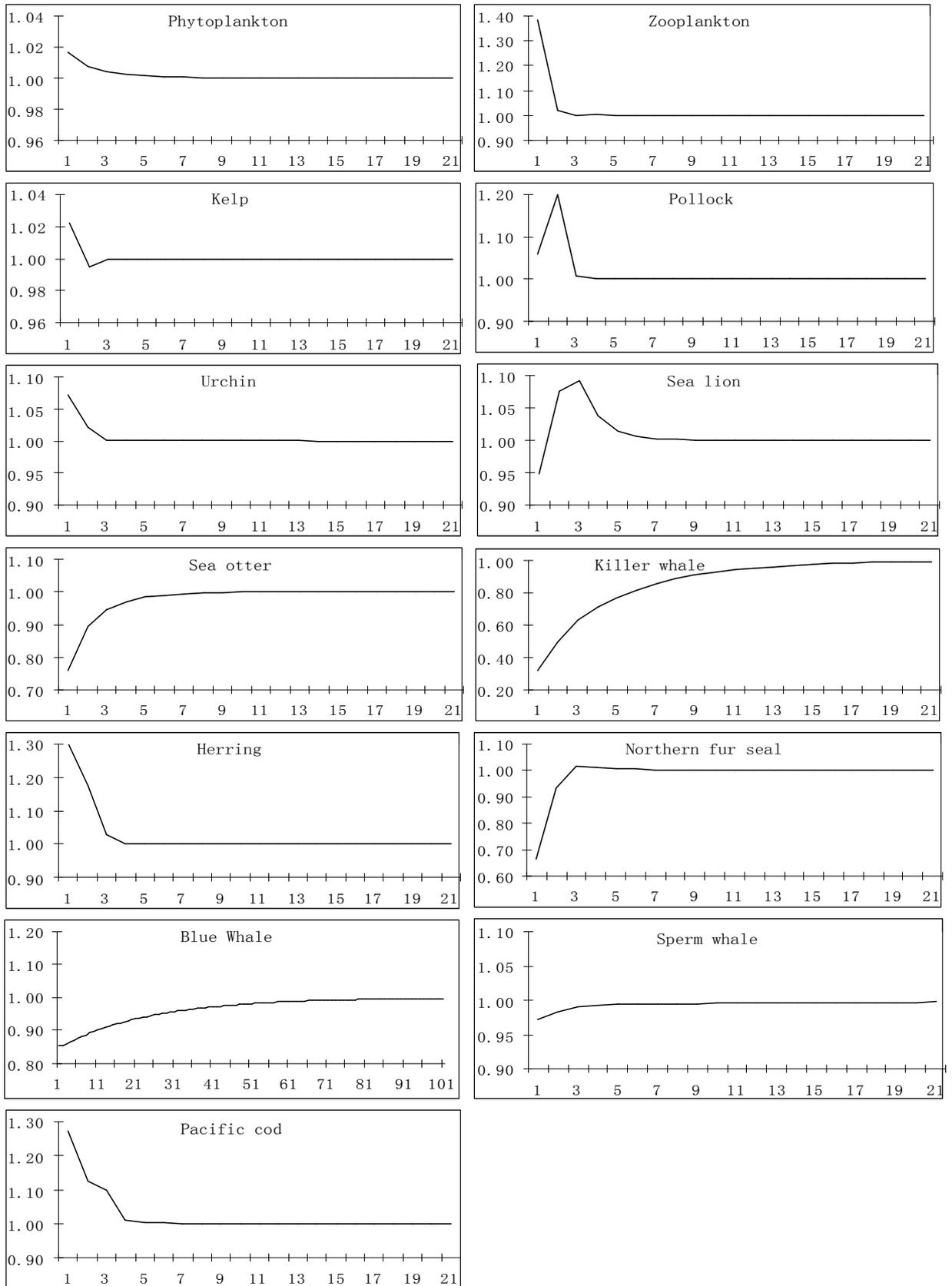
Figure 2 shows the stability of the GEEM system. If the shocks are within a certain reasonable range, all species in the system recover to the steady state no matter how the species was hit (directly or indirectly<sup>3</sup>) and how frequently the shocks hit. In that sense, the system is stable. Notice also that the converging paths of species demonstrate different patterns, which I will explain more in 2.5.1.2.

### 2.5.1.2 A Close Look at the Converging Path

Figure 3 illustrates how the ecosystem converges to the steady state starting from a random set of conditions. Figure 3 is different from Figure 2 in that 1) instead of shocks being added along the path, the ecosystem is allowed to converge to the steady state after the one-time shock so that there is no random noise along the

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<sup>3</sup> The indirect shock means shocks added to other species in the ecosystem, which will affect the species in discussion through species interactions.



**Figure 3:** Converging Path of GEEM from a Random Point

converging path; 2) the shocks are normally distributed with a standard deviation of 0.30 in stead of 0.03, which enables larger shocks to be added to the system.

The starting point is generated by letting the computer add a random percentage shock to the steady state population of each species. The shock is normally distributed with a mean of zero and a standard deviation of 0.30. Formally, the dynamics can be written as

$$N_i^t = \begin{cases} N_i^{ss}(1 + \varepsilon_i), & t = 1 \\ \Omega(\bar{N}^{t-1}), & t > 1 \end{cases} \quad (10)$$

where  $N_i^{ss}$  is the steady state population of species I;  $\Omega$  is the population updating function through GEEM;  $\varepsilon_i \sim i.i.dN(0, 0.3); i = 1, 2, \dots, 13$ .

As seen in Figure 3, although all species return to the steady state values eventually, the converging paths are quite diversified. Most species follow a smooth path to return to one, but some species overshoot (sea lion) or undershoot (kelp) the steady state value before finally converging to it. There is also disparity in the converging speeds of single species. Usually the farther the starting point is away from one, the longer it takes that species to return to one. But some species, such as zooplankton and northern fur seal, rebound to their steady state populations very quickly from relatively large shocks (39% and negative 34% respectively), while it takes much longer for others to return to the steady state. For example, the blue whale has to adjust to the effects of the negative 15% shock constantly for more than 90 periods before it hits the steady state. The speed of convergence is related to the lifespan parameter in the updating equation, since the lifespan parameter functions similarly to the internal growth rate in the logistic population function.

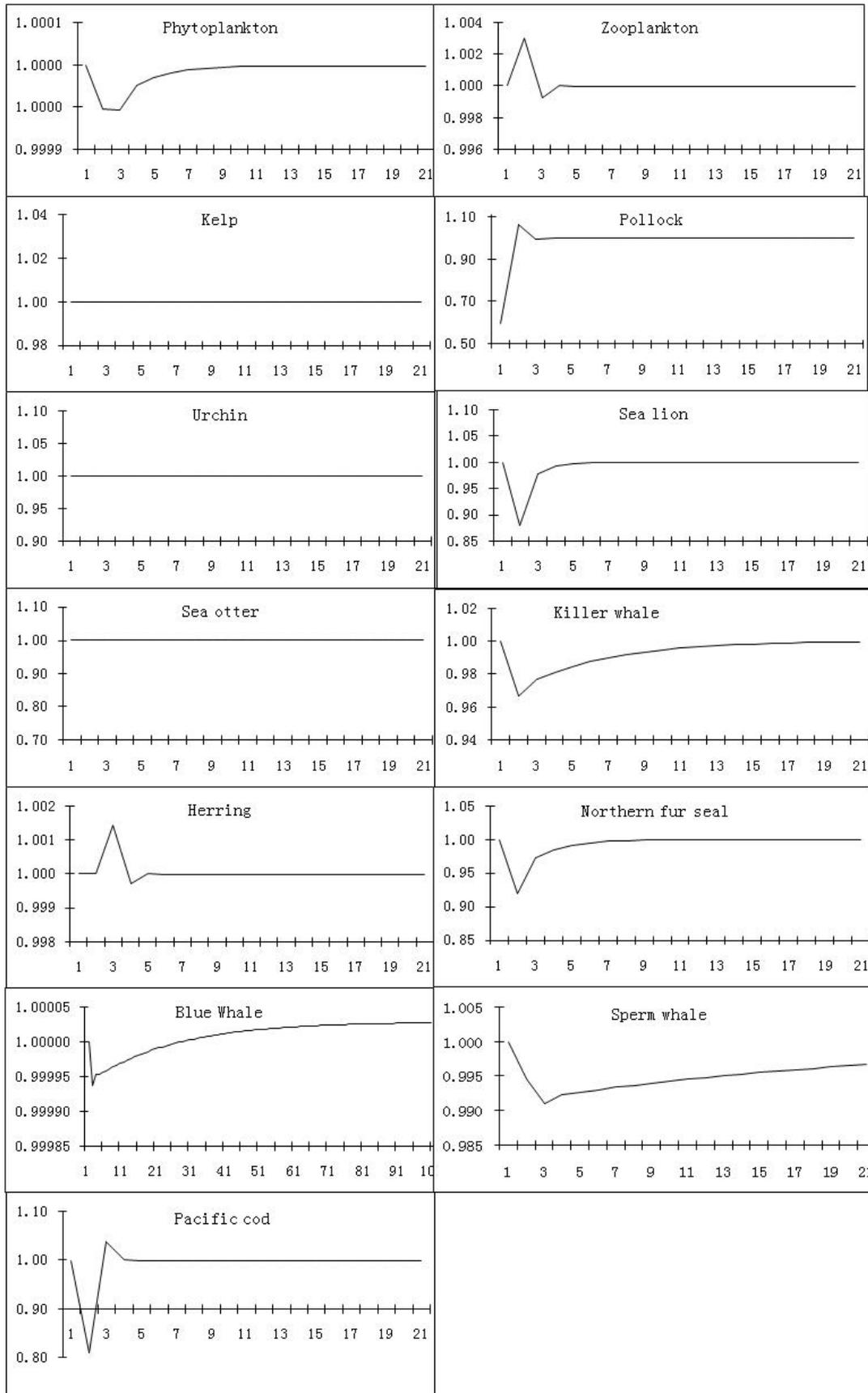
While the converging path information in Figure 3 can be used in making species protection plans and recovery programs, one must be careful about

generalizing the observed converging characteristics because the converging path and the starting state have a one-to-one correspondence. If the system starts from an alternative point, GEEM predicts different converging paths.

### **2.5.1.3 Dynamics Following Disturbance in One Species**

While last section and Figure 3 discuss how the system converges to the steady state from a random point where none of the species were at their steady-state values, this section shows in more detail how all species in the system respond to a disturbance in one species, assuming all other species start at their respective steady state.

Figure 4 illustrates the system dynamics when 40% of pollock are harvested in the first period (the population of the pollock is reduced to 60% of the steady-state value). The pollock population rebounds soon after the harvesting, overshoots before converging to the steady state at period 5. What is more interesting is how other species in the ecosystem responds to this pollock harvesting. As seen in Figure 4, pollock's prey, zooplankton, closely follows pollock's population changes in the opposite direction by increasing first (corresponding to decreased pollock population from harvesting), then decreasing (reflecting the quick recovery of the pollock population) before it reaches its steady state. Unsurprisingly, pollock's predators, sea lion, Northern fur seal, killer whale, and Pacific cod all show decreased populations following the pollock harvesting, then gradually recover to their steady states. While it is straight forward to predict and explain how those species that are in a direct predator-prey relationship with pollock respond to the pollock harvesting, the responses of other species are more complex. For example, the herring population increases first before it damps to the steady state. This dynamic is connected to the



**Figure 4: Dynamics following a 40% harvesting of pollock**

pollock harvesting through two pathways, one through pollock's prey, zooplankton, which is also prey to the herring. Along this energy flow, harvesting pollock is beneficial to the herring because of reduced competition for common prey. The other pathway is through pollock's predators, sea lion, Northern fur seal, and killer whale, which are predator of the herring too. Along this second pathway, harvesting pollock is detrimental to herring because predators switch from pollock to herring. In the case in Figure 4, the positive effect of pollock harvesting overpowers the negative effect, and herrings' population increases following the pollock harvesting. Other species, such as phytoplankton and sperm whale, also connect to the harvesting through energy flows and respond to the harvesting accordingly. Note that some of those indirect responses are quite small and reflect directional information rather than substantial population changes.

### **2.5.2 Functional and Numerical Responses of Predation**

With 22 multiple predator and prey relationships in the ecosystem, it is worth delving deeper into the predation behavior in GEEM. A variety of factors, including the food preferences, the energy content of the prey, and the density and quality of alternative prey, are known to influence the predation rate. In this section, I focus on the responses of predators to changing prey density.

#### **2.5.2.1 Previous Research on the Functional and Numerical Response in GEEM**

Solomon (1949) recognized two responses of predators to the density of their resources. They are a functional response, which describes how the consumption rate

changes with respect to the resource density, and a numerical response, which results in a change in the density of predators within a given feeding area.

Holling (1959a) identified three basic types of behavioral responses: Type I (linear) response describing a proportional increase in consumption with increasing prey density; Type II (cyrtoid.) response describing a decreasing increase, or a concave response; and Type III (sigmoid) response or an accelerating consumption increase at low levels of prey density and a decreasing increase at high levels of prey density. All three forms impose an upper limit on prey consumption and each type has a specific form reflecting aspects of predatory behaviors in relation to variation in prey abundance (Ruscoe et al, 2005).

Tschirhart (2004) identifies four cases to track functional responses in a GEEM in which the densities and the consumptions of both the predator and prey result from complex interactions among species, including but not exclusive to the predator and the prey, in the ecosystem. Functional response forms in three cases can be analytically obtained. In case (i) where the prey consumption is fixed, the functional response in GEEM is Type I while case (ii) where the total prey consumption is fixed implies a Type II functional response. Unlike case (i) and case (ii) in which the predator density is fixed, for case (iii) and (iv), both predator density and prey consumption are allowed to vary. It is mathematically proved in Tschirhart (2004) that with the predator density being allowed to adjust to a steady state in case (iv), the functional response of the predator is constant and independent of prey density. All the above analytical results apply to the extended GEEM in this dissertation.

In addition to changes in the predation rate, predators also respond to prey density through their own abundance, or numerical response. The numerical change usually results from the alteration in the reproductive activity of the predator. In

GEEM, this is implemented through the net energy term in the population updating equation.

There are three basic kinds of numerical responses: 1) a direct response, in which the population of the predator increase as that of its prey increases; 2) no response, in which the population of the predator stays the same as that of its prey increases and the entire response is functional; 3) an inverse response, in which the population of the predator decreases as that of its prey increases (Elseth and Baumgardner, 1981). Tschirhart (2004) suggested that if the predator's population is allowed to attain a steady state for each prey density (case iv), the numerical response is strictly concave.

### **2.5.2.2 Functional and Numerical Response in Case (iii)**

The only case without an analytical conclusion, and the case I shall focus on in this section, is case (iii) in which both the consumption and the predatory density are allowed to adjust over one reproductive cycle. It can be more than one cycle as long as the predatory density does not reach a steady state. But I will allow one period only in the simulations to catch the short-term functional response to a direct prey density change without involving residue functional responses to the density change in the past periods.

Note that unlike case (iii) presented in Tschirhart (2004) in which the major reason for not having an analytical solution is because of the transition feature of the system, we cannot find analytical results here with one cycle because it is complex to sign the Jacobian matrix and the numerator matrix. For example, when determining the direction of the functional response of a species  $i$  to the biomass change in its prey  $J(\partial x_{ij} / \partial N_j)$ , we can use Cramer's rule. Since this is in a system with 22 first order

conditions and 22 demand-supply equations, we need to sign two 44 by 44 matrices, the Jacobian matrix (the denominator) and the numerator matrix. It would be very difficult to do so and even if we could, the result cannot be generalized to other functional responses.

An alternative approach to shed some light on the functional response and numerical response in GEEM is to use statistics for estimating the shapes of the responses. Simulations are run for 12 prey species in Figure 1 separately. For each prey species, 100 simulations are generated. In each simulation, the system starts at the steady state with the prey density varied from 10% to 1000% of the steady state value. The densities and consumptions of all predators are tracked for estimating the functional and numerical response functions using a Box-Cox transformation (Box and Cox, 1964). For example, to track the functional and numerical response of predators of pollock, I generate 100 simulations. In each simulation, the species populations are at the steady state with the exception of the density of pollock which varies from 10% to 1000% of the steady state value. In the first simulation, the pollock density is set to be 10% of the steady-state value while all others are at their steady-state values. Then GEEM is allowed to run freely for one period without any constraints on the prey consumption (as in case (i) or (ii)), and reports the optimal consumptions of predators on the pollock (functional response) and the predator densities at the end of running (numerical response). The same procedure is repeated in the second (third, fourth, ..., hundredth) simulation except that the starting density of the pollock is set to 20% (30%, 40%, ..., 1000%) of the steady-state value. Because the only difference in each simulation is the prey density, I am catching the functional and numerical response of the predators on the pollock density holding all other

ecological factors in the model constant. Notice that predator density change is actually one period lagged, which is illustrated in equation (15) below.

To estimate the functional response of species *i* over the density change of its prey, species *j*, ecologists use various function forms, usually assuming one particular type of response. For example, Holling (1959) derives a Type II functional response taking the form of

$$x_{i,j}^t = \frac{aN_j^t}{1 + bN_j^t} \quad (11)$$

Since the types of the functional responses generated by GEEM are unknown, a more general function form that allows for more response types is used. Following Box and Cox (1964), I use equation (12)

$$\frac{(x_{i,j}^t)^\lambda - 1}{\lambda} = \alpha + \beta N_j^t + \varepsilon \quad (12)$$

where  $x_{i,j}^t$  is the consumption in time period *t*;  $N_j^t$  is the prey density in time period *t*;  $\lambda$  is the transformation power;  $\alpha$  is the constant;  $\beta$  is the density coefficient;  $\varepsilon$  is the error term and is assumed to be normally distributed. In a Box-Cox transformation function, the parameters as well as the response type (the function form) are estimated together. I will also estimate the parameters in the Holling's Type II response function as a comparison.

Using the chain rule, I can derive the functional response from equation (12)

$$\frac{\partial x_{i,j}^t}{\partial N_j^t} = \frac{\beta}{\lambda(x_{i,j}^t)^{\lambda-1}} = \frac{\beta}{\lambda}(x_{i,j}^t)^{1-\lambda} \quad (13)$$

and

$$\frac{\partial^2 x_{i,j}^t}{\partial N_j^{t^2}} = \frac{\beta}{\lambda}(1-\lambda)(x_{i,j}^t)^{-\lambda} \quad (14)$$

Thus, the functional response is an increasing function if  $\beta$  is greater than zero. Depending on whether  $\lambda$  is equal to or less than one, it is a Type I (linear) or II (concave) response. Note that for a Type III response, a spline regression can be used to determine the shape. That is, a regression at low levels of  $N_j^t$  and another at high levels of  $N_j^t$ .

The estimation of the numerical response is similar to the functional response. The Box-Cox transformation is represented as following:

$$\frac{(N_i^t)^\tau - 1}{\tau} = \gamma + \delta N_j^{t-1} + \varepsilon \quad (15)$$

where  $N_i^t$  is the predator density;  $N_j^{t-1}$  is the prey density in time period t-1;  $\tau$  is the transformation power;  $\gamma$  is the constant;  $\delta$  is the density coefficient;  $\varepsilon$  is the error term and is assumed to normally distributed.

From equation (15), the numerical response is derived as

$$\frac{\partial N_i^t}{\partial N_j^{t-1}} = \frac{\delta}{\tau(N_i^t)^{\tau-1}} = \frac{\delta}{\tau}(N_i^t)^{1-\tau} \quad (16)$$

and

$$\frac{\partial^2 N_i^t}{\partial N_j^{t-1^2}} = \frac{\delta}{\tau}(1-\tau)(N_i^t)^{-\tau} \quad (17)$$

The three basic kinds of numerical responses suggested by Baumgardner (1981) can be identified depending on the value of  $\delta$  and  $\tau$ . If  $\delta$  and  $\tau$  are of the same sign, there is a direct numerical response.  $\delta$  being zero implies no response while an inverse response corresponds to either  $\delta$  or  $\tau$  being negative. If a numerical response does exist, then  $\tau$  being greater than one implies a concave function.

### 2.5.2.3 Functional and Numerical Response to Pollock Density Change

This section reports the functional and numerical response of predators of pollock: sea lion, killer whale, northern fur seal, and Pacific cod. The functional and numerical response of predators of other species derived from the Box-Cox transformation and those derived from the Holling's Type II response function can be found in Appendix 5. Figure 5b in Appendix 7 illustrates the differences between the Box-Cox functional response and the Holling's Type II response function for all prey species except for pollock, which is shown in Figure 5a.

The steady-state density for pollock is 6.612, and the pollock density in the simulations varies between 0.6612 (10%) and 66.12 (1000%). As seen in Figure 5a, which plots the functional response of four predators, all Box-Cox transformed functional responses are Type II. This follows from the parameter estimation in Table 2 in which for all four predators  $\beta$  is positive and all four predators'  $\lambda$  is  $> 1$ . Notice that although both response functions are concave, we derived the shape of the Box-Cox transformation from the data while the concavity of the Holling's Type II response function is preassumed. As a result, the Box-Cox transformed functions fit GEEM data better than the Holling type II functions. This is shown in Figure 5a and 4b in which the GEEM data lines almost perfectly overlap with the Box-Cox transformed function curves for most species while the Holling function II estimate fits the data less well. In general, functional responses simulated from GEEM and Box-Cox transformation are flatter than those from the Holling type II function, which usually underestimate the consumption of the prey when the prey density is low or high and overestimate the consumption when the prey density is at a medium level.

Information in Table 2 can be used to derive an explicit function form for the functional response. For example, the functional response of sea lion to pollock density can be derived from

$$\frac{(x_{6,4}^t)^2 - 1}{2} = 9.7428 + 575406N_4^t \quad (18)$$

which can be transformed to

$$x_{6,4} = (9.7428 * 2 + 2 * 575406N_4^t + 1)^{0.5} = (20.4856 + 1150812N_4^t)^{0.5} \quad (19)$$

Note that most  $\lambda$  values in the functional responses are equal to or close to 2.

This is because in GEEM, we assume that all species' net energy following the same equation (1)

$$\begin{aligned} R_i &= \sum_j [e_j - e_{i,j}]x_{i,j} - \sum_k e_i [1 + t_i e_{k,i}]y_{i,k} - f^i(x_{i,j_1}, x_{i,j_2}, \dots) - \beta_i \\ &= \sum_j [e_j - e_{i,j}]x_{i,j} - \sum_k (e_i d_{i,k} (\sum_j x_{i,j})^5 [1 + t_i e_{k,i}]) - .5r_i (x_{i,j_1}^2 + x_{i,j_2}^2 + \dots + x_{i,j_1}x_{i,j_2} + \dots) - \beta_i \end{aligned} \quad (1)$$

and all predation-prey energy flow satisfy

$$N_k x_{k,j} = N_i y_{i,k} = N_i d_{i,k} (\sum_j x_{i,j})^5 \quad (5)$$

in which the exponential values for all species are the same. In other words, we assumed that all species' dynamics follows one specific function form although the number of terms and the parameter values are varied depending on the energy flow of the species. As a result, the GEEM simulation, which has been used to estimate the Box-Cox transformation, implies similar functional response (similar  $\lambda$ ) but different parameter values (varied  $\alpha$  and  $\beta$ ) for different species. Were the GEEM structures have varied exponential values across species, we would expect to get varied  $\lambda$  accordingly. This can also be a potential modification over current GEEM.

Similar analysis can be applied to the numerical response. While functional responses of the four predators of pollock demonstrate similarity, numerical responses for them are diversified. As shown Figure 6, northern fur seal has a numerical response which is obviously differently shaped from that of the other three predators

with concave numerical response. The parameter estimation in Table 3 reports a less-than-one  $\tau$  (0.9069), which suggests that northern fur seal has a convex numerical response to pollock density.

**Table 2: Functional Response to the Pollock Density**

	$\lambda$	$\alpha$	$\beta$
Sea Lion	2.00	9.7428	575460
Killer Whale	2.00	3.5012	223340
Northern Fur Seal	2.00	-0.4366	3597.7
Pacific Cod	2.00	-0.4643	2077.2

Note: All estimates are statistically significant at 99% level.

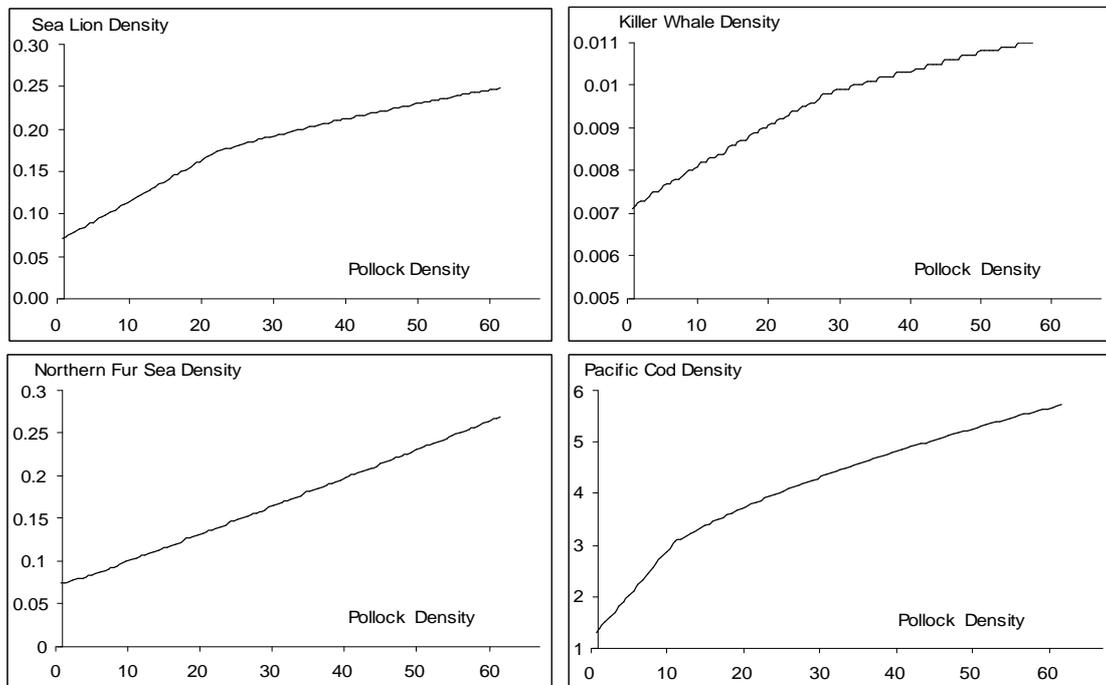
**Table 3: Numerical Response to the Pollock Density**

	$\tau$	$\gamma$	$\delta$
Sea Lion	2.3450	-0.4260	0.000267
Killer Whale	4.06	-0.2463	4.27E-11
Northern Fur Seal	0.9069	-1.0043	0.00386
Pacific Cod	2.5585	-0.2222	0.5461

Note: All estimates are statistically significant at 99% level.

According to GEEM, the energy price of the prey usually increases as the population of the predator increases, which explains why most species here have concave numerical response functions. Why would northern fur seal illustrate a different numerical response than the other three predators (sea lion, killer whale, and Pacific cod), which show concave functions? The answer may lie in the energy flow chart in Figure 1. In GEEM, the speed of the species population change (the shape of the numerical response function) depends on both the prey density and its predator behavior. In the northern fur seal case, as the pollock density increases, the energy price of pollock to the northern fur seal decreases, which leads to an increasing numerical response. At the same time, the energy price of pollock to the northern fur

seal's predator, the killer whale, is decreased too, which causes the killer whale to switch from the northern fur seal (currently constitutes 3% of its prey) to the pollock (currently constitutes 38% of its prey). It is this reduction in the predator pressure that makes the convex numerical response of the northern fur seal to the pollock possible. Among other predators, sea lion has energy flows similar to the northern fur seal, but the predator pressure reduction from the killer whale's prey switching behavior is not enough to cancel the "population effect" in which the increasing number of sea lions pushes up the energy price of pollock, which explains why the sea lion has a concave numerical response function to the pollock.



**Figure 6: Numerical responses of predators of pollock**

### 2.5.3 GEEM with Human Activity

Next, I introduce human activities into the GEEM and illustrate how the ecosystem responds to the interventions. In Chapter 4 I will answer the question of how humans and the ecosystem interact and how they respond to each other's

activities. For now, I assume humans are naïve and have no optimization goals in mind. Instead, they follow a simple regulatory rule, which states that they can harvest up to a fixed percent of all fish each year. For instance, in Figure 7 from Appendix 8 they harvest 20% of the populations of pollock, Pacific herring, and Pacific cod each year.

Formally the dynamics for species  $i$  is

$$N_i^t = \begin{cases} \Omega(\bar{N}^{t-1}) - h_i^{t-1} & \text{and } i = 4, 9, \text{ and } 13 \\ \Omega(\bar{N}^{t-1}), & \text{and } i \neq 4, 9, \text{ and } 13 \end{cases} \quad (19)$$

where  $\Omega$  is the population updating function through GEEM;  $h_i^{t-1}$  is the harvesting of species in period  $t-1$ , which equals 20% of  $N_i^{t-1}$ ;  $i=1,2,\dots,13$ .

Figure 7 in Appendix 8 shows the GEEM dynamics and new steady state with harvesting, or in ecological terms, numerical responses of species to the density change of fish resulting from harvestings. The original steady state is at one. The changes are proportional to the original states. All three fish are harvested by 20% of their current state, which means that the starting states of fish are 0.8 as shown in the graph.

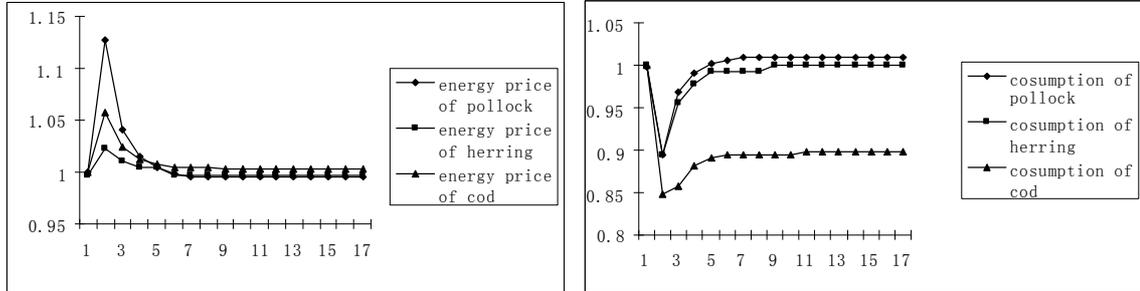
Not surprisingly, all three harvested fish species' new steady states are lower than their original ones. Although the harvesting percentage is 20% for all three species, the magnitudes in the decrease of the steady state are different. For pollock the steady state drops by 18%, herring 20%, and Pacific cod 29%. The reason why the Pacific cod steady state decreases by 29% is because of the population decrease of its prey, pollock. Recall from Figure 1 that pollock constitutes 21% of the energy to the Pacific cod. What is more interesting is the indirect influence of harvesting over other species in the food-web. For example, marine mammals that prey on fish reach a lower steady state while blue whale, which is a competitive predator to the fish over

zooplankton, reaches a higher steady state. The decreases in the marine mammals in turn affect the populations of the fish they prey on. For example, the population of pollock recovers to .82 from .80 after a few periods when the populations of its prey (sea lion, northern fur seal, Pacific cod, and killer whale) population decrease.

Figure 8 below and Figure 9 (in Appendix 9) illustrate the functional responses of predators, including the prey switching behavior and the energy prices. Usually when prey is abundant, less energy is needed for the capture of food and a correspondingly greater amount can be expended on reproductive activity. In GEEM terms, the energy price for that prey is lower. On the other hand, when suitable prey is rare, considerable energy must be spent on search and pursuit, or the energy price is higher. To maximize its net energy, an individual applies “feeding strategies” to lower the energy costs of search and pursuit. For example, when a certain kind of prey is common, predators tend to prey more on that species than other prey with higher energy prices. This is reflected in Figure 8 with an obvious negative relationship between the energy price and the consumption of each prey of sea lion.

Notice that the consumption of one prey species depends on not only the energy price of that species, but also on the energy prices for other prey. A simple linear relationship between energy prices and consumptions cannot explain why in period 2 the consumptions of both pollock and herring decrease about 10%, but the energy price of pollock increases much more than that of herring. Also we notice that in the new steady state, the energy prices of all prey are close to the original steady state energy price (the relative values on the y axis are close to one), but the consumption of cod in the new steady state is about 10% below the original steady state value. This prey switching behavior can also be explained by the marginal rule as in an economic problem. The sea lion, who is maximizing its total net energy, switches prey among

pollock, herring, and Pacific cod until the ratio of the marginal energy gain from consuming one more unit of a prey to that prey's energy price are equal for all three prey species.



**Figure 8: Sea lion's Consumptions and Energy Prices**

A more complicated example of prey switching behavior, the prey preferences of the top predator (killer whale) is illustrated in Figure 9 in Appendix 9. As the top predator, the killer whale preys on seven species, two of which, pollock and herring, are harvested by humans. Similar to the sea lion, the killer whale decreases its consumptions of pollock and herring when the harvestings start because the energy prices increase. But over time, the consumptions of pollock and herring converge to new steady states, which are very close to the original ones despite the fact that the populations of both fish in the new steady state are lower (see Figure 7). Notice that the energy prices of pollock and herring converge to the original steady states too. This can be explained as follows. When the fish densities initially decrease, the energy prices increase and each killer whale consumes less fish. But that means less net energy, which in turn leads to decreased killer whale density as shown in Figure 7. GEEM predicts that lower predator density will reduce the competition among predators and thus decrease energy prices and increase consumption over time, which is illustrated in Figure 9. While the consumptions of the fish are almost intact, the consumptions of prey species which are not harvested are adjusted in order to satisfy the net energy maximization conditions in GEEM. To be specific, the consumption of

northern fur seal, sea lion, and sperm whales decreases while that of sea otter and blue whales increases. These changes in the consumption of marine mammals are consistent with the population changes in Figure 7. For example, the increase in the blue whale consumption coincides with the increased density of blue whale while the decrease in the sperm whale consumption coincides with the increased density of sperm whale.

## **2.6 Conclusion and Future Extension**

The extended GEEM developed in this essay is used to simulate a 13-species marine ecosystem dynamics. To improve the prediction accuracy of GEEM as a population model, multiple predators and prey are added to the model and new data are used for the parameter calibration. In the empirical simulations, the stability analysis of the system, the converging path comparison, and the functional and numerical responses of predators are completed to yield more information on the interactions within the ecosystem and between the system and the economy.

Basically, GEEM extends economists' methodology to the ecosystem. Depending on how well those net energy functions are consistent with the species behavior and how accurate the parameter calibrations are, the ecosystem simulations provided by GEEM may be good or not so good. But with no doubt it offers an ecological framework that can be used either to model predator-prey systems or to integrate the ecosystem and the economy.

As discussed at the beginning of this chapter, GEEM leaves much space for improvement. With the multiple species interaction issue being addressed in this essay, several other possible extensions remain to be explored. For example, we can introduce harvesting into the calibration instead of assuming that the benchmark

system is in the steady state, which will give better estimated parameters. Another possible improvement is to change the species aggregation in GEEM. Although GEEM provides the microfoundation (the energy flow) for population dynamics, it is not a real individual-based model in ecological sense because GEEM assumes no difference among individuals within a species. A population model that focuses on the individual behavior like GEEM would benefit from distinguishing individuals of different characteristics.

Besides possible improvements of GEEM, it is also of importance to compare GEEM simulations with simulations from other ecological models, or better, real data series. Although GEEM uses economic research tools and serves for economic problems, it is a population model based on ecological theory in essence and needs to be tested in the ecologist's battlefield.

## Chapter 3

### REDUCED FORM OF THE GENERAL EQUILIBRIUM MODEL

#### -----An Alternative Population Dynamics Model for Interaction Species

In Chapter 1 I raised two questions on the success of integrating the GEEM (Finnoff and Tschirhart, 2003) with an economic model in application: how can we improve the prediction accuracy of GEEM as a population model and how well can variables from one model be effectively incorporated in the other? While the first question was answered in Chapter 2, Chapters 3 and 4 jointly answer the second question.

For the purpose of including the GEEM simulations in an economic problem, in this chapter I apply a vector autoregression (VAR) model to the simulations from GEEM and derive a linear system for population dynamics of interacting species. Since the derived population dynamics model is based on the simulations of the GEEM, I call it “the Reduced Form of the GEEM”, or R-GEEM for abbreviation.

This chapter is organized in the following ways: Section 3.1 presents the research motivations of deriving R-GEEM. After an overview of nonlinear model reduction methodology (Section 3.2), a vector autoregression model is built and the data generation algorithm is discussed in Section 3.3. Section 3.4 reports the econometric results, analyzes the stability of R-GEEM, and compares R-GEEM and GEEM from three perspectives: mathematical, graphic, and statistical.

Appendices 10-15 give more implementation details, such as the estimated matrix in R-GEEM, graphs of R-GEEM and GEEM responding to random shocks, and Q- statistics for single species under shocks of various scales.

### **3.1 The Motivations of the Deriving of R-GEEM**

There are two mutually dependent motivations behind my deriving R-GEEM: one is for the easy application of GEEM in resource management models and the other is for the contributions to the population ecology literature.

#### **3.1.1 Motivation A -- Application of GEEM in Economic Models**

The major reason why I estimate R-GEEM is the technical difficulty researchers will encounter if GEEM is used in an optimization problem. As discussed in Chapter II, GEEM can track both the interactions among species in the ecosystem and the interactions between the economy and the ecosystem, hence performing useful forecasting and policy-analysis functions. But GEEM variables are not easy to incorporate in an economics model because GEEM is a general equilibrium system of implicit functions without explicit solutions. As a result, to utilize GEEM information modelers have to include the complete general equilibrium model in the setup.

Including the complete GEEM may be achievable in a static model, but will be troublesome in a dynamic model since the modeler has to run GEEM multiple times for the population updating. For example, in the discrete time multiple species harvesting dynamic optimization model that I will illustrate in Chapter 4, to take advantage of the rich interaction information provided by GEEM, the complete GEEM needs to be included in the model as the population updating constraints. To get the global optimum of such a dynamic model, I need to use the numerical approach, which means that the complete GEEM will be run in each iteration. Although there are algorithms to avoid slow grid search, and optimization using simpler GEEM with less species has been accomplished, more complicated GEEM like the one presented in this paper could cause technological problems and we may

never be able to find solutions for such nonlinear dynamic problems. One way to tackle the above technological problem is to reduce the nonlinear GEEM to an explicit linear dynamic population system, R-GEEM. As will be seen later in this chapter, R-GEEM is a good approximation for GEEM iterations, and it enables researchers to solve dynamic optimization problems without losing the advantage of using the interaction information from GEEM.

### **3.1.2 Motivation B – Contributions to the Population Ecology Models**

Although the initial purpose of deriving R-GEEM is to solve the technical issues in economic models and offer a feasible method for economists to utilize the interaction information, R-GEEM also contributes to current ecology research, specifically the population dynamic models, in three ways.

First, R-GEEM presents a new mass-balanced population dynamics model. In terms of population dynamics, ecologists have long passed the stage where the logistic model was the main single-species model and the Lotka-Volterra model was the main multispecies competition and predation model (Kingsland 1985; Gutierrez, 1996). In the past two decades, ecologists have paid increasing attention to population models using mass-balance conditions, feeding interactions, and nutrient flow (Deangelis and Gross, 1992; Pauly and Christensen, 1993). One of the most applied biomass balanced models is the ECOPATH model. For example, to evaluate the impact of fishing on the ecosystem, Arreguin-Sanchez et al (2002) constructed a mass-balanced model of a benthic ecosystem using ECOPATH software (Christensen and Pauly, 1992a, b). For those who are not familiar with ECOPATH, it “consists of a set of linear equations representing each of the functional groups in the ecosystem, and describes the balance between biomass gains through production and losses, involving predation, fishing

and other exports” (Arreguin-Sanchez et al, 2002). The major limitation of the ECOPATH is that it is a static model, though this weakness can be dealt with using Ecosim, a time dynamic simulation method (Walters et al., 1997, 2000; Christensen and Walters, 2004). While ECOPATH models shed some light on the biomass flow in the ecosystem, they fail to provide important theoretical information about the kinds of dynamic behavior that can emerge from interactions between individuals. As an alternative biomass model, R-GEEM studies problems that cannot be addressed with ECOPATH models, such as the biomass flow among individuals, individual optimizing behavior, or the microfoundation of the population dynamics.

Second, R-GEEM is an attempt to build an ecosystem population model, which was once regarded “too complex” to build because “we ecologists have more parameters than we have pockets” (Elseth and Baumgardner, 1981). In recent years, researchers have attempted to build more complicated and realistic population dynamics models, such as incorporating environmental factors, management effects, cohort structures, and stochastic events (Williams et al. 2002). Researchers also have realized the importance of species interaction in a successful population model, and some proposed theoretic models for interacting species (Williams et al. 2002). As will be seen later in this essay, the function form of R-GEEM is consistent with the general model suggested by Williams et al. (2002). Some researchers have also attempted to build empirical dynamics models on the base of the ecosystems (Cox et al. 2002; Weisberg et al. 2002; Tews et al. 2006), although generally such ecosystem based population models are still rare.

Third, R-GEEM is a prediction model instead of retrospection models in most ecology literature. Some researchers have been criticizing ecology for its overemphasis on retrospection and lack of concern with prediction (Peters 1991).

Using time series technique, R-GEEM is a population prediction model incorporating past ecosystem information, which enables us to answer the question-- given present populations, what changes can we expect in the future and how can we affect those changes to our own ends?

Last but not the least, R-GEEM connects two major methods researchers employ to model natural phenomena: theoretical models and statistical approaches. Theoretical population models are based on assumptions, ecological knowledge, and mathematical equations. While more detail in theoretical models brings more realism, such descriptions require heavier computation with long simulation times and may be very difficult to understand. The other approach is the purely statistical approach. Researchers who prefer this approach usually model the population dynamics as a function of one or more independent variables, then apply statistical techniques to estimate the function forms and parameters in the functions. Statistical models can be quite precise, but without including any biological process they fail to illuminate the underlying population dynamic mechanism. Unlike most previous research which applies either the individual-based model or the statistical approach, R-GEEM is a statistical population dynamics model with a biomass-based ecological model, GEEM, as its micro foundation.

### **3.2 Methodology Discussion**

To find a reduced form with satisfactory accuracy for a complicated nonlinear and interrelated system like GEEM, researchers usually tackle the problem from two directions, mathematical or statistical. In this section, I will discuss the feasibility, advantages, and disadvantages of both methods.

### 3.2.1 The Mathematical Approach

In terms of the mathematical method, Taylor expansion (to certain degree, mostly one for the linearity) is the most commonly used model reduction method in the economics literature. The GEEM system discussed in Chapter 2 can be reduced by following the procedure:

1) Use first order Taylor expansion to linearize 22 first-order conditions from the net energy equations (equations in Appendix 1) and 22 demand-supply equations (equations in Appendix 2) around the steady state values of  $x_{i,j}$  and  $e_{i,j}$ ;

2) Solve the above linear system for 22  $x_{i,j}$  and 22  $e_{i,j}$  in terms of 13  $N_i$ , steady state values, and parameters;

3) Substitute  $x_{i,j}$  and  $e_{i,j}$  back to the 13 net energy equations to get the optimized  $R_i$  in terms of 13  $N_i$ , steady state values, and parameters;

4) Substitute optimized  $R_i$  back to the population updating equations (equation 7).

5) Use first order Taylor expansion again to linearize the population updating equations around the steady state values of 13  $N_i$ .

Note that the above procedure involves applying Taylor expansion twice, once in step 1) to solve for  $x_{i,j}$  and  $e_{i,j}$  in terms of 13  $N_i$ , steady state values, and parameters, and once in step 5) to linearize the updating equations so that the population dynamics is a linear system. This extra approximation procedure will add more noise to the derived system than a normal Taylor approximation.

Systems derived using first order Taylor approximation work well if operated in linear regime, or small departure from the equilibrium, but work poorly in a more general case (Chen, 1999). In other words, in the GEEM case, a linear system derived

from Taylor approximation will predict population dynamics reasonably well when the state is close to the steady state, but will do poorly once one or more species' populations move away from the steady state. Note that there is no guarantee that the perturbations on the equilibrium state in the GEEM are small. In fact, human activities affect the ecosystem so much that we can extinguish some species.

### **3.2.3 The Statistical Approach**

An alternative approach is to use statistical modeling. Similar to the statistical population modeling discussed in the last section, using the data from experiments, simulations, or natural observations researchers can estimate a system without theoretical perspectives. Statistics helps researchers select the model structure, estimate the parameters, and test the validity of the model. If applied appropriately, statistical models can approximate the original system to a quite high precision.

An example of application of statistical models is the VAR (vector autoregression) model in empirical macroeconomics. First applied by Christopher Sims (1980) in macroeconomics research to estimate a six-variable, four-lag dynamic system, a VAR is a  $n$ -equation,  $n$ -variable linear model in which each variable is explained by the lagged values of  $n$  variables. Since then, VAR has been used by macroeconomists extensively and has made major impact on new generations (Cogley et al. 2005). Since VAR provide a consistent and realistic approach to data description, forecasting, and policy analysis (Sims 1980), it suits my purpose to describe the GEEM data and generate a reliable reduced form for the population dynamics and tracking ecosystem responses to shocks.

There are three major uses of the VAR in the macroeconomics literature (Leeper and Zha, 1999). The first strand is to identify monetary shocks and test whether policy

shocks have contributed to business cycles (Leeper et al, 1996). The second strand tests whether the responses to policy shocks predicted by macroeconomics theories match those that VARs produce (Christiano et al, 1998a, 1998b). The third use involves forecasts with VAR models conditional on relatively long sequences of variables (Fackler and McMillin, 2002). The VAR model in this chapter entails all three uses. I will identify the VAR model (R-GEEM), use R-GEEM to predict the responses to various shocks, and test whether the responses in R-GEEM match those that GEEM predicts. For a more detailed summary of the VAR application in macroeconomics, please refer to the CREI archive for the “Macroeconomics and Reality, 25 Years Later” conference (CREI, 2005).

### 3.3 The Econometric Model

Depending on how many lags are in the model, a VAR model is called VAR(m) where m is the number of lags. After having tried nonlinear function forms combined with different VAR(m), I choose VAR(3) with linear terms only. For the comparison of linear and nonlinear estimation of the GEEM system, please see Q-statistics in the Table 9 in Appendix 12.

#### 3.3.1 The VAR Model Setup

The time-aggregated version of VAR with 3 lags is :

$$N^t = C + \Phi_1 N^{t-1} + \Phi_2 N^{t-2} + \Phi_3 N^{t-3} + \varepsilon^t \quad (20)$$

where  $N^t, N^{t-1}, N^{t-2}, N^{t-3}$  are vectors of populations of 13 species at time t, t-1, t-2, and t-3 respectively; C is a vector of constants;  $\Phi_1, \Phi_2, \Phi_3$  are  $13 \times 13$  matrices;

$$\varepsilon^t \sim iid(0, \Omega); \text{cov}(\varepsilon^i, \varepsilon^j) = 0 \text{ for } i \neq j.$$

The matrix  $[C \ \Phi_1 \ \Phi_2 \ \Phi_3]'$  is called the linear model or VAR matrix hereafter.

To test the nonlinearity of the system, I also applied a quadratic model:

$$N^t = C + \Psi_1 N^{t-1} + \Psi_2 N^{t-2} + \Psi_3 N^{t-3} + \Psi_4 (N^{t-1})^2 + \Psi_5 (N^{t-2})^2 + \Psi_6 (N^{t-3})^2 + \varepsilon^t \quad (21)$$

### 3.3.2 GEEM Simulations Generation

My next step is to use time series data generated from the GEEM in Chapter 2 to estimate  $\Phi_1, \Phi_2, \Phi_3$ . To ensure enough dynamics but not too much noise in the GEEM time series data, I start the populations at their steady-state values, then randomly add small shocks to any species in the system. In each period, the probability that no species is hit by a shock is  $0.978^{13} = 75\%$ . That is, the probability of at least one of 13 species being shocked is 25%. The number of the observations (time periods) the GEEM generated is 10,000.

Formally,

$$N_i^t = \begin{cases} N_i^{ss}, t = 1 \\ \Omega(N^{t-1}), t > 1 \text{ and } \phi_i^t \leq 0.978 \\ \Omega(N^{t-1})(1 + \mu_i^t), t > 1 \text{ and } \phi_i^t > 0.978 \end{cases} \quad (22)$$

where  $N_i^{ss}$  is the steady state population of species  $i$ ;  $\Omega$  is the population updating function through GEEM;  $\mu_i^t \sim i.i.dN(0, 0.10)$ ;  $\phi_i^t \sim U(0,1)$ ;  $i = 1, 2, \dots, 13$ ; and  $t = 1, 2, \dots, 10000$ .

Since the disturbance terms are not correlated, the VAR system is a seemingly unrelated regression model (SUR) with identical regressors, which means that the equations can be estimated separately by ordinary least squares (Greene, 2001). The GAUSS code for the estimation is available upon request.

### 3.4 The R-GEEM Estimate and Econometric Analysis

In this section, I will report the R-GEEM, analyze the stability of the system, and discuss the similarity of GEEM and R-GEEM from three perspectives: calculated steady states, graphic comparison, and a formal statistical test using Q-Statistics.

#### 3.4.1 The R-GEEM model

The R-GEEM matrix is reported in Table 5 in Appendix 5. All coefficients are rounded off to two decimals. While the matrix itself is easy to read, there are two things worth mentioning: First, the reported matrix corresponds to the linear model, which is the model I finally chose. I also estimated the quadratic model matrix and compared it with the linear model using a Q-test (see Table 9 in Appendix 12). The matrix for the quadratic model is available in Appendix 13 (Table 10). Q-test follows Cogley and Nason (1995) and I shall discuss the calculation of Q statistics more in detail in 3.4.3.3.

Second, for easy interpretation, the populations are divided by the steady state values and the predicted values are proportional to steady state populations. The matrix will be altered in the next chapter for the dynamic optimization problem so that R-GEEM predicts the populations in terms of the units used in the calibration, not the percentage to the steady state values. The matrix used in the numerical optimization problem in Section 4.3 is reported in Appendix 14.

Third, for easy analysis of the maximum principles in the dynamic problem in Section 4.2, I change the R-GEEM from equation (20) to

$$\Delta N = C + \Phi_1' N^{t-1} + \Phi_2 N^{t-2} + \Phi_3 N^{t-3} + \varepsilon^t \quad (23)$$

Note that  $\Phi_1$  becomes  $\Phi_1'$  when I move  $N_i^{t-1}$  to the left side to calculate

$\Delta N$ , which is a vector of 13 population updating rate.

### 3.4.2 Stability Analysis of R-GEEM

As discussed in 2.5.1, it is usually difficult to obtain all necessary information for the community stability analysis. But with the explicit form of R-GEEM, a mathematical analysis of the ecosystem analysis can be accomplished.

The VAR represented in the equation (20) can also be rewritten as a first-order model:

$$Y^t = C + \Phi Y^{t-1} + v^t \quad (24)$$

where

$Y^t = (N^{t'}, N^{t-1'}, N^{t-2}')$ ;  $v^t = (\varepsilon^{t'}, 0', 0')$ ;  $C$  is a vector of constants;  $v^t \sim iid(0, \Omega)$ ;

$$\text{cov}(v^i, v^j) = 0 \text{ for } i \neq j; \Phi = \begin{bmatrix} \Phi_1 & \Phi_2 & \Phi_3 \\ I_{13 \times 13} & 0 & 0 \\ 0 & I_{13 \times 13} & 0 \end{bmatrix} \text{ where } I_{13 \times 13} \text{ is a } 13 \times 13 \text{ identity matrix.}$$

The stationarity condition of R-GEEM dynamics, which is that all eigenvalues of the  $39 \times 39$  companion matrix  $\Phi$  are less than one in absolute value, is satisfied. The values for roots are in Appendix 15.

### 3.4.3 The comparison of R-GEEM and GEEM

In this section, I compare R-GEEM and GEEM from three perspectives: the steady state values, the model outputs, and a formal statistical test, the Q-test. All three approaches try to answer the same question: how well does R-GEEM resemble GEEM?

#### 3.4.3.1 Steady State Values in R-GEEM

Since we have proved in Section 3.4.2 that the R-GEEM is stable, the steady

state values of the system can be calculated by replacing  $N^t, N^{t-1}, N^{t-2}, N^{t-3}$  in equation (20) with  $N^{ss}$ , then solving for  $N^{ss}$ , which gives the formula:

$$N^{ss} = (I_{13 \times 13} - \Phi_1 - \Phi_2 - \Phi_3)^{-1} C \quad (25)$$

Substituting  $C, \Phi_1, \Phi_2, \Phi_3$  from the matrix in Table 6 to equation (25), I get the steady state values in R-GEEM, which are reported in Table 7. All 13 values are very close to 1, the steady state value in GEEM, which indicates a good resemblance at the steady state of two models.

**Table 7: Steady State Values in the R-GEEM**

Species	R-GEEM SS Value	Species	R-GEEM SS Value
Phytoplankton	0.999929	Killer whale	1.000725
Zooplankton	1.00056	Herring	1.000434
Kelp	0.999715	Northern fur seal	1.000419
Pollock	1.000401	Blue whale	0.998437
Urchin	0.999642	Sperm whale	1.001689
Sea lion	1.000771	Pacific cod	1.000279
Sea otter	1.000498		

### 3.4.3.2 Graphic Comparison

Further insight into the similarity of R-GEEM and GEEM can be obtained by looking at the converging paths of these two systems from the same random state, as plotted in Figure 10 in Appendix 11. The GEEM path is shown by the grey line and the R-GEEM path is shown by the black line. As before, the vertical values are in terms of the population percentage of the steady state value.

Species are under various shocks, positive or negative, small or large. This is incorporated in their starting populations. For example, the starting population of kelp is 1.34 (34% positive shock) while that of sperm whale is 0.29 (71% negative shock). R-GEEM and GEEM converge to the same steady state, as proved in 3.4.3.1. Although the converging paths are close for both small and large shocks, we cannot conclude that the dynamic mechanisms in the two systems are the same because

Figure 10 was generated from one random starting point. Should the systems start at alternative starting points, we would expect both systems to yield different dynamics. A formal statistical test is needed for assessing whether GEEM and R-GEEM have the same dynamic mechanisms.

### 3.4.3.3 Q Test

To test whether the R-GEEM is a good reduced form of GEEM, or to be specific, to test whether the impulse response functions in R-GEEM replicate the dynamics of GEEM under various shocks, I use a version of the Q-test proposed by Cogley and Nason (1995) by computing the generalized Q statistics, which can be defined as:

$$Q = (r_{GEEM} - r_{R-GEEM})'(V_{GEEM} + V_{R-GEEM})^{-1}(r_{GEEM} - r_{R-GEEM}) \quad (26)$$

The vectors  $r_{GEEM}$  and  $r_{R-GEEM}$  represent theoretical impulse response functions from GEEM and R-GEEM, respectively. They are calculated by averaging  $N (=1000)$  observations generated by GEEM or R-GEEM. That is,

$$r_j = (1/N) \sum_{i=1}^N r_{j,i} \quad (27)$$

where  $j = GEEM, R-GEEM$  and  $i$  is the iteration index. The generation procedures of the data are as follows: first, 1000 states are randomly chosen. Each state, which includes populations of 13 species, is input to GEEM and GEEM runs 10 periods to generate 1000 time series datasets, namely GEEM data. Then the same 1000 random states are input to R-GEEM, and R-GEEM runs 10 periods for prediction so that another 1000 time series datasets, R-GEEM data, are generated. The Q-test compares the resemblance of GEEM to R-GEEM data, or test how well R-GEEM predicts GEEM dynamics.

Unlike the Q-test in Cogley and Nason (1995) in which the covariance matrix is

the ensemble average of the outer product of the simulated impulse response functions, in equation (26) the covariance is the summation of  $V_{GEEM}$  and  $V_{R-GEEM}$ .  $V$  is computed as

$$V_j = N^{-1} \sum_{i=1}^N (r_{j,i} - r_j)(r_{j,i} - r_j)' \quad (28)$$

where  $j = GEEM, R-GEEM$  and  $i$  is the iteration index.

The test statistic  $Q$  has approximately a  $\chi^2$  distribution with degrees of freedom equal to the number of elements in  $r$ . For the single species test, the distribution is  $\chi^2(L)$  where  $L$  is the number of lags, or the number of time periods in each observation<sup>4</sup>. To make sure that GEEM and R-GEEM are similar both in short run and long run, I performed a  $Q$  test using a 1-period lag, 3-period lag, 5-period lag, and 10-period lag, respectively. For the complete system test, the distribution is  $\chi^2(13*L)$ <sup>5</sup>.

For the resemblance of R-GEEM and GEEM as complete systems, I test two competing hypotheses, **H0** and **H1**, which can be stated as:

**H0:** The R-GEEM and GEEM give the same dynamics;

**H1:** The R-GEEM and GEEM do not give the same dynamics.

If  $Q$  statistic is bigger than the critical value of  $\chi^2(13*L)$ , then **H0** is rejected in favor of **H1**, i.e. R-GEEM and GEEM do not give the same dynamics. Otherwise, we cannot reject **H0** that R-GEEM and GEEM give the same dynamics. In other words, we cannot reject the hypothesis that R-GEEM is statistically the same system as GEEM.

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<sup>4</sup> According to Cogley and Nason (1995), choosing too high a lag order reduces the power of the test while too low a lag order sacrifices information about the shape of the transitory impulse response function.

<sup>5</sup>  $130 = 13 * 10$  where 13 is the number of the species in the system and 10 is the number of lags.

Table 8 reports Q statistics for both the linear model (equation 20) and the quadratic model (equation 22) under various external shocks. As seen in the table, all statistics are very small compared with the 95% critical values, which means that **H0** holds for all models. For simplicity, I choose the linear model as the R-GEEM structure. Notice that R-GEEM provides good estimate of GEEM no matter the ecosystem is having big or small perturbations.

**Table 8: Q-test for complete systems**

Number of Lags(L)	95%critical value of $\chi^2_{(13*L)^6}$	Shock Distribution	Model			
			Linear Model		Quadratic Model	
			Q Statistics	Reject <b>H0</b> at 95% ?	Q Statistics	Reject <b>H0</b> at 95% ?
1	22.36	N(0,0.1)	9.06E-4	NO	4.59E-5	NO
		N(0,0.3)	9.67E-4	NO	1.25E-3	NO
		N(0,0.5)	1.05E-3	NO	2.18E-3	NO
3	54.57	N(0,0.1)	0.02	NO	0.02	NO
		N(0,0.3)	0.02	NO	0.02	NO
		N(0,0.5)	0.02	NO	0.02	NO
5	84.82	N(0,0.1)	0.39	NO	0.04	NO
		N(0,0.3)	0.04	NO	0.04	NO
		N(0,0.5)	0.04	NO	3.02	NO
10	157.6	N(0,0.1)	0.25	NO	0.24	NO
		N(0,0.3)	0.21	NO	0.20	NO
		N(0,0.5)	0.42	NO	1.27	NO

Similar econometric analysis can be applied to test single species dynamics.

Two competing hypothesis are:

**H0:** The R-GEEM and GEEM give the same dynamics for species n;

**H1:** The R-GEEM and GEEM do not give the same dynamics for species n.

If Q statistics is bigger than the critical value of  $\chi^2_{(10)}$ , then **H0** is rejected in favor of H1. As seen in Table 9a-9d in Appendix 12, H0 holds for all species estimated in R-GEEM for all time lags.

<sup>6</sup> Chi squared calculator from <http://www.fourmilab.ch>.

### **3.5 Conclusion**

This chapter presents the meaning, process, and results of deriving R-GEEM. A vector autoregression (VAR) model is applied to the simulations from GEEM and a linear system for population dynamics of interacting species, R-GEEM, is derived and tested using a mathematical, graphic, and statistical approach respectively. All tests indicated that R-GEEM is a good reduced form of GEEM and resembles GEEM dynamics under various shocks.

This essay partially answers the question raised in Chapter 1 on how we can incorporate variables from GEEM with an economic model. The economic problems discussed in the next chapter will complete the answer to this question.

## Chapter 4

### INCORPORATING GEEM IN ECONOMIC MODELS

This chapter provides application examples of the GEEM in resource management, and jointly with Chapter 3, completes the answer to the second question raised in Chapter 1 on integrating GEEM with economic models in application: how to effectively incorporate variables in one model into the other? The answer is comprised of two parts: theoretical models and policy simulations of harvesting in the Eastern Bering Sea (EBS).

This chapter is organized as follows: Section 4.1 presents an overview of multispecies models. In Section 4.2, a theoretical model with a profit-maximization objective and various constraints is set up and maximum principles are analyzed. In Section 4.3, the multispecies profit maximization model is applied to fishery management in the Eastern Bering Sea using real data, assuming single owner property rights. Results from the multispecies and single species approaches are compared and discussed first, then comparative simulations for parameters are reported and analyzed.

Appendices 16-21 give more details for the material discussed in this chapter, such as the estimation of the harvesting functions, more comparative simulation results for the parameters, etc.

#### 4.1 Introduction

Traditional biological resource management models usually assume the exploitation of a single stock that exists independent of other species. Take, for example, fishery management. Most fishery management models are largely

single-species based (Clark, 1984), although actual fisheries usually involve multispecies interactions.

The inadequacy of single species based management has become of “increasing consequence with the tremendous expansion in the intensity of fishing operations and an increase in the variety and trophic level of species harvested” (Mercer, 1982). In the past two decades, bioeconomists have taken a more realistic approach to management. The management of multi-species embraces not only the situation in which one type of gear takes more than one species, but also the effects harvesting one species has on other species. In a sense, multi-species fishery means management of the resource in a region where more than one species coexist and interact with each other. Clark (1990) divides interactions among resources into two categories: ecological interdependency which involves biological interactions such as predation and competition (Anderson, 1975 a, b; Begon et al., 1996; MRAG Americas 2000), and technical interdependency whereby capture of one species results in capture of other species (Clark, 1985; Flaaten and Stollery, 1996; Hartwick and Olewiler, 1986). In this essay, I focus on the role the ecological interdependency plays in multispecies management approach.

Most researchers agree that although short-term management objectives may be achievable in ignorance of their ecosystem, long-term, strategic management requires the consideration of species interactions, or the ecosystem mechanism (Bax, 1998). With rare exceptions, previous research on the optimal harvesting of species in the context of multiple species has been confined to two species which either form a predator-prey system (Goh et al, 1974; Clark, 1976; Ragozin and Brown, 1985, Strobele and Wacker, 1995; Hartwick and Olewiler, 1986) or a mutualistic system (Wacker, 1999). For example, Hartwick and Olewiler (1986) analyze optimal

utilization for two interacting species in a predator-prey system, shark and tuna, and demonstrate how interesting policy inferences can be drawn from such an exercise. Wacker (1999) analyzes the case of an optimization model with the context of a mutualistic system in which two regenerative natural resources interact. Although humans consume only one of the two resources, the other resource has a positive value for its positive feedback. Not surprisingly, the author concludes that at the optimum, society keeps a bigger resource stock than in the corresponding single-species case, where the positive feedback is neglected.

In recent years, some researchers have proposed the application of the ecosystem-based fishery management approach (National Marine Fisheries Service, 1999; Brodziak and Link. 2002; Pikitch et al, 2004), which implies more than two species and more complicated interactions than the models described above. But according to van Kooten and Bulte (1999), most multi-species models ignore many important relationships and are partial models due to incomplete information of ecosystems. Clark (1990) even argues that no marine system has probably been studied enough for sophisticated multi-species models. For instance, Flatten and Stolley (1996) examined the economic cost of predation of minke whales on economically valuable species such as herring and capelin. While they have shown that the cost of predation depends on the management regime of prey species, they neglect the interactions among prey species because modeling a more complete multispecies model of the ecological system proved to be very difficult. With GEEM or R-GEEM in the picture, it is actually possible to set up and solve complex multispecies bioeconomic models that involve ecological interdependencies. Although GEEM or R-GEEM is still a new ecological model the validity of which

remains to be tested, the multispecies models in this paper can be a further step in incorporating modern ecological science in economics.

In the rest of this chapter, I shall set up dynamic models depicting the role of GEEM in the optimal choices of a sole owner's profit maximization problem. That is, an intertemporal model of a sole-owner-managed fishery involving multiple species harvestings is adopted to illustrate how information in GEEM can be used in resource management. The methodology to solve the dynamic problem is discussed, the maximum principles are analyzed, and a numerical Alaskan fishery management model with real data is used as an application example.

## **4.2 The Model Setup**

In this section, I set up a dynamic optimization model in which a sole owner intends to maximize her total discounted profit from harvesting two species in the R-GEEM system.

### **4.2.1 Introduction**

As in previous chapters, I use the 13-species marine system GEEM as the ecological foundation for the dynamics optimization problems. For the technical reasons discussed in Chapter 3, I use the R-GEEM (in the form of equation (23)) as the population updating constraints instead of directly including the complete general equilibrium model in the optimization problem. Since humans harvest pollock and Pacific cod in this ecosystem, the choice variables are pollock and Pacific cod harvesting and there are 13 state variables in the system.

Although the dynamic model in this section addresses the optimization problem

in a particular ecosystem (the 13-species Alaskan marine system), its setup can be extended to dynamic optimization problems in other ecosystems that are suitable for GEEM simulations or many other multiple species interaction models. The choice variables can be more than two and the objectives are, of course, not limited to profit maximization. Depending on the economy and ecosystem setup, the dynamic models discussed in this section can have numerous variations, but the underlying principles are the same. What is worth mentioning is that R-GEEM is only an approximation of GEEM. That is, if the ecosystem is small enough (maybe a two or three species ecosystem) or the economic problem (maybe a static problem) is simple enough not to cause technological issues, GEEM is preferable to R-GEEM as the updating constraints. The methodology to solve a dynamic optimization problem with GEEM as constraints is similar to the numerical approach that will be discussed in the Section 4.3 for solving the dynamic problem with the R-GEEM as constraints.

#### **4.2.2 The Sole Owner Profit-Maximization Problem**

Now assume that the marine system is managed by a firm with well-defined property rights or a sole owner who is to maximize her discounted total profits from harvesting pollock and Pacific cod. Selective harvesting is available and there is no technical interdependency (Anderson, 1977) between pollock and Pacific cod harvesting. For simplicity, the owner does not care about other values of the ecosystem such as tourism. But the harvesting is subject to fishery regulations, which either set a cap to the harvesting or set a minimum safety population limit for the endangered species, or both. Depending on the policy setup, the regulatory constraints can exist in each period or a particular period. If the regulatory constraint exists in each period, the problem becomes a state constrained one. If the regulatory constraint

applies to only the last period, it can serve as a transversality condition. Other assumptions include fixed technology and market price over time, no market power in either fish markets or input markets, and perfect information for the owner. By perfect information, we mean that the owner knows current conditions in the ecosystem and is able to infer the populations in the future through GEEM or R-GEEM.

Using the 13-species R-GEEM as the updating constraint, the harvesting problem without a minimum safety limit<sup>7</sup> is

$$\mathit{Max}_{h_i^t} \quad \pi = \sum_{t=0}^{\infty} \left( \frac{1}{1+\delta} \right)^t \sum_{i=4,13} (p_i h_i^t - C_i(h_i^t, N_i^t))$$

*s.t.*

$$N_j^{t+1} - N_j^t = RG_j^t(N^t, N^{t-1}, N^{t-2}) - Ah_j^t = \alpha_j + \omega_{1,j}N^t + \omega_{2,j}N^{t-1} + \omega_{3,j}N^{t-2} - Ah_j^t$$

where  $j=1,2,\dots,13$ ;

$N^{-1}, N^{-2}, N^{-3}$  are given and  $h^{-1}, h^{-2}, h^{-3}$  are zeros.

(29)

Species  $i$  are the harvested species, pollock and Pacific cod;  $p_i$  is the price of species  $i$ ;  $C_i$  is the cost function of harvesting species  $i$ ,  $\frac{\partial C_i}{\partial h_i} > 0$ ,  $\frac{\partial C_i}{\partial N_i} < 0$ ,  $\delta$  is the discount rate in the economy;  $N^t, N^{t-1}, N^{t-2}$  are vectors of populations of all 13 species in period  $t, t-1$ , and  $t-2$  respectively;  $\alpha_j$  is the constant term in R-GEEM for species  $j$ ;  $\omega_{1,j}, \omega_{2,j}, \omega_{3,j}$  are vectors of coefficients from R-GEEM for species  $j$ ; and  $A = [00010000000001]$ .

There are two things in the GEEM updating equations that do not exist in a traditional single species model. First,  $N^t$  is a vector of all species in the ecosystem. In other words, this optimization problem has 13 state variables. Second,  $N^{t-1}, N^{t-2}$ ,

<sup>7</sup> A minimum safety limit will be added in next section when a numerical approach is used to solve the problem. It is left out here to avoid a state constrained dynamic problem so that the economic analysis of maximum principles is clearer.

which are the values of state variables in previous periods affect the population updating of species  $j$  in period  $t$ . As will be seen below, these elements in the GEEM updating constraint complicate the solutions to the problem and provide new perspectives to the economic analysis.

The Lagrangian expression for the problem presented in equation (29) is defined as

$$L = \sum_{t=0}^{\infty} \left( \frac{1}{1+\delta} \right)^t \left\{ \sum_{i=4,13} (p_i h_i^t - C_i(h_i^t, N_i^t)) + \sum_{j=1}^{13} \left( \frac{1}{1+\delta} \right) \lambda_j^{t+1} (N_j^t + RG_j^t(N^t, N^{t-1}, N^{t-2}) - Ah_j^t - N_j^{t+1}) \right\} \quad (30)$$

where  $\lambda_j^{t+1}$  is the costate variable for species  $j$ , and can be interpreted as the value of an additional unit of  $N_j^{t+1}$  in period  $t+1$ . Notice that the value is discounted by  $\frac{1}{1+\delta}$  to put it on the same period as the objective function. Thus, the expression in  $\{.\}$  in (30) is a value from the perspective of period  $t$ , and it is discounted by  $\left(\frac{1}{1+\delta}\right)^t$  back to the present, and discounted values from other periods are summed to calculate the present value of the Lagrangian.

First-order conditions with respect to the choice variables are

$$p_4 - \frac{\partial C_4}{\partial h_4} = \left( \frac{1}{1+\delta} \right) \lambda_4^{t+1} \quad (31)$$

and

$$p_{13} - \frac{\partial C_{13}}{\partial h_{13}} = \left( \frac{1}{1+\delta} \right) \lambda_{13}^{t+1} \quad (32)$$

Equation (31) and (32) imply that for a harvest strategy to be optimal the marginal net profit (RHS) from harvesting species  $i$  in period  $t$  must equal the opportunity cost (user cost),  $\left(\frac{1}{1+\delta}\right) \lambda_j^{t+1}$ , which is the discounted value of an additional

unit of the resource  $j$  in period  $t+1$ . These are similar to the optimum rules in the single species case, but since the owner is harvesting two species (two choice variables), equation (31) and (32) need to be satisfied simultaneously, together with 13 costate variable conditions that will be discussed below.

First-order conditions regarding the costate variables are more complicated and different from the single species case. For our problem, there are 13 equations for the costate variables (corresponding to 13 species):

$$\begin{aligned}
\frac{\partial L}{\partial N_m} = 0 = & \left( \frac{1}{1+\delta} \right)^t \left\{ - \frac{\partial C_m(h_m^t, N_m^t)}{\partial N_m} + \left( \frac{1}{1+\delta} \right) \lambda_m^{t+1} + \left( \frac{1}{1+\delta} \right) \lambda_m^{t+1} \frac{\partial RG_m^t(N^t, N^{t-1}, N^{t-2})}{\partial N_m} \right. \\
& \left. + \sum_{\substack{j=1 \\ \text{and} \\ j \neq m}}^{13} \left( \frac{1}{1+\delta} \right) \lambda_j^{t+1} \frac{\partial RG_j^t(N^t, N^{t-1}, N^{t-2})}{\partial N_m} \right\} - \left( \frac{1}{1+\delta} \right)^{t-1} \left( \frac{1}{1+\delta} \right) \lambda_m^t \\
& + \left( \frac{1}{1+\delta} \right)^{t+1} \left( \left( \frac{1}{1+\delta} \right) \lambda_m^{t+2} \frac{\partial RG_m^{t+1}(N^{t+1}, N^t, N^{t-1})}{\partial N_m} + \sum_{\substack{j=1 \\ \text{and} \\ j \neq m}}^{13} \left( \frac{1}{1+\delta} \right) \lambda_j^{t+2} \frac{\partial RG_j^{t+1}(N^{t+1}, N^t, N^{t-1})}{\partial N_m} \right) \\
& + \left( \frac{1}{1+\delta} \right)^{t+2} \left( \left( \frac{1}{1+\delta} \right) \lambda_m^{t+3} \frac{\partial RG_m^{t+2}(N^{t+2}, N^{t+1}, N^t)}{\partial N_m} + \sum_{\substack{j=1 \\ \text{and} \\ j \neq m}}^{13} \left( \frac{1}{1+\delta} \right) \lambda_j^{t+3} \frac{\partial RG_j^{t+2}(N^{t+2}, N^{t+1}, N^t)}{\partial N_m} \right)
\end{aligned} \tag{33}$$

Equation (33) can be simplified and rewritten as

$$\begin{aligned}
\lambda_m^t = & - \frac{\partial C_m(h_m^t, N_m^t)}{\partial N_m} + \left( \frac{1}{1+\delta} \right) \lambda_m^{t+1} \left( 1 + \frac{\partial RG_m^t(N^t, N^{t-1}, N^{t-2})}{\partial N_m} \right) + \sum_{\substack{j=1 \\ \text{and} \\ j \neq m}}^{13} \left( \frac{1}{1+\delta} \right) \lambda_j^{t+1} \frac{\partial RG_j^t(N^t, N^{t-1}, N^{t-2})}{\partial N_m} \\
& + \left( \frac{1}{1+\delta} \right)^2 \left( \lambda_m^{t+2} \frac{\partial RG_m^{t+1}(N^{t+1}, N^t, N^{t-1})}{\partial N_m} + \sum_{\substack{j=1 \\ \text{and} \\ j \neq m}}^{13} \lambda_j^{t+2} \frac{\partial RG_j^{t+1}(N^{t+1}, N^t, N^{t-1})}{\partial N_m} \right) \\
& + \left( \frac{1}{1+\delta} \right)^3 \left( \lambda_m^{t+3} \frac{\partial RG_m^{t+2}(N^{t+2}, N^{t+1}, N^t)}{\partial N_m} + \sum_{\substack{j=1 \\ \text{and} \\ j \neq m}}^{13} \lambda_j^{t+3} \frac{\partial RG_j^{t+2}(N^{t+2}, N^{t+1}, N^t)}{\partial N_m} \right)
\end{aligned} \tag{34}$$

Before we continue to explain specific terms in (34), it is worth elaborating on the meanings of two sets of elements in this costate condition for species  $m$ ,  $\lambda_m^t$ , and

partial derivatives  $\frac{\partial RG_j^t(N^t, N^{t-1}, N^{t-2})}{\partial N_m}$ .  $\lambda_j^t$  is the shadow value of an additional

unit of the species  $j$  in period  $t$  while  $\frac{\partial RG_j^t(N^t, N^{t-1}, N^{t-2})}{\partial N_m}$  indicates how species  $i$

influences the growth of species  $j$ . The product of the shadow value and the partial derivative represents the economic effect of a change in species  $m$  in terms of value change of species  $j$ . In other words, this product term reflects how the ecological interaction caused by an ecological variable change ( $\partial N_m$ ) can be valued in terms of economic value. Following Wacker (1999), the summation of the product terms for all species in the ecosystem is defined as the sum of “multi-species effect”.

While equation (34) looks daunting, its interpretation is actually quite simple if we compare it with the first-order condition to the state variable in a single species model which can be written as

$$\lambda_m^t = -\frac{\partial C_m(h_m^t, N_m^t)}{\partial N_m} + \left(\frac{1}{1+\delta}\right)\lambda_m^{t+1}\left(1 + \frac{\partial G(N_m^t)}{\partial N_m}\right) \quad (35)$$

where  $G(N_m^t)$  is the growth function of  $N_m$ , and other variables are defined as in the problem presented in (29).

According to equation (35), in a single species model, when the species is optimally harvested,  $\lambda_m^t$ , the value of an additional unit of the species in period  $t$ ,

equals the current period marginal profit,  $-\frac{\partial C_m(h_m^t, N_m^t)}{\partial N_m}$ , plus the marginal value

that an unharvested unit will be worth in period  $t+1$ ,  $\left(\frac{1}{1+\delta}\right)\lambda_m^{t+1}\left(1 + \frac{\partial G(N_m^t)}{\partial N_m}\right)$ , which

is the value of the marginal unit and its marginal growth discounted by one period.

For discussion purposes, I rewrite equation (34) as

$$\lambda_m^t = Z1 + Z2 + Z3 + Z4 + Z5 \quad (36)$$

Comparing (34) and (35), we can see that the state variable first-order conditions for (29) have three extra terms, Z3, Z4, and Z5. Z3 reflects the ecological interdependencies among species. It is similar to the extra term in a two-species model which has the following first-order condition:

$$\lambda_m^t = -\frac{\partial C_m(h_m^t, N_m^t)}{\partial N_m} + \left(\frac{1}{1+\delta}\right)\lambda_m^{t+1}\left(1 + \frac{\partial G(N_m^t)}{\partial N_m}\right) + \left(\frac{1}{1+\delta}\right)\lambda_k^{t+1} \frac{\partial RG_k^t(N_m^t, N_k^t)}{\partial N_m} \quad (37)$$

where m represents the other species.

In the present model, the ecological interdependency term, Z3, is composed of 12 terms, one for each species except for species m, the growth of which is included in the second term, Z2. Each of the 12 terms has a user cost of species m, and a “cross growth rate”,  $\frac{\partial RG_k^t(N_m^t, N_k^t)}{\partial N_m}$ , which describes how the stock of species m affects the growth of the stock of species j. As discussed before, the summation term is defined as the sum of “multi-species effect”. Depending on the sign and magnitude of each individual multi-species, a species in the ecosystem may decrease or increase the user cost of species m,  $\lambda_m^t$ , along the optimal path.

Z4 and Z5 may seem a bit puzzling, but not if we take into account the effect of  $N^{t-1}, N^{t-2}$  in the R-GEEM updating equation. Z4 can be interpreted as effects of species m in period t on the values of one more unit of other species in period t+2 discounted to present value. Notice that Z4 is a summation of 13 values, including the value of one more unit of species m in period t+2. So the Z4 term includes both inter-species interactions and dynamic (across time) effect. Similarly Z5 represents how the population of species m in current period t affects all 13 species in period t+3. Again this term is from the lagged term in the R-GEEM equations. Note that Z4 and

Z5 come from lags in VAR. Should the R-GEEM take a different form, these two time lag terms would be different too. A more general analysis is given later in equation (44) through (47).

As a summary, equation (34), the costate variable condition for the ecosystem based optimization problem, states that in each period  $t$ , the value of an additional unit of the species  $m$  (LHS) equals the summation (RHS) of the marginal profit from harvesting species  $m$  in period  $t$  (Z1), the marginal value of species  $m$  in period  $t+1$  (Z2), current value of multi-species effects in period  $t+1$ (Z3),  $t+2$  (Z4), and  $t+3$  (Z5). Note that while two first order conditions for choice variables (equation 31 and 32) are pure economic conditions, equation (34) involves both economic and ecological information. To satisfy equation (34), not only are traditional economic elements such as marginal profit, discount rate, and shadow values taken into consideration, ecological interactions (as partial derivatives terms) are also measured and play an important role. This is a key difference between single species model and ecosystem based model. It is this difference that makes ecosystem based model both powerful and difficult. More discussion on comparing optimal rules of single species model and that of ecosystem based models can be found in next section when a R-GEEM based model is applied to an empirical problem.

Now that we have 28 difference equations (2 first order conditions, 13 equations of movement for costate variables, and 13 population updating constraints) to derive feasible optimal harvesting rules for pollock and Pacific cod. It is extremely difficult to solve for closed-form equations for a dynamic system with so many difference equations. And unlike continuous time models in which we can derive some modified Ramsey rule at steady state, the analysis on the first-order conditions to our problem will not yield an explicit harvesting rule. Nevertheless, evaluating equation (31), (32),

and (34) assuming the system is at steady state can shed some light on the optimal harvesting choices of the resources. As shown below, we can derive a modified "fundamental equation of renewable resources" (Clark, 1990).

At steady state,  $N_j^{t+1} = N_j^t$ ,  $\lambda_j^{t+1} = \lambda_j^t$ , and  $h_j^{t+1} = h_j^t$  so that all time subscripts in the first-order conditions can be suppressed. Taking pollock for example, at steady state, the first-order conditions for pollock are

$$p_4 - \frac{\partial C_4}{\partial h_4} = \lambda_4 \left( \frac{1}{1 + \delta} \right) \quad (38)$$

and

$$\lambda_4 = -\frac{\partial C_4}{\partial N_4} + \left( \frac{1}{1 + \delta} \right) \lambda_4 + \left( \frac{1}{1 + \delta} + \frac{1}{(1 + \delta)^2} + \frac{1}{(1 + \delta)^3} \right) \sum_{j=1}^{13} \lambda_j \frac{\partial RG_j}{\partial N_4} \quad (39)$$

Substitute (38) into (39) and rearrange, we have

$$\delta = \frac{\partial RG_4}{\partial N_4} - \frac{\frac{\partial C_4}{\partial N_4}}{p_4 - \frac{\partial C_4}{\partial h_4}} + \left( \frac{1}{1 + \delta} + \frac{1}{(1 + \delta)^2} \right) \frac{\partial RG_4}{\partial N_4} + \left( 1 + \frac{1}{1 + \delta} + \frac{1}{(1 + \delta)^2} \right) \sum_{\substack{j=1 \\ \text{and} \\ j \neq 4}}^{13} \lambda_j \frac{\partial RG_j}{\partial N_4} \quad (40)$$

Equation (40) is the modified "fundamental equation for renewable resource" the interpretation of which is quite straightforward if we compare it with the fundamental equation for renewable resource in a single-species model:

$$\delta = \frac{\partial RG_4}{\partial N_4} - \frac{\frac{\partial C_4}{\partial N_4}}{p_4 - \frac{\partial C_4}{\partial h_4}} \quad (41)$$

As in equation (41), the LHS of equation (40) is the discount rate in the society and represents the opportunity cost of deferring harvesting one more unit of pollock. On the RHS, the first term is the marginal net growth rate of pollock. The second term has been referred to in literature as the marginal stock effect (Clark, 1990), reflects the

impact of the biomass on the harvesting cost, or values of the stock relative to the marginal value of harvest. In our model, the larger the size of the biomass, the lower is the harvesting cost ( $\frac{\partial C_4}{\partial N_4} < 0$ ), and the greater the net profit from the exploitation of the resource. The RHS of (41) can be interpreted as the internal rate of return of the resource in a single species case without lagged values.

Similar to the single species case, for a multiple species model, at optimal steady state, the internal rate of return of the resource should equal to the discount rate in society, as shown in equation (40). Compared with equation (41), the internal rate of return in a multiple species with lagged values, which is represented in RSH of equation (40) has two extra terms. The third term represents sum of discounted values from marginal growth of an unharvested unit of pollock in period t+2 and period t+3. As discussed earlier, this term is from the lagged values in the R-GEEM updating equations.

The fourth term is of special interest with ratios of shadow prices and cross species partial derivatives. This multispecies effect term as defined earlier is composed of two piece of information:  $\frac{\partial RG_j}{\partial N_4}$  represents ecological interactions between pollock and species j, and  $\frac{\lambda_j}{\lambda_4}$  represents economic relationship of the two species. The fourth term reflects the impact of pollock over other species in period t+1, t+2, and t+3, or the indirect increase of cost due to the harvesting of pollock. The multispecies effect is discounted to present by multiplying the discount term in the bracket, which is composed of three discount factors responding to period t+1, t+2, and t+3 respectively.

The summation of all four terms in RHS reflects the opportunity cost of harvesting one more unit of pollock. The fundamental rule requires that the optimal steady-state values of the harvesting and biomass of pollock satisfy the condition that the discounting rate in the economy equals the marginal growth rate accounting for the marginal stock effect and the multi-species effect across three periods, or the opportunity costs of harvesting and holding harvesting one more unit of pollock are equal. In other words, the forgone interest the owner can earn from the profit of harvesting one more unit of pollock should equal the summation of the current value of reduced harvesting cost, extra pollock growth in the next three periods, and values changes of other species in terms of pollock values in the next three periods, should the owner keep that unit of pollock in the sea instead of harvesting it.

A similar analysis can be applied to Pacific cod, which yield the fundamental equation for cod as

$$\delta = \frac{\partial RG_{13}}{\partial N_{13}} - \frac{\frac{\partial C_{13}}{\partial N_{13}}}{p_{13} - \frac{\partial C_{13}}{\partial h_{13}}} + \left( \frac{1}{1+\delta} + \frac{1}{(1+\delta)^2} \right) \frac{\partial RG_{13}}{\partial N_{13}} + \left( 1 + \frac{1}{1+\delta} + \frac{1}{(1+\delta)^2} \right) \sum_{\substack{j=1 \\ \text{and} \\ j \neq 13}}^{13} \frac{\lambda_j}{\lambda_{13}} \frac{\partial RG_j}{\partial N_{13}} \quad (42)$$

Combine equation (40) and (42), we have

$$\begin{aligned} \delta &= \frac{\partial RG_4}{\partial N_4} - \frac{\frac{\partial C_4}{\partial N_4}}{p_4 - \frac{\partial C_4}{\partial h_4}} + \left( \frac{1}{1+\delta} + \frac{1}{(1+\delta)^2} \right) \frac{\partial RG_4}{\partial N_4} + \left( 1 + \frac{1}{1+\delta} + \frac{1}{(1+\delta)^2} \right) \sum_{\substack{j=1 \\ \text{and} \\ j \neq 4}}^{13} \frac{\lambda_j}{\lambda_4} \frac{\partial RG_j}{\partial N_4} \\ &= \frac{\partial RG_{13}}{\partial N_{13}} + \frac{\frac{\partial C_{13}}{\partial N_{13}}}{p_{13} - \frac{\partial C_{13}}{\partial h_{13}}} + \left( \frac{1}{1+\delta} + \frac{1}{(1+\delta)^2} \right) \frac{\partial RG_{13}}{\partial N_{13}} + \left( 1 + \frac{1}{1+\delta} + \frac{1}{(1+\delta)^2} \right) \sum_{\substack{j=1 \\ \text{and} \\ j \neq 13}}^{13} \frac{\lambda_j}{\lambda_{13}} \frac{\partial RG_j}{\partial N_{13}} \end{aligned} \quad (43)$$

Equation (43) can be read as the fundamental rule of a multi-species model and requires that the opportunity costs of harvesting one more unit of pollock and that of Pacific cod are equal and coincides with the discounting rate in the economy. What is worth mentioning here is that there are no clear-cut expectations on the connection of the multispecies terms in these two harvested species. For example, the fact that the Pacific cod prey on pollock implies a positive  $\frac{\partial RG_{13}}{\partial N_4}$  and a negative  $\frac{\partial RG_4}{\partial N_{13}}$  in the usual case, but not in our model. As seen in Figure 1, the Pacific cod and pollock are connected through another important relationship: both are prey to the sea lion. Having a common predator implies a positive  $\frac{\partial RG_{13}}{\partial N_4}$  and a positive  $\frac{\partial RG_4}{\partial N_{13}}$ . But this is not the end of the story. Pollock compete with herring over zooplankton, which implies a negative  $\frac{\partial RG_9}{\partial N_4}$ . Herring, however, is connected to the Pacific cod through their common predator, sea lion. So we have a positive  $\frac{\partial RG_{13}}{\partial N_9}$ , which in turn indicates a negative  $\frac{\partial RG_{13}}{\partial N_4}$  by the chain rule.

Note that all above analysis is based on the VAR(3) R-GEEM derived in Chapter 3. I chose VAR(3) because having tried nonlinear function forms combined with different VAR(m), VAR (3) was one of the simplest models yet provided best fit for GEEM as proved by the Q-test in Section 3.4.3.3. If, however, the updating equations are not from the VAR(3) R-GEEM but from a more general multiple species ecosystem with n species and the lag term is not three but s, and the harvested species is not two but x, the forgoing analysis can still be applied to such problems.

Consider the following problem:

$$\text{Max}_{h_i^t} \quad \pi = \sum_{t=0}^{\infty} \left( \left( \frac{1}{1+\delta} \right)^t \sum_{i=\{x\}} (p_i h_i^t - C_i(h_i^t, N_i^t)) \right)$$

s.t.

$$N_j^{t+1} - N_j^t = G_j^t(N^t, N^{t-1}, \dots, N^{t-s+1}) - Ah_j^t \quad (44)$$

where  $j=1,2,\dots,n$ ;

$N^{-1}, N^{-2}, N^{-3}$  are given and  $h^{-1}, h^{-2}, h^{-3}$  are zeros.

First-order conditions with respect to the choice variables are

$$p_i - \frac{\partial C_i}{\partial h_i} = \left( \frac{1}{1+\delta} \right) \lambda_i^{t+1} \quad (45)$$

where  $i=\{x\}$ .

And first-order conditions with respect to the state variables are

$$\begin{aligned} \lambda_m^t = & -\frac{\partial C_m(h_m^t, N_m^t)}{\partial N_m} + \left( \frac{1}{1+\delta} \right) \lambda_m^{t+1} \left( 1 + \frac{\partial G_m^t(N^t, N^{t-1}, \dots, N^{t-s+1})}{\partial N_m} \right) + \sum_{\substack{j=1 \\ \text{and} \\ j \neq m}}^n \left( \frac{1}{1+\delta} \right) \lambda_j^{t+1} \frac{\partial G_j^t(N^t, N^{t-1}, \dots, N^{t-s+1})}{\partial N_m} \\ & + \sum_{k=2}^s \left\{ \left( \frac{1}{1+\delta} \right)^k (\lambda_m^{t+k}) \frac{\partial G_m^{t+k-1}(N^t, N^{t-1}, \dots, N^{t-s+1})}{\partial N_m} + \sum_{\substack{j=1 \\ \text{and} \\ j \neq m}}^n \lambda_j^{t+k} \frac{\partial G_j^{t+k-1}(N^t, N^{t-1}, \dots, N^{t-s+1})}{\partial N_m} \right\} \end{aligned}$$

where  $m=\{n\}$

(46)

The fundamental rule at steady state can be written as

$$\begin{aligned} \delta = & \frac{\partial G_i}{\partial N_i} - \frac{\frac{\partial C_i}{\partial N_i}}{p_i - \frac{\partial C_i}{\partial h_i}} + \left( \frac{1}{1+\delta} + \frac{1}{(1+\delta)^2} \right) \frac{\partial G_i}{\partial N_i} + \left( 1 + \frac{1}{1+\delta} + \frac{1}{(1+\delta)^2} \right) \sum_{\substack{j=1 \\ \text{and} \\ j \neq i}}^n \frac{\lambda_j}{\lambda_i} \frac{\partial G_j}{\partial N_i} \\ & + \dots + \left( 1 + \frac{1}{1+\delta} + \frac{1}{(1+\delta)^2} + \dots + \frac{1}{(1+\delta)^{s-1}} \right) \sum_{\substack{j=1 \\ \text{and} \\ j \neq i}}^n \frac{\lambda_j}{\lambda_i} \frac{\partial G_j}{\partial N_i} \end{aligned}$$

(47)

where  $i=\{x\}$ .

The interpretation of equation (44) through (47) is similar to the discussion on equation (29)- (43).

### **4.3 An Empirical Example of Economics Analysis Using R-GEEM**

As discussed earlier, it is difficult to find an exact solution analytically for the dynamic system of so many variables or analyze its stability. That being said, it is not impossible to apply the model to solve real optimization problems. An alternative method, the numerical approach using computers, is available for the solution.

In this section, I apply the profit maximization setup in Section 4.2 to a real economic problem: the profit maximization by the sole owner in the Eastern Bering Sea. Real data from the Alaskan fishery industry is used for the parameter calibrations in the problem. In practice, complex nonlinear optimal control problems are typically solved numerically by programs like GAMS that are designed to solve large constrained optimization problems.

Since the objective function is quadratic and constraints are linear, it is a quadratic programming problem, which can be solved by the Nonlinear Programming (NLP) package in GAMS. However, it is worth noting that the numerical solution to a nonlinear programming problem may not be the global optimum. If the software used to solve the problem is flexible enough, the researcher should check the solution carefully to make sure that it is reasonable and not sensitive to starting values.

The empirical example applied here is to answer two specific questions: 1) does the multispecies resource management lead to different harvesting behaviors than applying the single species approach? and 2) how do the exogenous parameters such as interest rate and species price affect the optimal choice?

#### **4.3.1 The Benchmark Joint Harvesting Model**

First, assume that the Eastern Bering Sea fishery is managed by a sole owner who harvests pollock and Pacific cod and is subjected to the sea lion minimum safety

population regulation. The owner has perfect foresight for the ecosystem (deterministic R-GEEM) and cares about only the current value of total harvesting of both fish over 1000 periods (there are no ecological values of other species to him). He has no market power either in the product markets or in the factor markets. That is, both prices and cost coefficients for pollock and cod are exogenous parameters. There is no technology interaction between the harvests of two species which is connected solely through the energy flows in the ecosystem as shown in Figure 1.

Assuming that harvests occur according to the Schaefer harvest function (Schaefer, 1957) which is commonly used in bioeconomic analysis, I set up the harvesting function for pollock and cod as

$$h_i^t = q_i (e_i^t)^{a_i} (N_i^t)^{b_i} \quad (48)$$

where  $i = 4, 13$ ;  $h_i^t$  is the harvest of species  $i$  in time period  $t$ ;  $q_i$  is the catchability coefficient;  $e_i^t$  is the effort spent on harvesting species  $i$  in time period  $t$ ;  $a_i$  and  $b_i$  are harvesting parameters.

The profit function can be written in terms of harvests as following:

$$\pi_i^t = p_i h_i^t - c_i \left( \frac{h_i^t}{q_i (N_i^t)^{b_i}} \right)^{a_i} \quad (48)$$

The benchmark profit maximization model with multispecies management is:

$$\mathbf{Max}_{h_i^t} \quad \pi = \sum_{t=0}^{1000} \left\{ \left( \frac{1}{1+r} \right)^t \sum_{i=4,13} (p_i h_i^t - c_i \left( \frac{h_i^t}{q_i (N_i^t)^{b_i}} \right)^{a_i}) \right\} \quad (49)$$

s.t.

$$\begin{aligned} N_6^t &\geq N_6^{\min}; N^t \text{ are at steady state and } h_4^t = 0 \text{ for } t = -1, -2, -3; \\ N_j^{t+1} - N_j^t &= RG_j(N^t, N^{t-1}, N^{t-2}) - Ah_j^t = \alpha_j + \omega_{1,j} N^t + \omega_{2,j} N^{t-1} + \omega_{3,j} N^{t-2} - Ah_j; \\ j &= 1, 2, \dots, 13; \mathbf{A} = [00 \ 01 \ 0000000001] \end{aligned}$$

To simulate the infinite time horizon, I choose to maximize the profit over 1000 time periods. The population updating constraint follows R-GEEM as in equation (23).

Table 13 reports the parameter values used in the benchmark model. The harvesting functions are borrowed from Finnoff (2006) who kindly summarized the estimation process in Appendix 16.

**Table 13: Parameter Values in the Benchmark Model**

Parameters		Values
Price (\$/ million tons)	Pollock( $p_4$ )	0.000614
	Cod( $p_{13}$ )	0.000489
Cost (\$/ unit of harvesting effort)	Pollock( $c_4$ )	7.3688
	Cod( $c_{13}$ )	0.3168
Sea Lion Minimum Safety Density (Individual/ $KM^{-1}$ ): $N_6^{\min}$		0.0769
Catchability Coefficient	Pollock( $q_4$ )	4574.616
	Cod( $q_{13}$ )	4.2370
$a_4$		0.2245
$b_4$		0.2494
$a_{13}$		0.6888
$b_{13}$		0.4506

Note: all monetary values were converted to be in terms of millions of 2000 dollars.

#### 4.3.2 Joint Harvesting Model VS. Separate Harvesting Model

In the benchmark problem stated in equation (49), the owner harvests pollock and Pacific cod, and chooses two optimal harvestings simultaneously subject to the ecological interactions among all species in the ecosystem, including the two harvested species. With perfect information, we know that to maximize the total profit from two harvestings, the owner should follow the harvesting rules yield by (49). But what if the owner is not aware of the economic connections (through ecological interactions) between the two harvested species? Instead of following the multispecies harvesting problem in (49), suppose she applies single choice variable management. Will the separate models the owner applies lead to different harvesting behaviors than the joint model? To address this question, first I need to set up comparable separate models.

Consider that the owner determines the optimal harvest path based on a one-species approach, but the problem is subjected to R-GEEM. That is, instead of

choosing the harvests of pollock and cod simultaneously to maximize the summation of the profits from two fisheries, the owner chooses the harvests of two species separately to maximize the profit associated with the specific species. All other conditions stay the same as in the joint model, including the parameter values and the multi-species interactions in R-GEEM. The owner's problem becomes two separate problems presented in equation (50) and (51). Note that (50) and (51) are not traditional single species models because they take into account the multi-species interactions presented in the updating equations. The purpose of including multi-species updating equations in the separate models is to make the optimal solutions from the joint model and the separating harvesting models comparable. If we use the traditional logistic single species population model as the updating equation in (50) and (51), then the optimal rule from the joint harvesting and the separate harvestings are not comparable economically because more of the difference is from the ecosystem simulation than from the optimization behavior.

Back to our separate harvesting models, the owner solves:

$$\mathop{Max}_{h_4^t} \quad \pi = \sum_{t=0}^{1000} \left(\frac{1}{1+r}\right)^t (p_4 h_4^t - c_4 \left(\frac{h_4^t}{q_4 (N_4^t)^{b_4}}\right)^{a_4}) \quad (50)$$

s.t.

$$\begin{aligned} N_6^t &\geq N_6^{\min}; N^t \text{ are at steady state and } h_4^t = 0 \text{ for } t = -1, -2, -3; \\ N_j^{t+1} - N_j^t &= RG_j(N^t, N^{t-1}, N^{t-2}) - Ah_j^t = \alpha_j + \omega_{1,j}N^t + \omega_{2,j}N^{t-1} + \omega_{3,j}N^{t-2} - Ah; \\ j &= 1, 2, \dots, 13; A = [00010000000001] \end{aligned}$$

and

$$\mathop{Max}_{h_{13}^t} \quad \pi = \sum_{t=0}^{1000} \left(\frac{1}{1+r}\right)^t (p_{13} h_{13}^t - c_{13} \left(\frac{h_{13}^t}{q_{13} (N_{13}^t)^{b_{13}}}\right)^{a_{13}}) \quad (51)$$

s.t.

$$\begin{aligned} N_6^t &\geq N_6^{\min}; N^t \text{ are at steady state and } h_4^t = 0 \text{ for } t = -1, -2, -3; \\ N_j^{t+1} - N_j^t &= RG_j(N^t, N^{t-1}, N^{t-2}) - Ah_j^t = \alpha_j + \omega_{1,j}N^t + \omega_{2,j}N^{t-1} + \omega_{3,j}N^{t-2} - Ah; \\ j &= 1, 2, \dots, 13; A = [00010000000001] \end{aligned}$$

Mathematically we expect that the joint model solutions satisfy equation (31) and (32) simultaneously and its steady state satisfies equations (40), (42), and (43). However, in a separate model setup, the solutions and the steady states for the pollock model satisfy equation (31) and (40) while those of the Pacific cod model satisfy equation (32) and (42). According to the simulation results summarized in Figure 11 and 12, compared with the single species approach, the multispecies resource management does lead to different harvesting behaviors, which in turn influence the ecosystem dynamics.

Figure 11 reports the optimal harvesting paths in the joint model and separate model, respectively. For most of the 1000 time periods, both pollock and cod have lower optimal harvest levels in the joint model than that in the separate models. A reason for this result is that both pollock and cod are prey to sea lion<sup>8</sup>. Because of the prey switching behavior of the sea lion discussed in Chapter 2, we expect positive  $\frac{\partial RG_{13}}{\partial N_4}$  and  $\frac{\partial RG_4}{\partial N_{13}}$ . That is, the existence of more pollock (cod) provides an incentive (lower energy price for pollock (cod)) for the sea lion to switch from cod (pollock) to pollock (cod), thus increasing the cod (pollock) population. In a separate model, the owners consider the profit from harvesting one species and fails to take into account how the harvesting affects the density of the other species through the common predator, sea lion, and in turn affects the profit from harvesting the other species because of the density variable in the harvest functions. As a result, the owner tends to over-harvest in the separate model compared to the optimal harvest level in the joint model in which the owner takes into account two kinds of interactions: the ecological interaction between the two prey of sea lion (similar to the marginal rate of substitution), and the economic interaction between the profits from two fisheries

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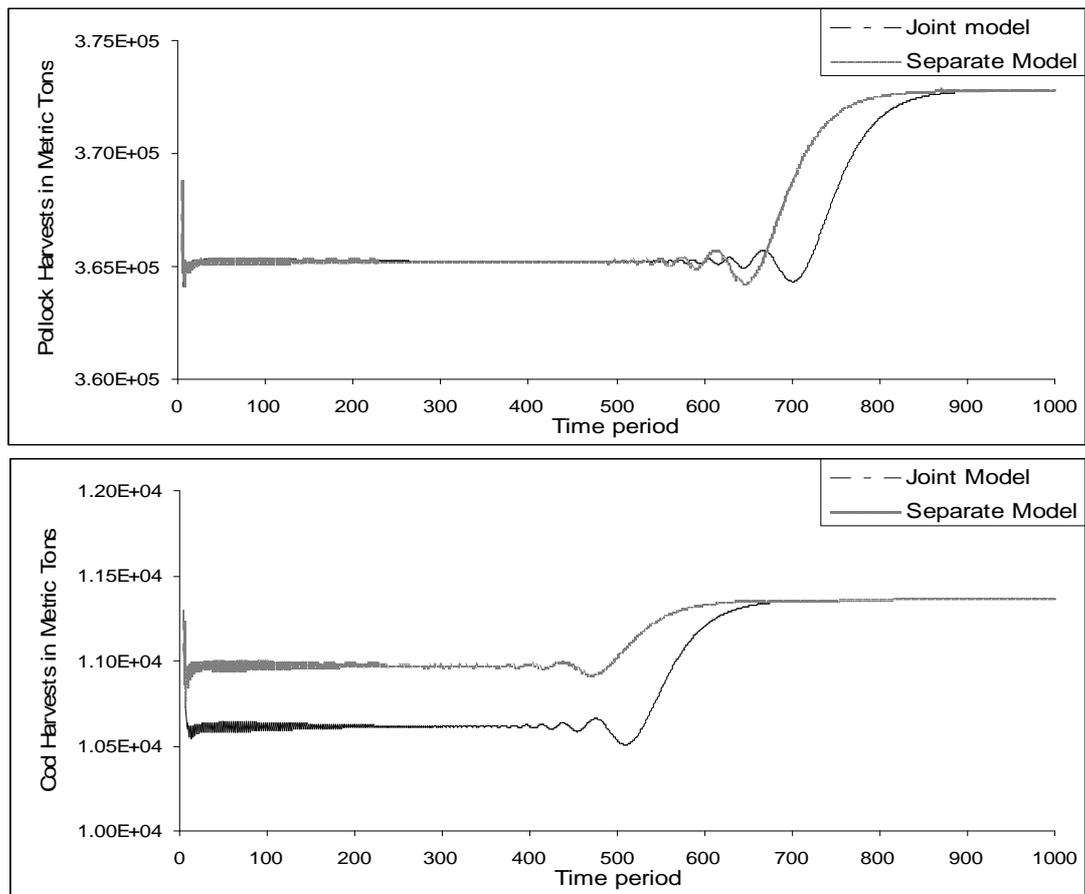
<sup>8</sup> Pollock composes 45% of the sea lion diet while Pacific cod composes 5% of the diet.

(similar to the marginal rate of technological substitution).

Another interesting difference between the joint model and separate models is the time when the owner's harvesting jumps. Recall that the optimal harvesting rules state that in each period  $t$ , the opportunity cost of leaving one unit of pollock in the sea (the interest rate in the society) should equal the opportunity cost of harvesting one more unit of pollock in period  $t$  (the summation of all future generated value from this unit discounted to period  $t$ ). Although we have 1000 periods in the problem, this is not a real infinite horizon problem. As a result, after a certain point of time, because of shorter time period until the termination point, the discounted summation of future value of an extra unit of pollock (the opportunity cost of harvesting) drops so much that it is not worth saving as much pollock for future harvesting as before. While both the joint model and separate model have shown this jump at harvesting, the jump in the joint model happens later than that in the separate model. This is consistent with the behavior difference discussed earlier that the owner fails to take into consideration how the harvesting of pollock affects the density of cod through the common predator, sea lion, and in turn affects the profit from harvesting cod because of the density variable in the harvest functions. Because of this ignorance of the economic value of the ecological interaction, the opportunity cost of harvesting one more unit of pollock (discounted summation of all future values) is underestimated, and the harvesting jump point is earlier in the separate model than in the joint model. Notice that the discount rate in the society influences the jump point too. More discussion follows later in the comparative simulation section.

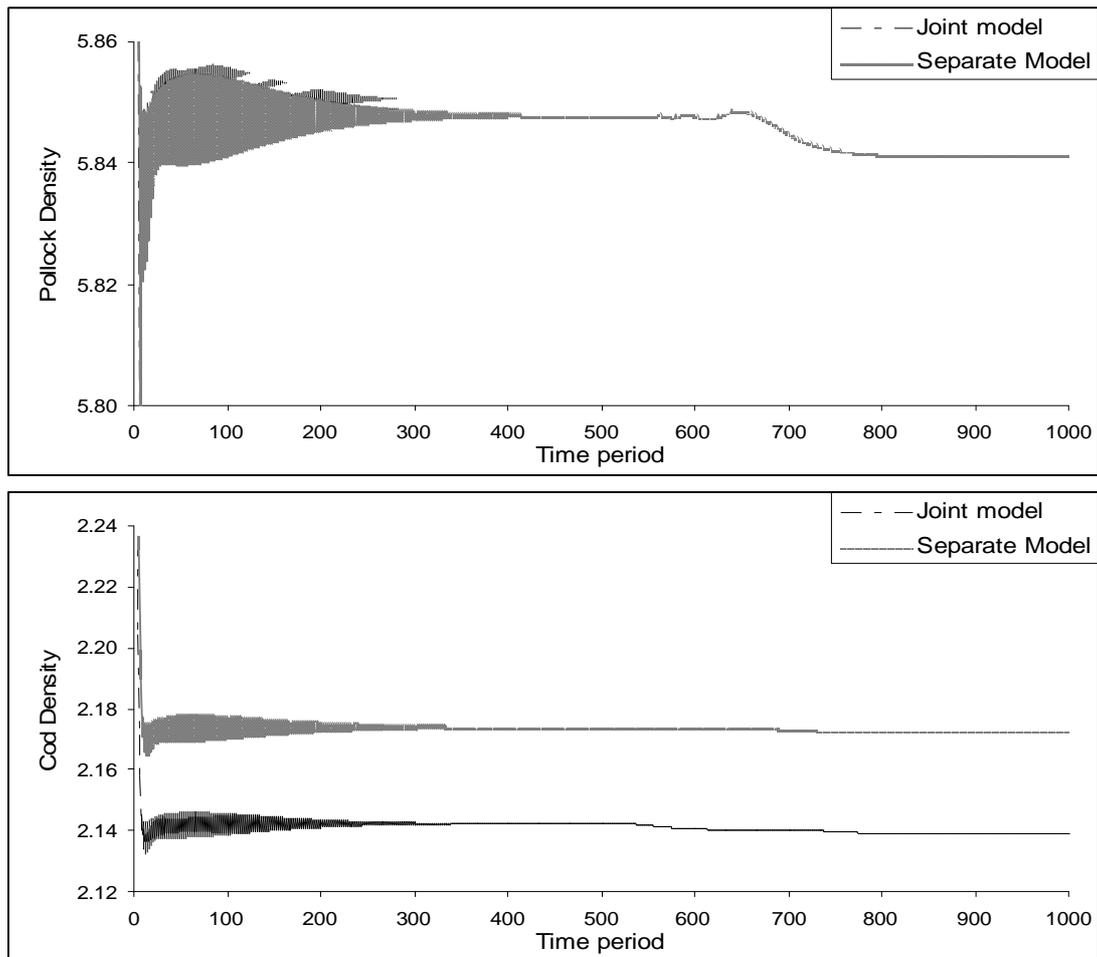
Figure 12 reports harvested species densities over time in joint model and separate model respectively. For most of the time, pollock density (the upper graph) in the joint model is higher than that in the separate model while the opposite is true for

the cod density (the lower graph). Considering that pollock and cod have a common



**Figure 11: Optimal Harvesting Path in Joint Model and Separate Model**

predator, this finding is quite curious. But we can explain the results easily using the information on the multi-species interactions in Figure 1. Besides the fact that both pollock and cod are prey to a common predator, sea lion, there is another important interaction between these two harvested species, namely the predator-prey interaction. As seen in Figure 1, pollock composes 21% of the Pacific cod's diet. A higher cod density implicitly hurts the profit from the pollock harvesting by reducing the pollock density through preying. There are also other implicit interactions between pollock and cod, some beneficial and others harmful. For example, as discussed before more pollock can harm cod by competing for zooplankton with herring, which is beneficial to the cod because both herring and cod are prey to the sea lion. In a joint harvesting model, the owner takes all this interactions into account and the relative salience of



**Figure 12: Species Density in Joint Model and Separate Model**

implicit costs and benefits decides what the optimal populations are. For the cod, the summation of implicit costs from a higher density of cod on the pollock is larger than the summation of implicit benefits, which explains why a separate model that ignores those implicit costs on the pollock yields higher cod density than that in a joint model.

Notice that we cannot directly compare the maximized profit from the joint model with the summation of the maximized profits from two separate models because in the latter the owner updates the ecosystem assuming there is only one species harvested while she is actually harvesting both.

### 4.3.3 Comparative Simulation Study of Parameters

In this section, I will discuss how changes in the parameters in the model affect

the optimal choices, both in terms of optimal harvesting paths and optimal steady states.

As discussed in 4.2, an analytical comparative result for this multispecies model is not forthcoming, because of the complexity and large number of the first-order conditions. If the updating equations are in continuous time, we can derive a rule for the optimal harvesting path overtime (similar to the Ramsay rule), then use the modified Ramsay rule to analyze how changes in the values of the parameters affect the optimal harvesting choices and states of the ecosystem. Such an approach, however, is inapplicable with discrete time updating equations. Instead, we can use a numerical approach to apply a comparative simulation study. In the rest of this section, I will vary parameter values in the benchmark models to address the question of how exogenous parameters affect the optimal choice in a dynamic multispecies model. Discussion on the impacts of discount rate, own price, and cross price are provided while numerical graphs on the cost parameter and safety minimum rule are reported in appendixes for readers' reference.

Table 16 lists the parameter values in the comparative simulations. Six parameters are varied and in each simulation, I vary one parameter using its high or low value. The benchmark values are the same as in Table 13. All comparative results are reported in figures in Appendix 17-21.

First, let's have a look at how the discount rate affects the optimal harvest choice and the ecosystem dynamics, the simulation of which is illustrated in Figure 13a and 13b. In a single species model, a higher discount rate increases the opportunity cost of lower resource exploitation and is usually associated with faster harvests (Clark, 1990; Conrad, 1999). While one may be attempted to apply the same reasoning to a multispecies management model, Figures 13a and 13b tells a different story which is

not as simple as "the higher the discount rate, the faster the harvests" reasoning.

**Table 16: Parameter Values in the Comparative Simulations**

Parameters		Benchmark Values	Low Value	High Value
Price (\$/ million tons)	Pollock( $P_4$ )	0.000614	0.000307	0.000921
	Cod( $P_{13}$ )	0.000489	0.000244	0.000733
Cost (\$/ unit of harvesting effort)	Pollock( $C_4$ )	7.3688	3.6844	11.0532
	Cod( $C_{13}$ )	0.3168	0.1584	0.4753
Sea Lion Minimum Safety Density $N_6^{\min}$ (Individual/ $KM^{-1}$ ):		0.0769	0.0481	0.0936
Discount Rate		0.03	0.01	0.10

In most periods, compared with the benchmark model, the owner harvests pollock faster when the discount rate is higher, as seen in the first graph in Figure 13a. This tendency is especially clear when we blow up the first 10 harvesting periods, as shown in the first graph in Figure 13b where we see three wavy lines with the high interest line on the top, the benchmark interest line in the middle, and the low interest line at the bottom. Note that this argument is not absolute since the optimal harvesting path actually oscillates over time and in some periods the owner harvest more in the case of a lower discount rate than a higher discount rate (the lines cross sometimes). A piece of more striking evidence that higher discount rate is not necessarily associated with faster harvesting (as in single species case) is from the harvesting behavior of cod shown in the second graph in Figure 3b. Again the owner's optimal cod harvestings are shown in three wavy lines. Contrary to the pollock harvesting, the low interest line is on the top, the benchmark interest line is in the middle, and the high interest line is at the bottom. This curious result can be explained by equation (40), the modified "fundamental equation for renewable resource", which is

$$\delta = \frac{\partial RG_4}{\partial N_4} - \frac{\frac{\partial C_4}{\partial N_4}}{p_4 - \frac{\partial C_4}{\partial h_4}} + \left( \frac{1}{1+\delta} + \frac{1}{(1+\delta)^2} \right) \frac{\partial RG_4}{\partial N_4} + \left( 1 + \frac{1}{1+\delta} + \frac{1}{(1+\delta)^2} \right) \sum_{\substack{j=1 \\ \text{and} \\ j \neq 4}}^{13} \frac{\lambda_j}{\lambda_4} \frac{\partial RG_j}{\partial N_4} \quad (40)$$

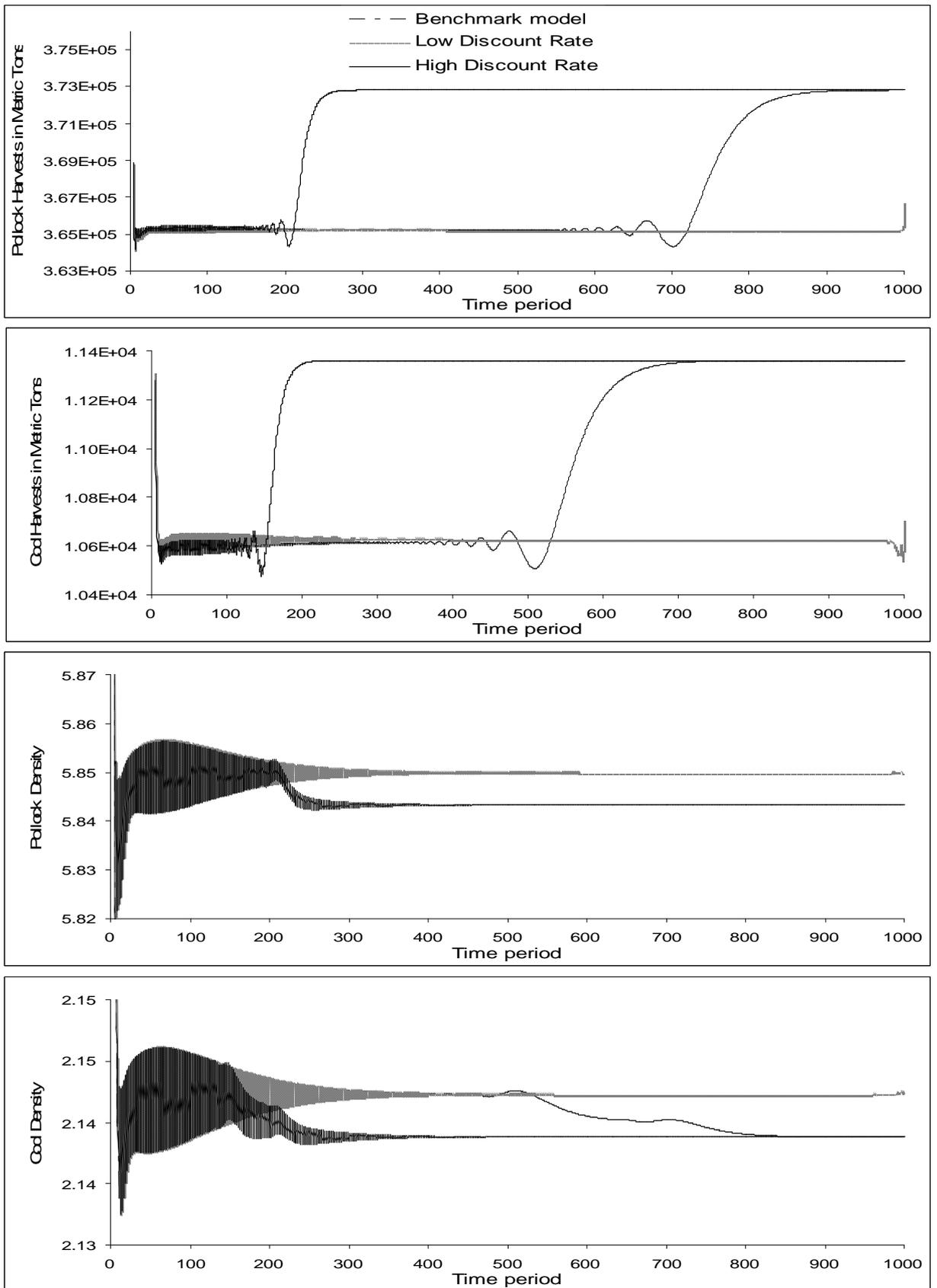


Figure 13a: Comparative simulations of the Discount Rate

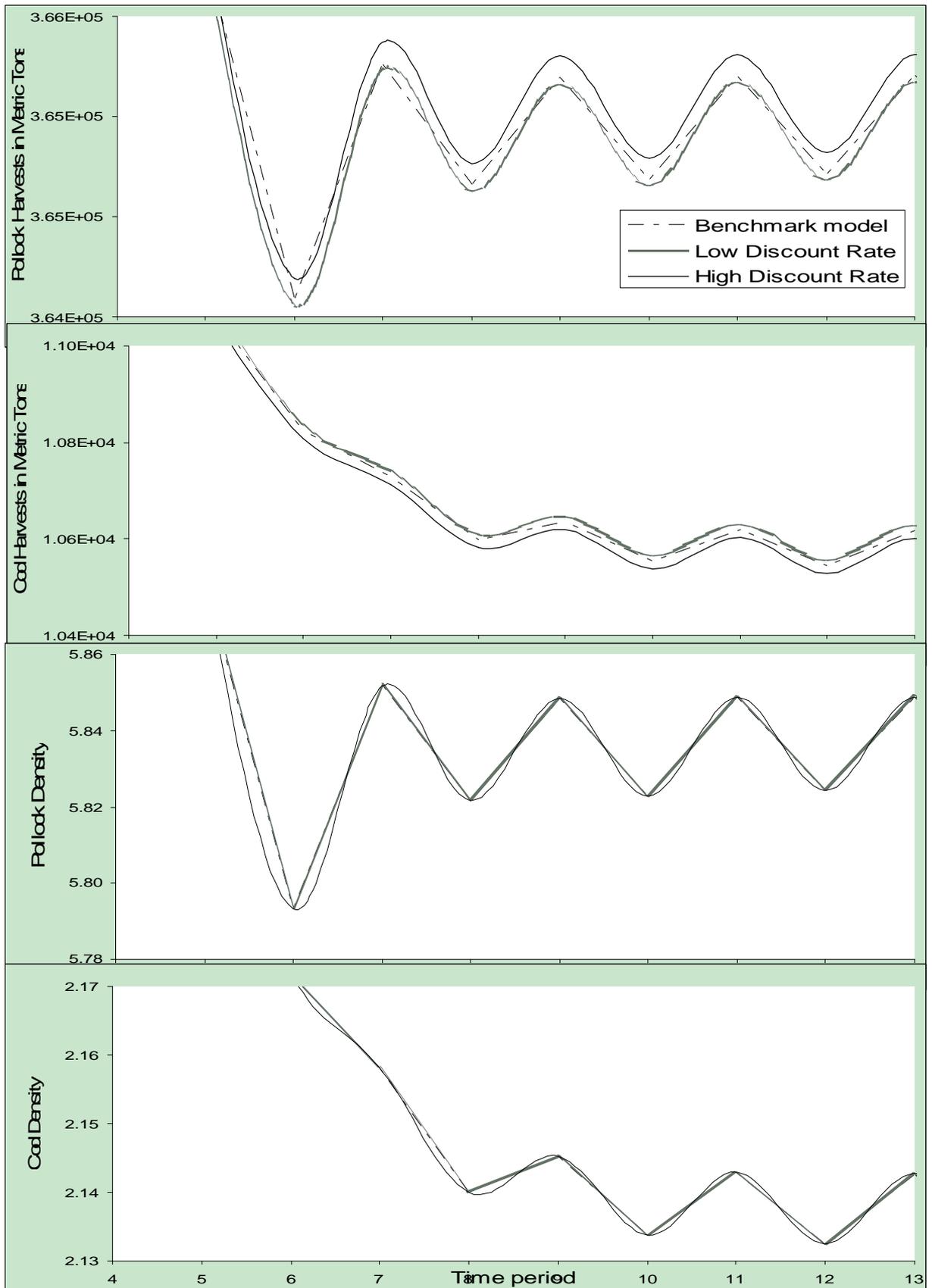


Figure 13b: Comparative simulations of the Discount Rate (first 10 harvesting periods)

Recall that the fundamental equation for renewable resource in a single species model is:

$$\delta = \frac{\partial RG_4}{\partial N_4} - \frac{\frac{\partial C_4}{\partial N_4}}{p_4 - \frac{\partial C_4}{\partial h_4}} \quad (41)$$

As discussed in Clark (1990), a higher discount rate increases the opportunity cost of lower resource exploitation (LHS of equation 41) and is usually associated with faster harvests so that the internal rate of return of the resource (RHS of equation 41) equals the discount rate. In a multiple species model, however, we have two extra terms, the lagged value term (the third term), and the multispecies terms (the fourth term) in the RHS as seen in equation (40). Both terms are scaled using the discount rate, which complicates the impact of changing the discount rate. For example, a higher discount rate (opportunity cost of deferring harvesting one more unit of the species) is no longer monotonically associated with faster harvesting because the higher discount rates in the third and fourth term actually reduce the internal rate of return of the resource when the marginal growth of an unharvested unit of pollock in period  $t+2$  and period  $t+3$  (the third term) are discounted to present by multiplying a lower discount term in the bracket. The fourth term, which is composed of twelve multispecies effect terms,  $\frac{\lambda_j}{\lambda_4} \frac{\partial RG_j}{\partial N_4}$ , further complicates the analysis since the multispecies effect, or the indirect increase of cost due to the harvesting of pollock, can be either positive or negative depending on the signs of  $\lambda_j$  and  $\frac{\partial RG_j}{\partial N_4}$ . As a result, a higher discount rate, or a lower discount term in the bracket before the fourth term, can either decrease or increase the RHS value.

In summary, when the interest rate increases, it influences the optimal harvesting

in three ways. First, it increases the opportunity cost of saving the resource for future harvesting because the owner could earn a higher return if she harvests today. Second, a higher interest rate decreases the opportunity cost of harvesting the resource today, because the values of future populations of some species are discounted more if they have positive value, such as pollock, cod, and their prey. The third effect is actually the opposite of the second one in that higher interest rate increases the opportunity cost of harvesting the resource, because some species have negative values, such as pollock's and cods' predators. These negative values are discounted more too, which raises the opportunity cost of harvesting the resource now. For example, when the owner harvests one unit of pollock today, beside the profit she gets from the harvesting, she also reduces future populations of pollock's predators. Since pollock's predators probably have negative values to the owner, by harvesting pollock, she gains another benefit, namely reduced negative values of pollock's predators in the future. A higher interest rate makes these reduced negative values in the future worth less now, which explains the existence of the third effect.

Note that the first two effects of a higher interest rate encourages higher harvesting by either increasing the opportunity cost of deferring harvesting or decreasing the opportunity cost of the harvesting, while the third effect reduces harvesting by increasing the opportunity cost of the harvesting. The three effects discussed above work jointly to determine whether a higher interest rate is associated with higher harvesting or not. In the first graph of Figure 13b, for the pollock harvesting, most of the time the first two effects overpower the third one, which explains why the higher interest rate line is mostly on the top. Occasionally, the third effect wins and causes the lines to cross. For the cod, however, the first two effects are rarely big enough to cancel out the third one, and the low interest rate line is on the

top. One reason for this curious finding is because cod preys on pollock, which makes the shadow value of cod smaller. As a result, the second effect, which increases harvesting, is smaller than if cod does not have a negative effect on the pollock.

Another interesting observation here is the disparity in the harvesting jump points. As discussed before, the jump in the harvesting reflects a point in time when the opportunity cost of harvesting one more unit of the resource is reduced so much because of shorter duration until the terminal point, that it is not worth to save as much resource for the future as before. Because the jump point is partly determined by the opportunity cost of harvesting, which is inversely related to the discount rate, a higher discount rate is expected to be associate with an earlier jump point and a significantly low discount rate predicts a late jump, possible very close to the terminal point. This is indeed true in Figure 13a.

As one would expect, the harvest behavior disparity resulting from the different discount rate also influences the ecosystem dynamics. As seen in the third and fourth graphs in Figures 13a and 13b, high, benchmark, and low interest population lines cross with each other multiple times, which indicates that a higher discount rate can cause either higher population or lower population depending on associated harvesting.

Besides the discount rate, I also did comparative simulations for species prices and harvest costs, the results of which are reported in Figure 14-17 in Appendix 17-21. The first thing I look at is the own price elasticity on harvesting. Economic intuition expects a positive own price elasticity, which is supported by the numerical results mapped into graphs in Appendix 17. In the first graph of Figure 14a, a higher pollock price is linked to a higher pollock harvest over time. Similar reasoning applies to the

harvesting of pacific cod and is supported by the numerical graph in Figure 15 (second graph) where higher cod price is associated with higher cod harvest.

While the own price elasticity is straightforward, the cross price elasticity, however, is not so clear-cut. As seen in the first graph of Figure 15, a higher cod price accompanies a lower pollock harvest for most of the time, which indicates a negative cross price affect. But in the second graph of Figure 14 in which the influence of pollock price on the cod harvest is reported, at first a higher pollock price is associated with a lower cod harvest, then a higher one. While the ambiguity of the cross price effect is probably caused by complex ecological interactions between pollock and cod, analysis in Section 4.2 can help us to better understand how the ecological interactions influence the cross price elasticity here.

Recall that first order conditions for optimal harvesting include:

$$p_4 - \frac{\partial C_4}{\partial h_4} = \left(\frac{1}{1+\delta}\right)\lambda_4^{t+1} \quad (31)$$

$$p_{13} - \frac{\partial C_{13}}{\partial h_{13}} = \left(\frac{1}{1+\delta}\right)\lambda_{13}^{t+1} \quad (32)$$

and

$$\begin{aligned} \lambda_m^t = & -\frac{\partial C_m(h_m^t, N_m^t)}{\partial N_m} + \left(\frac{1}{1+\delta}\right)\lambda_m^{t+1} \left(1 + \frac{\partial RG_m^t(N^t, N^{t-1}, N^{t-2})}{\partial N_m}\right) + \sum_{\substack{j=1 \\ \text{and} \\ j \neq m}}^{13} \left(\frac{1}{1+\delta}\right)\lambda_j^{t+1} \frac{\partial RG_j^t(N^t, N^{t-1}, N^{t-2})}{\partial N_m} \\ & + \left(\frac{1}{1+\delta}\right)^2 (\lambda_m^{t+2} \frac{\partial RG_m^{t+1}(N^{t+1}, N^t, N^{t-1})}{\partial N_m} + \sum_{\substack{j=1 \\ \text{and} \\ j \neq m}}^{13} \lambda_j^{t+2} \frac{\partial RG_j^{t+1}(N^{t+1}, N^t, N^{t-1})}{\partial N_m}) \\ & + \left(\frac{1}{1+\delta}\right)^3 (\lambda_m^{t+3} \frac{\partial RG_m^{t+2}(N^{t+2}, N^{t+1}, N^t)}{\partial N_m} + \sum_{\substack{j=1 \\ \text{and} \\ j \neq m}}^{13} \lambda_j^{t+3} \frac{\partial RG_j^{t+2}(N^{t+2}, N^{t+1}, N^t)}{\partial N_m}) \end{aligned} \quad (33)$$

From (33), we can derive

$$\begin{aligned}
\lambda_4^t = & -\frac{\partial C_4(h_4^t, N_4^t)}{\partial N_4} + \left(\frac{1}{1+\delta}\right)\lambda_4^{t+1} \left(1 + \frac{\partial RG_4^t(N^t, N^{t-1}, N^{t-2})}{\partial N_4}\right) \\
& + \left(\frac{1}{1+\delta}\right) \left(\lambda_{13}^{t+1} \frac{\partial RG_{13}^t(N^t, N^{t-1}, N^{t-2})}{\partial N_4} + \sum_{\substack{j=1 \\ \text{and} \\ j \neq 4,13}}^{13} \left(\frac{1}{1+\delta}\right)\lambda_j^{t+1} \frac{\partial RG_j^t(N^t, N^{t-1}, N^{t-2})}{\partial N_4}\right) \\
& + \left(\frac{1}{1+\delta}\right)^2 \left(\lambda_4^{t+2} \frac{\partial RG_4^{t+1}(N^{t+1}, N^t, N^{t-1})}{\partial N_4} + \lambda_{13}^{t+2} \frac{\partial RG_{13}^t(N^t, N^{t-1}, N^{t-2})}{\partial N_4} + \sum_{\substack{j=1 \\ \text{and} \\ j \neq 4,13}}^{13} \lambda_j^{t+2} \frac{\partial RG_j^{t+1}(N^{t+1}, N^t, N^{t-1})}{\partial N_4}\right) \\
& + \left(\frac{1}{1+\delta}\right)^3 \left(\lambda_4^{t+3} \frac{\partial RG_4^{t+2}(N^{t+2}, N^{t+1}, N^t)}{\partial N_4} + \lambda_{13}^{t+3} \frac{\partial RG_{13}^t(N^t, N^{t-1}, N^{t-2})}{\partial N_4} + \sum_{\substack{j=1 \\ \text{and} \\ j \neq 4,13}}^{13} \lambda_j^{t+3} \frac{\partial RG_j^{t+2}(N^{t+2}, N^{t+1}, N^t)}{\partial N_4}\right)
\end{aligned} \tag{52}$$

and

$$\begin{aligned}
\lambda_{13}^t = & -\frac{\partial C_{13}(h_{13}^t, N_{13}^t)}{\partial N_{13}} + \left(\frac{1}{1+\delta}\right)\lambda_{13}^{t+1} \left(1 + \frac{\partial RG_{13}^t(N^t, N^{t-1}, N^{t-2})}{\partial N_{13}}\right) \\
& + \left(\frac{1}{1+\delta}\right) \left(\lambda_4^{t+1} \frac{\partial RG_{13}^t(N^t, N^{t-1}, N^{t-2})}{\partial N_{13}} + \sum_{\substack{j=1 \\ \text{and} \\ j \neq 4,13}}^{13} \left(\frac{1}{1+\delta}\right)\lambda_j^{t+1} \frac{\partial RG_j^t(N^t, N^{t-1}, N^{t-2})}{\partial N_{13}}\right) \\
& + \left(\frac{1}{1+\delta}\right)^2 \left(\lambda_{13}^{t+2} \frac{\partial RG_{13}^{t+1}(N^{t+1}, N^t, N^{t-1})}{\partial N_{13}} + \lambda_4^{t+2} \frac{\partial RG_4^t(N^t, N^{t-1}, N^{t-2})}{\partial N_{13}} + \sum_{\substack{j=1 \\ \text{and} \\ j \neq 4,13}}^{13} \lambda_j^{t+2} \frac{\partial RG_j^{t+1}(N^{t+1}, N^t, N^{t-1})}{\partial N_{13}}\right) \\
& + \left(\frac{1}{1+\delta}\right)^3 \left(\lambda_{13}^{t+3} \frac{\partial RG_{13}^{t+2}(N^{t+2}, N^{t+1}, N^t)}{\partial N_{13}} + \lambda_4^{t+3} \frac{\partial RG_4^t(N^t, N^{t-1}, N^{t-2})}{\partial N_{13}} + \sum_{\substack{j=1 \\ \text{and} \\ j \neq 4,13}}^{13} \lambda_j^{t+3} \frac{\partial RG_j^{t+2}(N^{t+2}, N^{t+1}, N^t)}{\partial N_{13}}\right)
\end{aligned} \tag{53}$$

Working together, equation (31), (32), (52) and (53) can partially explain the irregular cross price elasticity observed in Figure 14 and 14. Consider how the cod price influences the optimal pollock harvest as an example. Although  $p_{13}$  does not appear in equation (31) directly, it has an effect on the pollock harvesting,  $h_4$ , through the shadow price of the pollock in next period,  $\lambda_4^{t+1}$ , which is connected to  $\lambda_{13}^t$  through equation (53).  $\lambda_{13}^t$ , the shadow price of the Pacific cod is in turn associated with the cod price according to equation (32). Note that the foregoing analysis only partially explains the ambiguous cross price elasticity because besides

the direct connections between those first order conditions corresponding to two species, there are also indirect connections between cod and pollock through the shadow prices of other species in the ecosystem according to equation (33).

The impact of the cod price on the pollock harvesting can also be explained in a more intuitive way if we refer to the ecosystem food web presented in Figure 1. When the price of cod increases, the owner is tempted to harvest more cod. This increase in cod harvest driven by higher cod price has at least two effects on the pollock harvest. 1) It decreases pollock harvest because both cod and pollock are prey to a common predator, sea lion. Increased cod harvest leads to decreased cod biomass, which causes the sea lion to switch to pollock the population of which will be decreased accordingly. Because of the marginal stock effect discussed before, the owner will reduce the pollock harvest. 2) The increase in cod price increases cod harvest because there is also predator-prey relationship between cod and pollock. Increased harvest of cod from a higher cod price decreases the cod biomass, which leads to increased population in its prey (pollock). More pollock in turn implies higher harvest of pollock. Beside the two conflicting effects we just discussed, there also exist other indirect effects according to Figure 1. For example, a changing cod price can also be connected to a changing pollock harvest by herring, which has a common predator with cod and pollock, and a zooplankton, which is prey to both herring and pollock.

Similar analysis can apply to the comparative simulations for the species costs as illustrated in Figure 16 and 16 in Appendix 19 and 21 respectively. Again, I find that the harvest cost of both species have clear negative affect on their own harvest but the cross affects are vague. Figure 18 in Appendix 21 reports the comparative analysis of the minimum safety constraint on sea lion. The owner generally harvests slightly more in the low minimum safety case than in the high one. Although this is

intuitively true and supported by Figure 18, the optimal harvesting path is not very sensitive to the constraint because of the set up of the model and its parameters. A different model may yield more observable responses. This can be an interesting extension in future research. Imagine an optimization case in which the discounting rate is much higher than the example here so that it is optimal for the owner to harvest much faster (higher harvesting now and lower in the future). However, since both fish are prey to the sea lion, harvesting more fish will reduce the population of the sea lion. Although there is no direct quota on the fishing, a bounded minimum safety constraint actually sets a cap on the maximum amount of harvesting.

What is worth mentioning here is that although the analyses given in this section apply to this particular problem only, the methodology, the way we incorporate the economy and the ecosystem, can be applied in general cases.

#### **4.4 Summary and Conclusion**

The primary focus of this chapter is on completing the answer to the second question raised in the introduction chapter: how to effectively incorporate variables in one model in the other when incorporate GEEM with economic models?

A theoretical multispecies model with the R-GEEM as the updating constraints is set up and the maximum principles are analyzed first, then the model is applied to the fishery management in the Eastern Bering Sea with real data, assuming sole property right.

The simulation results show that in this particular profit maximization problem, 1) compared with the multispecies optimal harvests, the single species approach tends to over-harvest the resources; and 2) parameters in the optimization problem have

important effects on the harvest choice and ecosystem dynamics, as predicted by the maximum principles of the theoretic model.

The methodology used in this chapter can be applied in general case given necessary data available.

## Chapter 5

### CONCLUSIONS

This chapter summarizes the main contributions made by this dissertation and suggests some directions for further research.

The research presented in this dissertation focuses on answering the two questions raised in **Chapter 1**: how to improve the GEEM as a realistic population model, and how to efficiently incorporate GEEM in economic models.

**Chapter 2** answers the first question by extending GEEM from an 8 to a 13-species marine system with several multiple predator-prey relations, and provides simulations of the ecosystem dynamics under various influences, especially human activities. Functional and numerical responses in the ecosystem are identified and discussed. This chapter contributes to ecological as well as economic research.

**Chapter 3** uses vector autoregression (VAR) to derive a linear dynamic population model for interactive species, the reduced form of GEEM. The stability of the R-GEEM is discussed and the resemblance of GEEM and R-GEEM are tested using three methods: mathematical, graphic, and statistical. All tests indicate that R-GEEM is a good estimate of the GEEM.

**Chapter 4** applies R-GEEM to the dynamic optimization problem with multiple species harvesting and endangered species protection plans. This chapter provides both theoretical and empirical examples of the GEEM applications in resource management and jointly with Chapter 3 completes the answer to the second question raised in Chapter 1 on the integrating of GEEM with an economics model in application.

In many ways, the research reported here is only a first step. In spite of being quite extensive, several interesting questions have been left aside in this paper:

comparing GEEM simulations with real data or simulations from other population models, making GEEM an ecological individual based model by allowing heterogeneous individuals within a species, introducing uncertainty into GEEM or assuming imperfect information for economic agent, considering more complicated economic models such as economies with a richer endogenous dynamics or CGE model, etc. These are some of the interesting extensions of this work.

## Appendix 1

### Net Energy Objective Functions for Representative Individuals

Phytoplankton (labeled as species 1):

$$R_1 = (e_{0,1} - e_{1,0})x_{1,0} - r_1 x_{1,0}^2 - d_{1,2}e_1(1 + t_1 e_{2,1})x_{1,0}^5 - b_1;$$

Zooplankton (labeled as species 2):

$$R_2 = (e_1 - e_{2,1})x_{2,1} - r_2 x_{2,1}^2 - d_{2,4}e_2(1 + t_2 e_{4,2})x_{2,1}^5 - d_{2,9}e_2(1 + t_2 e_{9,2})x_{2,1}^5 - d_{2,11}e_2(1 + t_2 e_{11,2})x_{2,1}^5 - b_2;$$

Kelp (labeled as species 3):

$$R_3 = (e_{0,3} - e_{3,0})x_{3,0} - r_3 x_{3,0}^2 - d_{3,5}e_3(1 + t_3 e_{5,3})x_{3,0}^5 - b_3;$$

Pollock (labeled as species 4):

$$R_4 = (e_2 - e_{4,2})x_{4,2} - r_4 x_{4,2}^2 - d_{4,6}e_4(1 + t_4 e_{6,4})x_{4,2}^5 - d_{4,10}e_4(1 + t_4 e_{10,4})x_{4,2}^5 - d_{4,13}e_4(1 + t_4 e_{13,4})x_{4,2}^5 - d_{4,8}e_4(1 + t_4 e_{8,4})x_{4,2}^5 - b_4$$

Sea urchin (labeled as species 5):

$$R_5 = (e_3 - e_{5,3})x_{5,3} - r_5 x_{5,3}^2 - d_{5,7}e_5(1 + t_5 e_{7,5})x_{5,3}^5 - b_5;$$

Sea lion (labeled as species 6):

$$R_6 = (e_4 - e_{6,4})x_{6,4} + (e_9 - e_{6,9})x_{6,9} + (e_{13} - e_{6,13})x_{6,13} - r_6(x_{6,4} + x_{6,9} + x_{6,13}) - .5r_6(x_{6,4}^2 + x_{6,9}^2 + x_{6,13}^2 + x_{6,4}x_{6,9} + x_{6,4}x_{6,13} + x_{6,9}x_{6,13}) - d_{6,8}e_6(1 + t_6 e_{8,6})(x_{6,4} + x_{6,9} + x_{6,13})^5 - b_6;$$

Sea Otter (labeled as species 7):

$$R_{07} = (e_{05} - e_{0705})x_{0705} - r_{07}x_{0705}^2 - d_{0708}e_{07}(1 + t_{07}e_{0807})x_{0705}^5 - b_{07};$$

Killer Whale (labeled as species 8):

$$R_8 = (e_4 - e_{8,4})x_{8,4} + (e_6 - e_{8,6})x_{8,6} + (e_7 - e_{8,7})x_{8,7} + (e_9 - e_{8,9})x_{8,9} + (e_{10} - e_{8,10})x_{8,10} + (e_{12} - e_{8,12})x_{8,12} + (e_{11} - e_{8,11})x_{8,11} - r_8(x_{8,4} + x_{8,6} + x_{8,7} + x_{8,9} + x_{8,10} + x_{8,11} + x_{8,12}) - .5r_8(x_{8,4}^2 + x_{8,6}^2 + x_{8,7}^2 + x_{8,9}^2 + x_{8,10}^2 + x_{8,11}^2 + x_{8,12}^2 + x_{8,4}x_{8,6} + x_{8,4}x_{8,7} + x_{8,4}x_{8,9} + x_{8,4}x_{8,10} + x_{8,4}x_{8,11} + x_{8,4}x_{8,12} + x_{8,6}x_{8,7} + x_{8,6}x_{8,9} + x_{8,6}x_{8,10} + x_{8,6}x_{8,11} + x_{8,6}x_{8,12} + x_{8,7}x_{8,9} + x_{8,7}x_{8,10} + x_{8,7}x_{8,11} + x_{8,7}x_{8,12} + x_{8,9}x_{8,10} + x_{8,9}x_{8,11} + x_{8,9}x_{8,12} + x_{8,10}x_{8,11} + x_{8,10}x_{8,12} + x_{8,11}x_{8,12}) - b_8$$

Herring (labeled as species 9):

$$R_9 = (e_2 - e_{9,2})x_{9,2} - r_9 x_{9,2}^2 - d_{9,6}e_9(1 + t_9 e_{6,9})x_{9,2}^5 - d_{9,8}e_9(1 + t_9 e_{8,9})x_{9,2}^5 - d_{9,10}e_9(1 + t_9 e_{10,9})x_{9,2}^5 - b_9$$

Northern Fur Seal (labeled as species 10):

$$R_{10} = (e_4 - e_{10,4})x_{10,4} + (e_9 - e_{10,9})x_{10,9} - r_{10}(x_{10,4} + x_{10,9}) - 5r_{10}(x_{10,4}^2 + x_{10,9}^2 + x_{10,4}x_{10,9}) - d_{10,8}e_{10}(1 + t_{10}e_{8,10})(x_{10,4} + x_{10,9})^5 - b_{10}$$

Blue whale (labeled as species 11):

$$R_{11} = (e_2 - e_{11,2})x_{11,2} - r_{11}x_{11,2}^2 - d_{11,8}e_{11}(1 + t_{11}e_{8,11})x_{11,2}^5 - b_{11}$$

Sperm Whale (labeled as species 12):

$$R_{12} = (e_{12} - e_{12,13})x_{12,13} - d_{12,8}e_{12}(1 + t_{12}e_{12,13})x_{12,13}^5 - r_{12}x_{12,13}^2 - b_{12}$$

Pacific Cod (labeled as species 13):

$$R_{13} = (e_4 - e_{13,4})x_{13,4} - r_{13}x_{13,4}^2 - d_{13,6}e_{13}(1 + t_{13}e_{6,13})x_{13,4}^5 - d_{13,12}e_{13}(1 + t_{13}e_{12,13})x_{13,4}^5 - b_{13}$$

## Appendix 2

### Supply-Demand Equilibrium Equations

$$\tau_1 Area_0 = N_1 x_{1,0}$$

$$N_2 x_{2,1} = N_1 d_{1,2} x_{1,0}^5$$

$$\tau_3 Area_3 = N_3 x_{3,0}$$

$$N_4 x_{4,2} = N_2 d_{2,4} x_{2,1}^5$$

$$N_5 x_{5,3} = N_3 d_{3,5} x_{3,0}^5$$

$$N_6 x_{6,4} = N_4 d_{4,6} x_{4,2}^5$$

$$N_6 x_{6,9} = N_9 d_{9,6} x_{9,2}^5$$

$$N_6 x_{6,13} = N_{13} d_{13,6} x_{13,4}^5$$

$$N_7 x_{7,5} = N_5 d_{5,7} x_{5,3}^5$$

$$N_8 x_{8,4} = N_4 d_{4,8} x_{4,2}^5$$

$$N_8 x_{8,6} = N_6 d_{6,8} (x_{6,4} + x_{6,9} + x_{6,13})^5$$

$$N_8 x_{8,7} = N_7 d_{7,8} x_{7,5}^5$$

$$N_8 x_{8,9} = N_9 d_{9,8} x_{9,2}^5$$

$$N_8 x_{8,10} = N_{10} d_{10,8} (x_{10,4} + x_{10,9})^5$$

$$N_8 x_{8,11} = N_{11} d_{11,8} x_{11,4}^5$$

$$N_8 x_{8,12} = N_{12} d_{12,8} x_{12,13}^5$$

$$N_9 x_{9,2} = N_2 d_{2,9} x_{2,1}^5$$

$$N_{10} x_{10,4} = N_4 d_{4,10} x_{4,2}^5$$

$$N_{10} x_{10,9} = N_9 d_{9,10} x_{9,2}^5$$

$$N_{11} x_{11,2} = N_2 d_{2,11} x_{2,1}^5$$

$$N_{12} x_{12,13} = N_{13} d_{13,12} x_{13,4}^5$$

$$N_{13} x_{13,4} = N_4 d_{4,13} x_{4,2}^5$$

### Appendix 3

**Table 1: The Parameters Calibration Table**

	Variables		Parameters							
	Populations $N_i^a$ (units $\text{km}^{-2}$ )	Biomass or Biomass Flow $x_{ij}$	Embodied Energy $e_i$	Light Absorption $e_{0i}$	Resting Metabolic Rate $b_i$	Weight $w_i$	Predation $d_{ij}^{bq}$		Plant Congestion $\tau_i^{br}$	Var. Resp. $r_i^{bs}$ (kcal $\text{yr}^{-1}$ )
PHYTOPLANKTON	87.692 <sup>3b</sup> 1 unit = $1 \times 10^{12}$ ind.	435.6 <sup>0</sup> kg $\text{unit}^{-1}$	400 <sup>ad</sup> kcal $\text{kg}^{-1}$	15150 <sup>an</sup> kcal $\text{kg}^{-1} \text{yr}^{-1}$	395,939 <sup>aq</sup> kcal $\text{unit}^{-1} \text{yr}^{-1}$	435.6 <sup>bd</sup> kg $\text{unit}^{-1}$	PREDATOR	$d_{ij}$	0.029	5.640
							ZOOPLANKTON	158.093		
ZOOPLANKTON	162.30 <sup>8c</sup> 1 unit = $1 \times 10^9$ ind.	1782.7 <sup>p</sup> kg $\text{unit}^{-1} \text{y}^{-1}$	559 <sup>ae</sup> kcal $\text{kg}^{-1}$	NA <sup>ao</sup>	178270 <sup>ar</sup> kcal $\text{unit}^{-1} \text{yr}^{-1}$	3.75 <sup>7be</sup> kg $\text{unit}^{-1}$	PREDATOR	$d_{ij}$	NA	0.084
							POLLOCK	6.690		
							HERRING	0.721		
							BLUE WHALE	0.002		
POLLOCK	6.1621 <sup>5d</sup> 1 unit = 1000 ind.	7440 <sup>q</sup> kg $\text{unit}^{-1} \text{y}^{-1}$	1128 <sup>af</sup> kcal $\text{kg}^{-1}$	NA <sup>ao</sup>	1247688 <sup>as</sup> kcal $\text{unit}^{-1} \text{yr}^{-1}$	1000 <sup>bf</sup> kg $\text{unit}^{-1}$	PREDATOR	$d_{ij}$	NA	0.024
							NORTH HERN FUR SEAL	0.035		
							SEA LION	0.482		
							KILLER WHALE	0.024		
							PACIFIC COD	0.672		
SEA LION	0.0961 <sup>54e</sup> 1 unit = 1 ind	PREY	$x_{ij}$ (kg $\text{unit}^{-1} \text{y}^{-1}$ )	2000 <sup>ag</sup> kcal $\text{kg}^{-1}$	NA <sup>ao</sup>	853214 <sup>at</sup> kcal $\text{yr}^{-1}$	250 <sup>g</sup> kg	0.579	NA	0.210
		POLLOCK	2663 <sup>r</sup>							
		HERRING	132.94 <sup>s</sup>							
		PACIFIC COD	299.74 <sup>s</sup>							

KILLER WHALE	0.0077 <sup>f</sup> 1 unit = 0.1 ind.	PREY	$x_{ij}$ (kg unit <sup>-1</sup> ·y <sup>-1</sup> )	NA	NA <sup>ao</sup>	651780 <sup>au</sup> kcal unit <sup>-1</sup> yr <sup>-1</sup>	399. <sup>6bh</sup> kg unit <sup>-1</sup>	NA	NA	0.275	
		SEA LION	401.0985 <sup>t</sup>								
		SEA OTTER	221.6014 <sup>t</sup>								
		SPERM WHALE	12.03637 <sup>3</sup>								
		BLUE WHALE	0.048635 <sup>t</sup>								
		NORTHERN FUR SEAL	168.5885 <sup>50</sup>								
		HERRING	82.81998 <sup>6</sup>								
		POLLOCK	1659.079 <sup>7</sup>								
SEA OTTER	0.0506 <sup>31g</sup> 1 unit = 100 ind.	255,500 <sup>v</sup> kg unit <sup>-1</sup> y <sup>-1</sup>		1810 <sup>ah</sup> kcal kg <sup>-1</sup>	NA <sup>ao</sup>	32193000 <sup>a</sup> kcal unit <sup>-1</sup> yr <sup>-1</sup>	2800 <sup>bi</sup> kg unit <sup>-1</sup>	0.067	NA	0.0005	
URCHIN	10.769 <sup>2h</sup> 1 unit = 1 x 10 <sup>7</sup> ind.	330,000 <sup>w</sup> kg unit <sup>-1</sup> y <sup>-1</sup>		717 <sup>ai</sup> kcal kg <sup>-1</sup>	NA <sup>ao</sup>	67732500 <sup>a</sup> kcal unit <sup>-1</sup> yr <sup>-1</sup>	8760 <sup>0bj</sup> kg unit <sup>-1</sup>	2.082	NA	0.0006	
KELP	1076.9 <sup>2i</sup> 1 unit = 1x10 <sup>4</sup> ind.	21024 <sup>x</sup> kg unit <sup>-1</sup>		821 <sup>aj</sup> kcal kg <sup>-1</sup>	650 <sup>ap</sup> kcal kg <sup>-1</sup> yr <sup>-1</sup>	819936 <sup>ax</sup> kcal unit <sup>-1</sup> yr <sup>-1</sup>	2102 <sup>4bk</sup> kg unit <sup>-1</sup>	22.966	870.814	0.0006	
SPERM WHALE	0.63 <sup>j</sup> 1 unit = 0.01 ind.	23.03 <sup>y</sup> kg unit <sup>-1</sup> y <sup>-1</sup>		2000 <sup>ak</sup> kcal kg <sup>-1</sup>	NA <sup>ao</sup>	94.78 <sup>ay</sup> kcal unit <sup>-1</sup> yr <sup>-1</sup>	280 <sup>bl</sup> kg unit <sup>-1</sup>	0.031	NA	0.480	
NORTHERN FUR SEAL	0.088 <sup>k</sup> 1 unit = 1 ind.	PREY	$x_{ij}$ (kg unit <sup>-1</sup> ·y <sup>-1</sup> )	2000 <sup>ak</sup> kcal kg <sup>-1</sup>	NA <sup>ao</sup>	1042.40 <sup>az</sup> kcal unit <sup>-1</sup> yr <sup>-1</sup>	135 <sup>bm</sup> kg unit <sup>-1</sup>	0.940099	NA	0.637	
		POLLOCK	210.51 <sup>z</sup>								
		HERRING	37.15 <sup>z</sup>								
PACIFIC COD	2.2323	160 <sup>aa</sup>		1050 <sup>al</sup>	NA <sup>ao</sup>	54144 <sup>ba</sup> kcal unit <sup>-1</sup>	310 <sup>bn</sup>	PREDATOR	d <sub>ij</sub>	NA	2.529

	87 <sup>l</sup> 1 unit = 100 ind.	kg unit <sup>-1</sup> y <sup>-1</sup>	kcal kg <sup>-1</sup>		yr <sup>-1</sup>	kg unit <sup>-1</sup>	SEA LION	1.021		
							SPER M WHALE	0.514		
HERRING	1.709 <sup>m</sup> 1 unit = 1000 ind.	2890.8 <sup>ab</sup> kg unit <sup>-1</sup> y <sup>-1</sup>	1950 <sup>am</sup> kcal kg <sup>-1</sup>	NA <sup>ao</sup>	484787 <sup>bb</sup> kcal unit <sup>-1</sup> yr <sup>-1</sup>	180 <sup>bo</sup> kg unit <sup>-1</sup>	PREDATOR	d <sub>ij</sub>	NA	0.05 9
							SEA LION	0.139		
							KILLER WHALE	0.007		
							NORT HERN FUR SEAL	0.036		
BLUE WHALE	0.0254 <sup>n</sup> 1 unit = 0.001 ind.	432 <sup>ac</sup> kg unit <sup>-1</sup> y <sup>-1</sup>	2000 <sup>ak</sup> kcal kg <sup>-1</sup>	NA <sup>ao</sup>	1574.94 <sup>bc</sup> kcal unit <sup>-1</sup> yr <sup>-1</sup>	64.3 48 <sup>bp</sup> kg unit <sup>-1</sup>	0.0007		NA	0.00 9

### Notes

NA – not applicable or not needed.

<sup>a</sup> Individuals are aggregated into population units and the units are divided by ocean surface area to yield population units per square kilometer. Pelagic populations are divided by  $1.3 \times 10^6$  km<sup>2</sup>, the approximate area of the EBS, and nearshore populations are divided by 26,000 km<sup>2</sup>, the approximate area along the Aleutian Islands. Killer whales are divided by both areas.

<sup>b</sup> An aggregate of multiple phytoplankton producer and saprophage species (Petipa et al. 1970, Table 1). The data are from the Black Sea but assumed to be transferable to the EBS. Populations in Petipa et al. are given in individuals per square meter; thus, when extrapolating to the EBS, the number of individuals is in an unmanageable sextillions. Consequently for phytoplankton and other species in Table 1 populations are converted to population units, then placed on a square kilometer basis.

<sup>c</sup> An aggregate of multiple zooplankton herbivore species (Petipa et al. 1970, Table 1) The data are from the Black Sea but assumed to be transferable to the EBS.

<sup>d</sup> Finnoff and Tschirhart (2003), page 170.

<sup>e</sup> The Stellar sea lion population was estimated to be 125,000 (NMFS 2000), and on a km<sup>2</sup> basis:  $125,000/1,300,000 \text{ km}^2 = 0.096154$ .

<sup>f</sup> Based on 1024 individuals (NMFS 2000). Because killer whale habitat includes both ocean and nearshore systems, the population was divided by 1,300,000 + 26,000 to put on a square kilometer basis.

<sup>g</sup> Based on 131,631 individuals extrapolated from Estes and Duggins (1995) estimates of populations in Aleutians island groups.

<sup>h</sup> Individuals from multiple sea urchin species at 153 randomly selected sites in the Aleutians (Estes and Duggins 1995).

<sup>i</sup> Kelp density of multiple species is about 10% of urchin at the same 153 sites in the Aleutians (Estes and Duggins 1995).

<sup>j</sup> Based on  $1,900,000 * 0.62 * 0.04 = 47120$  individuals in Northeast Pacific. The area is 7,503,000 km<sup>2</sup>. So the population on a km<sup>2</sup> basis is 0.0063 individual, or 0.63 units (Trites et al. 1997).

<sup>k</sup> Based on  $1,200,000 * 0.55 = 660,000$  individuals in Northeast Pacific (Trites et al. 1997).

<sup>l</sup> Pacific cod biomass estimates for the year 1980 are  $9 \times 10^8$  kgs (The Bering Sea Ecosystem 1996, pg 91). This is 692.3 Kg/ km<sup>2</sup>. The average weight of Pacific cod is 3.1 Kg ([http://atn-riac.agr.ca/seafood/mini\\_pacific\\_cod-e.htm](http://atn-riac.agr.ca/seafood/mini_pacific_cod-e.htm)). So the population density is 2.232387 units/ km<sup>2</sup>.

<sup>m</sup> Herring biomass estimates for the year 1980 are  $4 \times 10^8$  kgs (The Bering Sea Ecosystem 1996, pg 106). This is 307.69 Kg/ km<sup>2</sup>, which is 1709.4 ind./ km<sup>2</sup> since the average weight of herring is 0.18 Kg ( bo).

<sup>n</sup> Based on  $14,000 * 0.34 * 0.04 = 190.4$  individuals in Northeast Pacific (Trites et al. 1997).

<sup>o</sup> A weighted average of phytoplankton species' body weights ( $4.35615 \times 10^{-10}$  kg., Petipa et al. 1970, Table 1), in units of  $1 \times 10^{12}$  phytoplankton.

<sup>p</sup> A weighted average of zooplankton species indicates an individual weighs  $3.757 \times 10^{-6}$  gm. and consumes 130% of its weight in phytoplankton per day (Petipa et al. 1970, Table 1). This yields a consumption of  $1782.7 \text{ kg unit}^{-1} \text{ yr}^{-1}$ .

<sup>q</sup> Trites et al. (1997) p. 186. pollock eat mostly zooplankton (Witherell 2000) although adults may eat smaller fish including juvenile pollock. Here their diet is assumed to be 80% zooplankton.

<sup>r</sup> From Appendix D, SAFE, in 1990s Steller diet was 76% fish, of which 69% was groundfish and we assume 60% was pollock. Therefore, of the 5840 kg/yr taken by an individual sea lion (based on Rosen and Trites 2000), the pollock consumption was  $(.76) (.60) (5840) = 2663 \text{ kg/yr}$ .

<sup>s</sup> According to Table 4.9 in *The Bering Sea Ecosystem*, 1996, Stellar sea lion's major prey types include Demersal fishes, pelagic and semidemersal fishes. In our foodweb, the sea lion's major prey include pollock, herring, and Pacific cod. We assume that the proportions of those prey in the sea lion's diet are the same as the proportion of their biomass in the EBS area.

<sup>t</sup> Killer whale's major prey types include demersal fishes, octopus and squids, and marine mammals (*The Bering Sea Ecosystem*, 1996, Table 4.10). 65% of its diet are fishes, 20% are squids, and 15% are mammals. It eats 3-4% of its body weight daily. So every unit of the killer whale eats  $399.6 \times 3.5\% \times 365 \times 15\% = 765.73$  kg marine mammals ([www.seaworld.org](http://www.seaworld.org)) per year. We assume that around 1980 the proportions of marine mammals in the killer whale diet was the same as the proportions of their populations in the sum of the populations of all marine mammals in the EBS region as reported in Trites et al. (1997).

<sup>u</sup> Yearly consumption of fishes by a unit of killer whale is  $399.6 \times 3.5\% \times 365 \times 65\% = 3318.16$  kg. 59% of the total biomass of all groundfish in EBS is pollock. We assume that proportions of fishes in the sea lion's diet are the same as the proportion of their biomass.

<sup>v</sup> Otter eat 20-30% of body weight per day and on average an adult weighs 28 kg. (Costa 1978). Otter eat mostly sea urchins (Mason and Macdonald 1986), and here they are assumed to eat only sea urchins.

<sup>w</sup> Urchin weighing 0.00876 kg are assumed to grow by 38% in one year to 0.01201 (Estes and Duggins 1995, Table 11). This implies production of 0.003329 and if they consume ten times their production implies 0.03329 of biomass flow per individual. This is rounded to 333000 per population unit.

<sup>x</sup> Average biomass of an urchin is 0.00876 kg (Estes and Duggins 1995) and multiplied by the urchin population (vii) yields 943382 kg for the population. Assuming prey biomass is 1.2 times predator biomass (Kerr 1974), and assuming 5% of predation on kelp is by sea urchin, yields a biomass for kelp of  $943382 \times (1.2) / 0.05$ . Per population unit this is 21024 kg.

<sup>y</sup> Sperm whale's major prey type is demersal fish, which is Pacific cod in our foodweb. The total estimated annual food consumption by the population in the EBS is  $952.8 \times 10^6$  kgs, of which  $171.5 \times 10^6$  kgs (18%) is fish (Perez and McAlister 1993). 11% of catch in the Alaska groundfish fishery is Pacific cod. So we assume that 11% of fish in the sperm whale's diet is Pacific cod, which gives us  $23.03 \text{ kg unit}^{-1} \text{ y}^{-1}$ .

<sup>z</sup> Northern fur seal's diet includes Waleye pollock, Pacific salmon, Northern smoothtongue, Pacific herring, Pacific sand lance, *Gonatopsis borealis/berryteuthis magister*, *Gonatus madokai*/ *Gonatus middendorffi*, etc (National Marine Mammal Laboratory). Trites (1992) estimated 133,000,000 kg of pollock are consumed by northern fur seals in the EBS. So the biomass flow from pollock to northern fur seal is  $133,000,000 / 660,000 = 210.51 \text{ kg unit}^{-1} \text{ y}^{-1}$ .

<sup>aa</sup> In the Gulf of Alaska, Pacific cod's major diets include capelin, pollock (21%), pandalids, misc. fish, euphausiids, crabs, ect. (Yang 2004, Figure 5). On average, a typical Pacific cod consume  $2715 \times 0.21 / 130 = 4.38$  g pollock, which give the yearly biomass of  $160 \text{ kg unit}^{-1} \text{ y}^{-1}$ .

<sup>ab</sup> Trites et al. (1997) p. 186. Herring feed primarily on zooplankton such as copepods and other crustaceans. Their Consumption/biomass ratio is adapted from Pauly (1989).

<sup>ac</sup> A blue whale preys primarily on large zooplankton (Pauly, 1998) and eats 3,600 kg of krill (one of zooplankton groups) each day for about 120 days, which is  $432 \text{ kg unit}^{-1} \text{ y}^{-1}$ . From <http://www.buschgardens.org/infobooks/Baleen/dietbw.html>, and Zooplankton Laboratory, Fisheries and Oceans Canada, [http://www.pac.dfo-mpo.gc.ca/sci/OSAP/projects/plankton/zoolab\\_e.htm](http://www.pac.dfo-mpo.gc.ca/sci/OSAP/projects/plankton/zoolab_e.htm).

<sup>ad</sup> Weighted average of caloricity measures of three phytoplankton species groupings (Petipa et al. 1970, Table 7).

<sup>ae</sup> Weighted average of caloricity measures of three zooplankton species groupings (Petipa et al. 1970, Table 7).

<sup>af</sup> In a captive situation,  $7.2 \text{ kg d}^{-1}$  of pollock was fed to sea lions and its energy content was  $4.72 \text{ kJ g}^{-1}$  (Rosen and Trites 2000); therefore, the kcal embodied energy in pollock is  $(4.72 \text{ kJ g}^{-1}) (1 \text{ Mcal} / 4.184 \text{ MJ}) (1 \text{ MJ} / 1000 \text{ kJ}) (1000 \text{ kcal Mcal}^{-1}) (1000 \text{ g kg}^{-1}) = 1128 \text{ kcal kg}^{-1}$ .

<sup>ag</sup> Estimated based on blubber content in a sea lion versus otter which have no blubber. (Costa 1978) (See <sup>w</sup>).

<sup>ah</sup> Estes et al. (1998).

<sup>ai</sup> Costa (1978).

<sup>aj</sup> Lembi and Waalan (1988).

<sup>ak</sup> Assume that embodied energies in the marine mammals are the same as in the sea lion.

<sup>al</sup> From [weightlossforgood.co.uk](http://weightlossforgood.co.uk).

<sup>am</sup> From [weightlossforgood.co.uk](http://weightlossforgood.co.uk).

<sup>an</sup> 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. suggest a 20% transfer rule for ocean communities. Therefore, equate 20% of the energy taken by phytoplankton to the energy taken by zooplankton:  $(20\%) N_1 x_{10} e_{01} = N_2 x_{21} e_1$  and solve to obtain  $e_{01} = 15150 \text{ kcal kg}^{-1} \text{ yr}^{-1}$ . (Note  $N_1$  is from <sup>b</sup>,  $x_{10}$  from <sup>0</sup>,  $N_2$  from <sup>c</sup>,  $x_{21}$  from <sup>p</sup> and  $e_1$  is from <sup>ae</sup>).

<sup>ao</sup> Not applicable because only plants photosynthesize.

<sup>ap</sup> Using the 20% transfer rule (See <sup>an</sup>), equate 20% of the energy taken by kelp to the energy taken by urchin:  $(20\%) N_2 x_{20} e_{02} = N_6 x_{62} e_2$  and solve to obtain  $e_{02} = 650 \text{ kcal kg}^{-1} \text{ yr}^{-1}$ .

<sup>aq</sup> An average of respiration as a % of body weight over multiple phytoplankton species yields 6%. (Petipa et al. 1970, Table 2). Incoming phytoplankton energy is  $e_{01} x_{10} = (15149.2)(435.6)$ , and 6% of this is 395,939 kcal yr<sup>-1</sup>.

<sup>ar</sup> An average of respiration as a % of body weight over multiple zooplankton species yields 25%. (Petipa et al. 1970, Table 2). Calculations are similar to <sup>aq</sup>.

<sup>as</sup> pollock are assumed to have an average respiration of 30%. Their incoming energy from zooplankton is 7440 kg unit<sup>-1</sup> y<sup>-1</sup> 559 kcal kg<sup>-1</sup> which is then multiplied by 30%.

<sup>at</sup> For mammals, resting metabolic rate in kcal d<sup>-1</sup> (M) is related to body weight (W) by the formula  $M = 67.61W^{0.756} \pm 5\%$  (Kleiber 1975). Using 250 kg as sea lion weight and extrapolating to one year yields 1603786 kcal yr<sup>-1</sup>. The RMB used in the simulations is lowered by (76%)(70%) to reflect that sea lions are preying on more than just Pollock, herring, and Pacific cod (See <sup>r</sup> and <sup>s</sup>). 70% is the approximate proportion of three fish prey of sea lion's in the EBS area's fish biomass (See <sup>t</sup>).

<sup>au</sup> Use the formula from <sup>at</sup> and an average weight of 399.6 kg. The RMB used in the simulations is lowered to 50% of this figure to reflect that killer whales are preying on more than just marine mammals and fishes in our food web (See <sup>t</sup>).

<sup>av</sup> Use the formula from <sup>bg</sup> and an average weight of 28 kg and a +5% because otter have high metabolic rates (Costa 1978).

<sup>aw</sup> Similar to the estimate in <sup>ar</sup> except urchin are assumed to respire at about 25%.

<sup>ax</sup> Calculated as in <sup>aq</sup> except algae respiration (kelp) is assumed to be 15% of the value of photosynthesis (Petipa et al. 1970, Table 2).

<sup>ay</sup> Use the formula from <sup>at</sup> and an average weight of 280 kg/unit. The RMB used in the simulations is lowered by (18%)(11%) to reflect that sperm whales are preying on more than just Pacific cod(See <sup>y</sup>.)

<sup>az</sup> Use the formula from <sup>at</sup> and an average weight of 135 kg/unit. The RMB used in the simulations is scaled by  $(210.51+37.15)*660,000/432,400,000=0.378$  to reflect that Northern fur seals are preying on more than just pollock and herring (See <sup>z</sup>.)

<sup>ba</sup> Assuming that Pacific cod has an average respiration of 30%. Their incoming energy from pollock is 160 kg unit<sup>-1</sup> y<sup>-1</sup> \*1128 kcal kg<sup>-1</sup> which is then multiplied by 30%.

<sup>bb</sup> Assuming that Pacific herring has an average respiration of 30%. Their incoming energy from zooplankton is 2890.8 kg unit<sup>-1</sup> y<sup>-1</sup>\* 559 kcal kg<sup>-1</sup> which is then multiplied by 30%.

<sup>bc</sup> Use the formula from <sup>at</sup> and an average weight of 64.348kg/unit.

<sup>bd</sup> . Finnoff and Tschirhart (2003).

<sup>be</sup> Average of multiple zooplankton herbivore species (Petipa et al. 1970, Table 1).

<sup>bf</sup> Average of adult and juvenile, both are taken by fisheries and Steller sea lions. (See <sup>d</sup>.)

<sup>bg</sup> Based on weights of immature sea lions in Rosen and Trites (2000) and adult weights in Audubon Field Guide to North American Mammals (1980).

<sup>bh</sup> Average of male and female adults is 3996 kg (Estes et al. 1998).

<sup>bi</sup> Average of male and female adults is 28 kg (Costa 1978).

<sup>bj</sup> Urchins at six locations in the Aleutians averaged 8.76 gm each with a wide variance (Estes and Duggins 1995, Table 2).

<sup>bk</sup> Kelp are plants; therefore, weight is given in <sup>x</sup>.

<sup>bl</sup> Nicole Leboeuf, Texas Marine Mammal Stranding Networking.

<sup>bm</sup> North Pacific University Marine Mammal research Consortium.

<sup>bn</sup> [http://atn-riae.agr.ca/seafood/mini\\_pacific\\_cod-e.htm](http://atn-riae.agr.ca/seafood/mini_pacific_cod-e.htm).

<sup>bo</sup> NOAA-NMFS-NWFSC TM-45: Status Review of Pacific Herring (*Clupea pallasii*) in Puget Sound, Washington, Figure 37b.

<sup>bp</sup> An average weight for an adult blue whale is about 64,348 kg ( [www.seaworld.com](http://www.seaworld.com) ).

<sup>bq</sup> In population units  $\text{km}^2$ . 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.

<sup>br</sup> 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 space.

<sup>bs</sup> In  $\text{kcal yr}^{-1}$ . Derived from calibration. The benchmark biomasses and biomass flows 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

## Appendix 4

**Table 4: Functional and Numerical Response in GEEM – Box-Cox Estimate**

Prey	Predators' Functional And Numerical Response		$\lambda(\tau)$	$\alpha(\gamma)$	$\beta(\delta)$
Phytoplankton	Zooplankton	Functional	2.00	-0.4168	18120.3
		Numerical	2.40	2608.5	999.2
Zooplankton	Pollock	Functional	2.00	-0.4304	170520
		Numerical	2.2247	-1.3555	0.2143
	Herring	Functional	2.00	-0.4870	25743.4
		Numerical	2.3110	-0.4192	2.3110
	Blue Whale	Functional	2.00	-0.5020	574.9
		Numerical	4.2359	-0.2361	2.8E-11
Kelp	Urchin	Functional	1.6538	45841846	421443
		Numerical	2.0298	4.2109	0.0647
Pollock	Sea Lion	Functional	2.00	9.7428	575406
		Numerical	2.3450	-0.4260	0.000267
	Killer Whale	Functional	2.00	3.5012	223340
		Numerical	4.06	-0.2463	4.27E-11
	Northern Fur Seal	Functional	2.00	-0.4366	3597.7
		Numerical	0.9069	-1.0043	0.00386
	Pacific Cod	Functional	2.00	-0.4634	2077.2
		Numerical	2.5585	-0.2222	0.5461
Urchin	Sea Otter	Functional	2.00	45263.1	3.0308E+9
		Numerical	3.0547	-0.2980	0.000013
Sea Lion	Killer Whale	Functional	2.00	7.8081	836561
		Numerical	1.0071	-0.9856	0.000611
Sea Otter	Killer Whale	Functional	2.00	-5.8061	484972
		Numerical	3.00	-0.333	3.577E-8
Herring	Sea Lion	Functional	2.00	-0.5009	5170.6
		Numerical	3.00	-0.333	2.298E-6
	Killer Whale	Functional	2.00	-0.4996	2006.8
		Numerical	4.1360	-0.2418	-1.61E-12
	Northern Fur Seal	Functional	2.00	-0.4917	403.8
		Numerical	3.00	-0.3331	6.101E-6
Northern Fur Seal	Killer Whale	Functional	2.00	-0.4992	161489
		Numerical	3.98	-0.2510	1.32E-10
Blue Whale	Killer Whale	Functional	2.0385	-0.4906	0.0426
		Numerical	-3.00	-730140	-9.49E-10
Sperm Whale	Killer Whale	Functional	2.00	-0.50	115
		Numerical	-3.00	-730140	1.738E-11
Pacific Cod	Sea Lion	Functional	2.00	-0.1814	20122.3
		Numerical	3.00	-0.333	4.888E-6
	Sperm Whale	Functional	2.00	-0.4881	118.8
		Numerical	0.6915	-0.4131	0.00797

Note: All functional response functions follow equation (12) and all numerical response functions

follow equation (15). All F statistics are significant at 95% level.

## Appendix 5

**Table 5: Functional Response in GEEM – Holling Type II Estimate**

Prey	Predators' Functional Response	a	b
Phytoplankton	Zooplankton	20.5026	0.00267
Zooplankton	Pollock	46.2301	0.00144
	Herring	17.9626	0.00144
	Blue Whale	2.6843	0.00144
Kelp	Urchin	311.9	0.000217
Pollock	Sea Lion	435.8	0.0380
	Killer Whale	271.5	0.0380
	Northern Fur Seal	43.4534	0.0380
	Pacific Cod	26.1867	0.0380
Urchin	Sea Otter	23927.6	0.0217
Sea Lion	Killer Whale	4207.0	2.4322
Sea Otter	Killer Whale	4414.1	4.619
Herring	Sea Lion	78.4523	0.1368
	Killer Whale	48.8747	0.1368
	Northern Fur Seal	21.9234	0.1368
Northern Fur Seal	Killer Whale	1932.1	2.6576
Blue Whale	Killer Whale	1.9291	9.1913
Sperm Whale	Killer Whale	19.2684	0.3712
Pacific Cod	Sea Lion	135.4	0.1048
	Sperm Whale	10.4044	0.1048

Note: All functional response functions follow equation (11) and All F statistics are significant at 95% level.

## Appendix 6: Functional Response From GEEM, Box-Cox, and Holling Equation

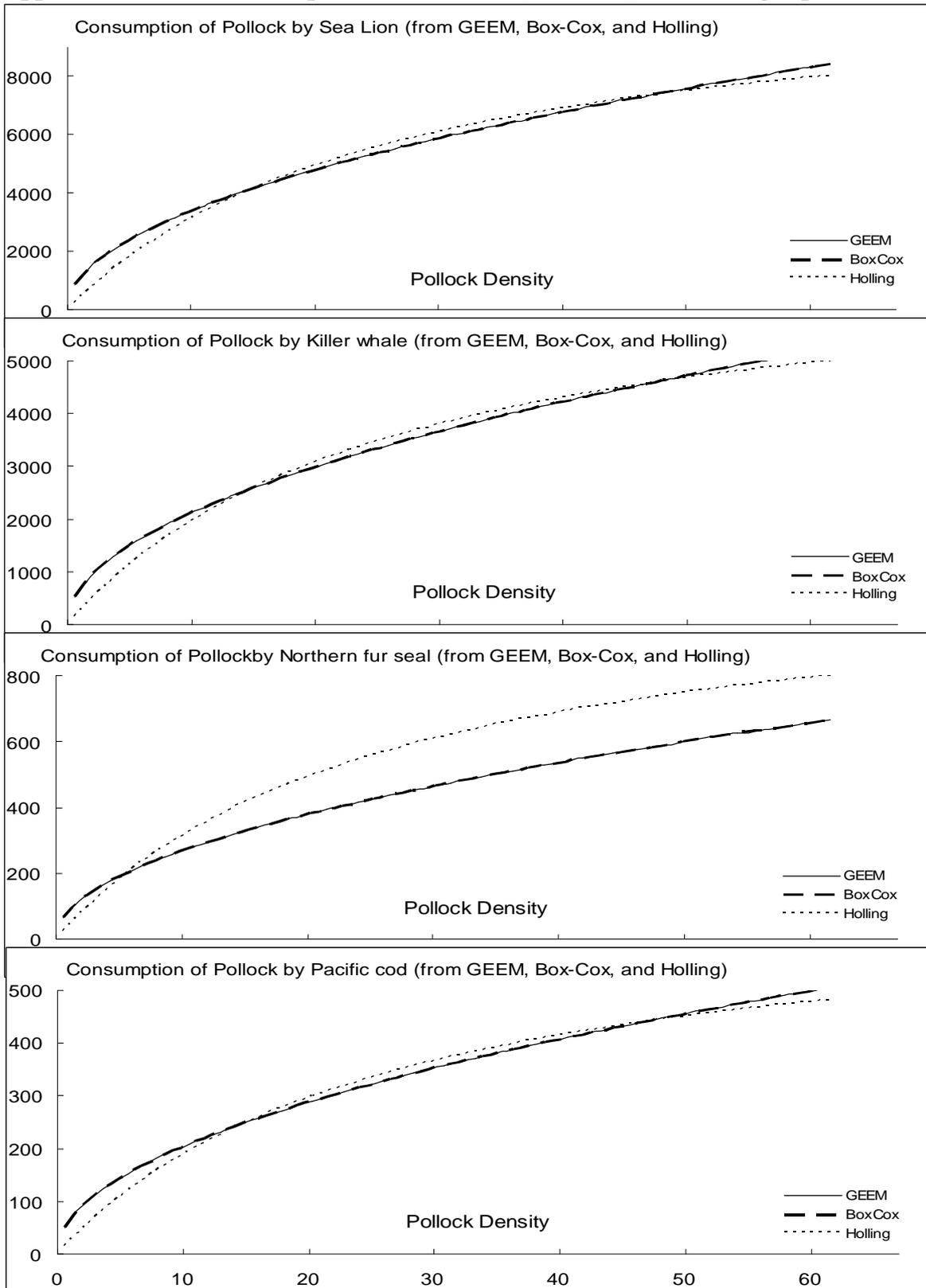
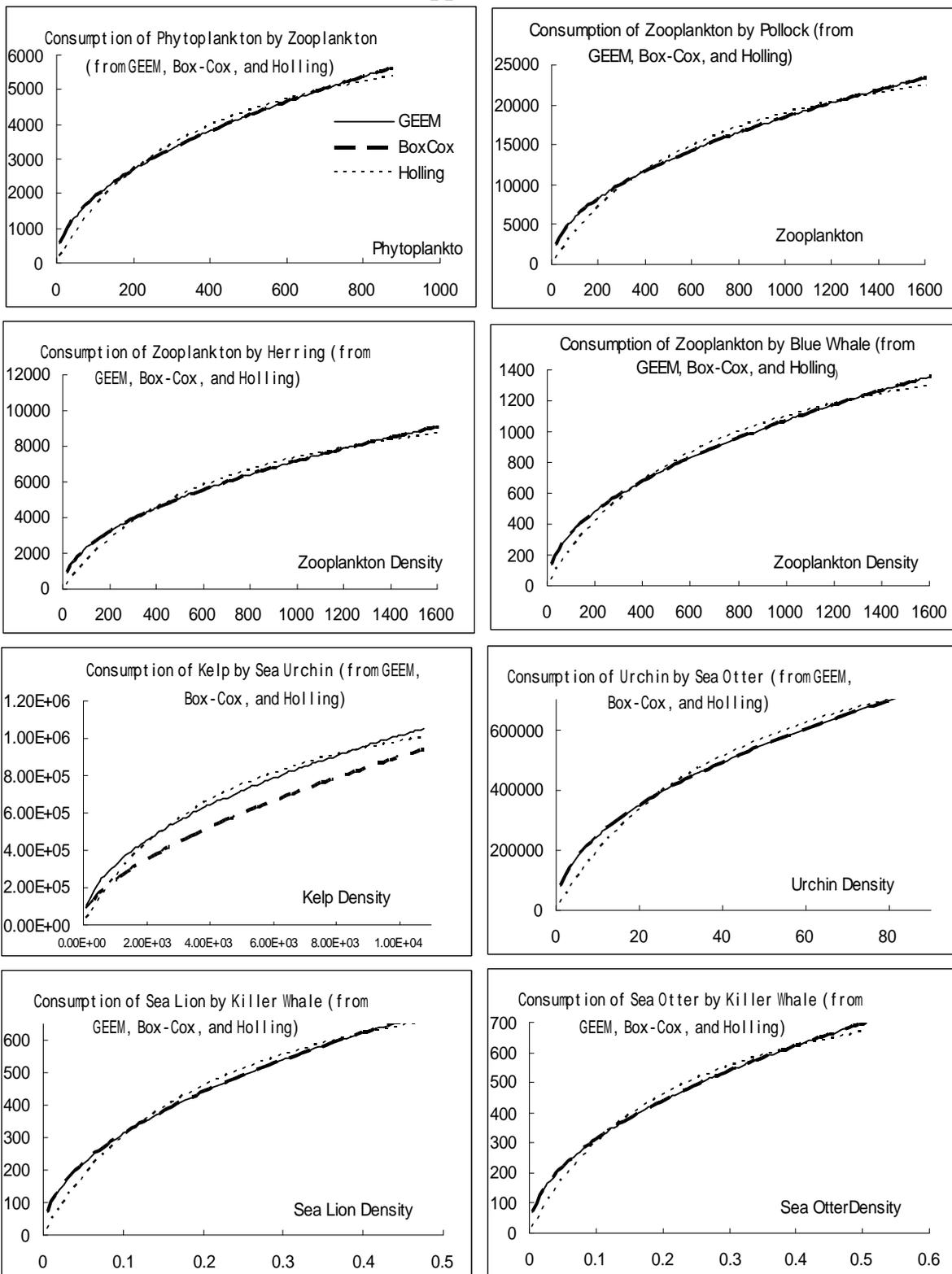
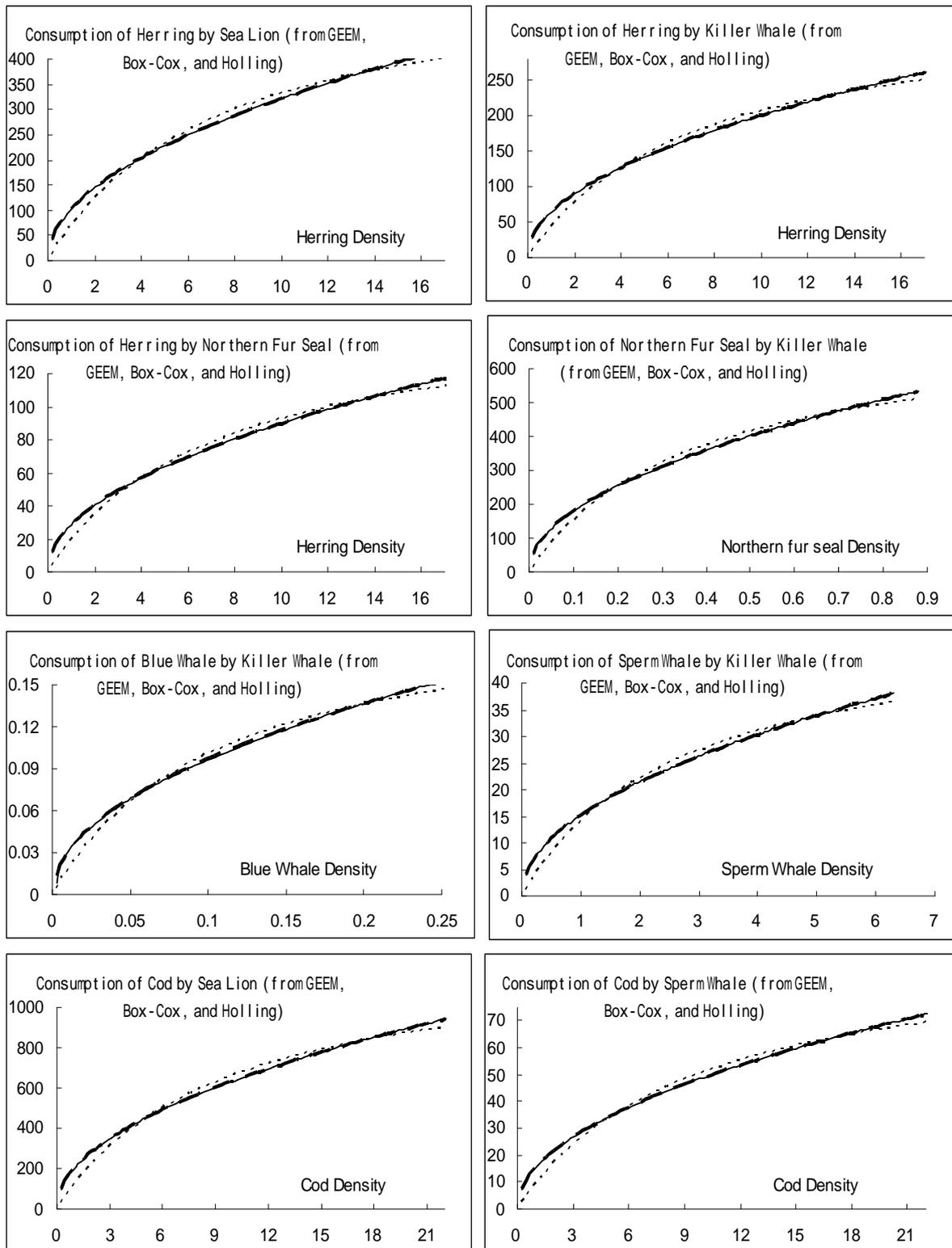


Figure 5a: Functional Responses of Pollock's Predators Estimated from GEEM, Box-Cox, and Holling Equation

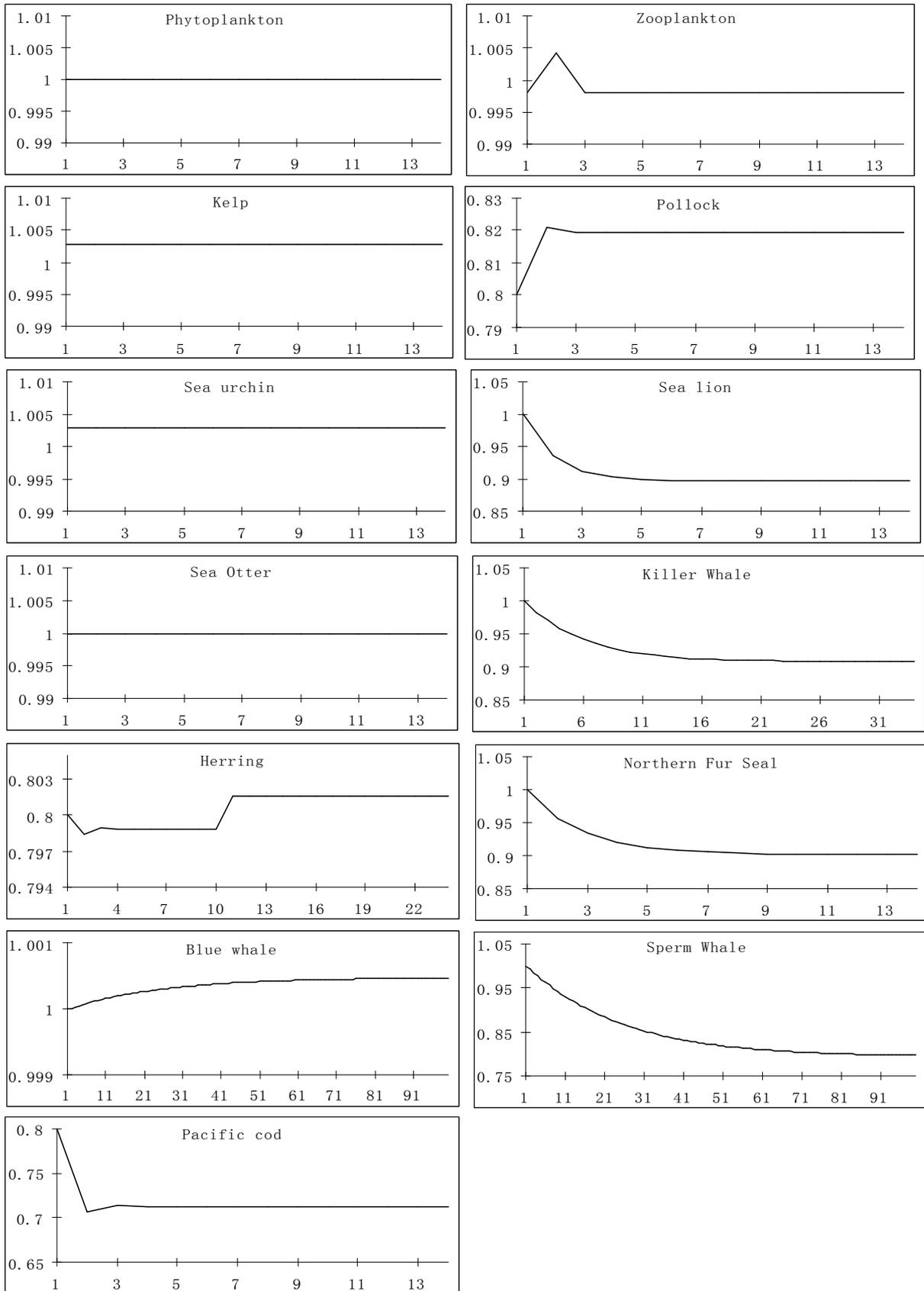
## Appendix 7





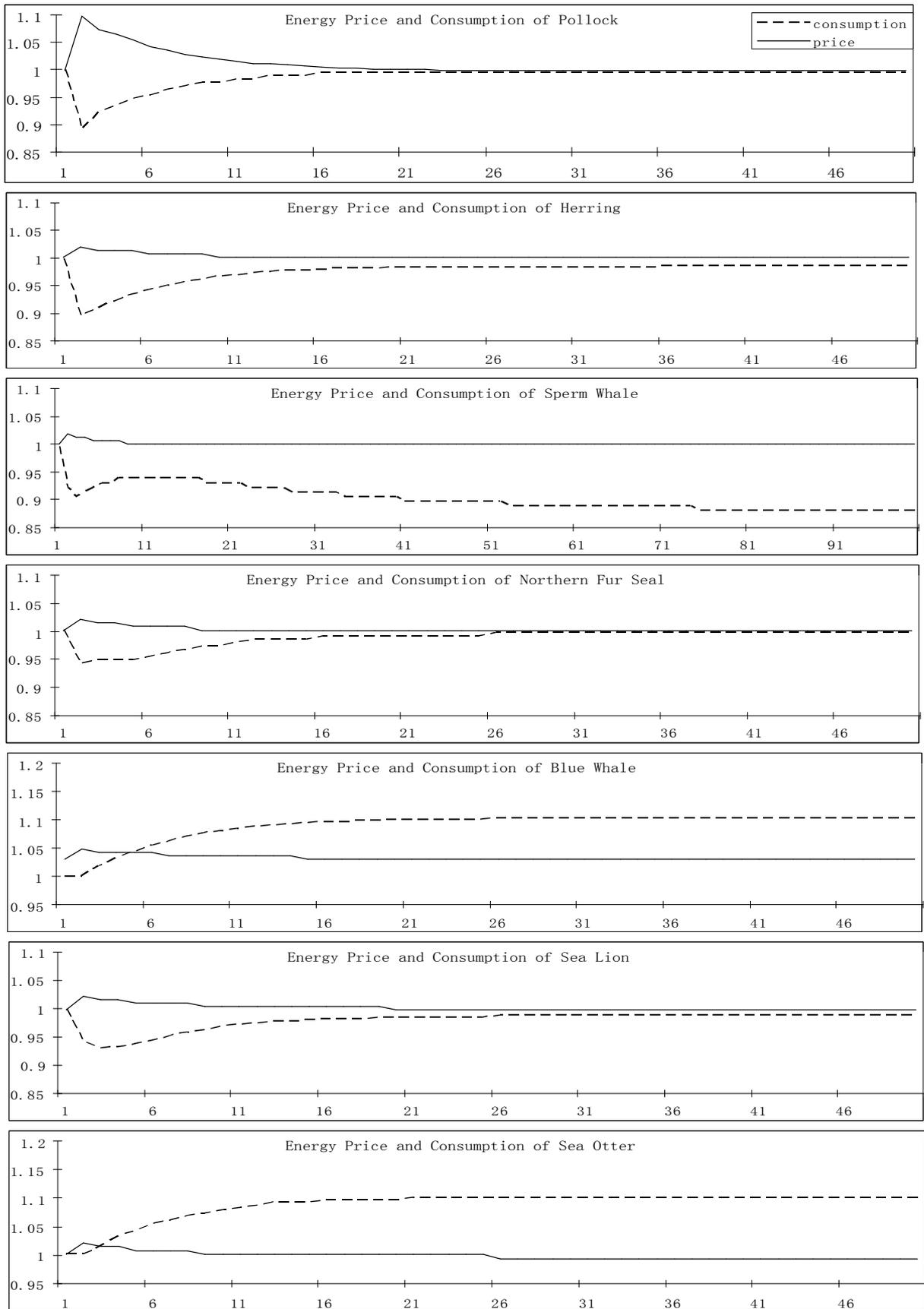
**Figure 5b: Functional Responses of Predators Estimated from GEEM, Box-Cox, and Holling Equation**

## Appendix 8



**Figure 7: GEEM with Constant Percentage Harvesting**

## Appendix 9



**Figure 9: Killer Whale's Consumptions and Energy Prices**

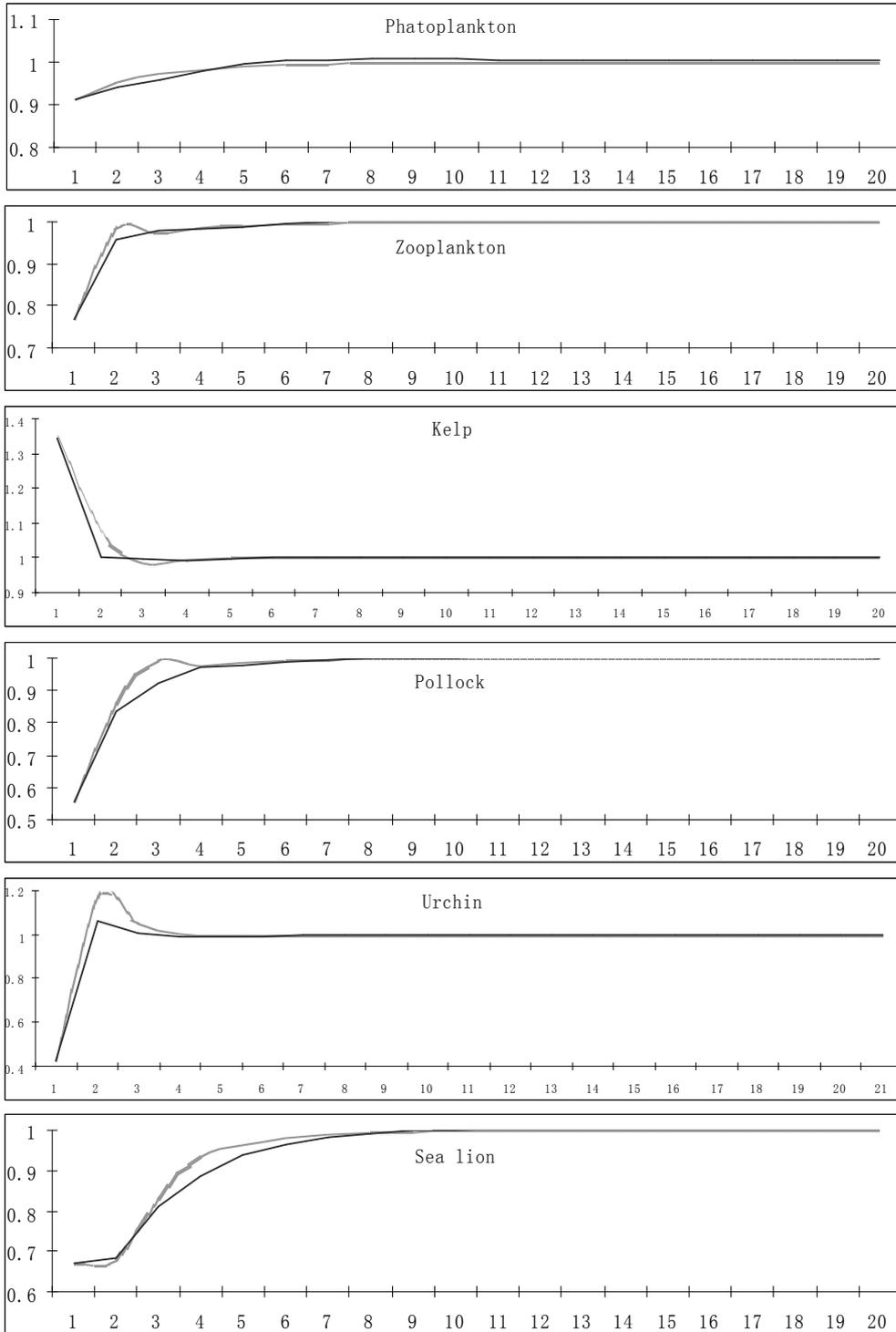
## Appendix 10

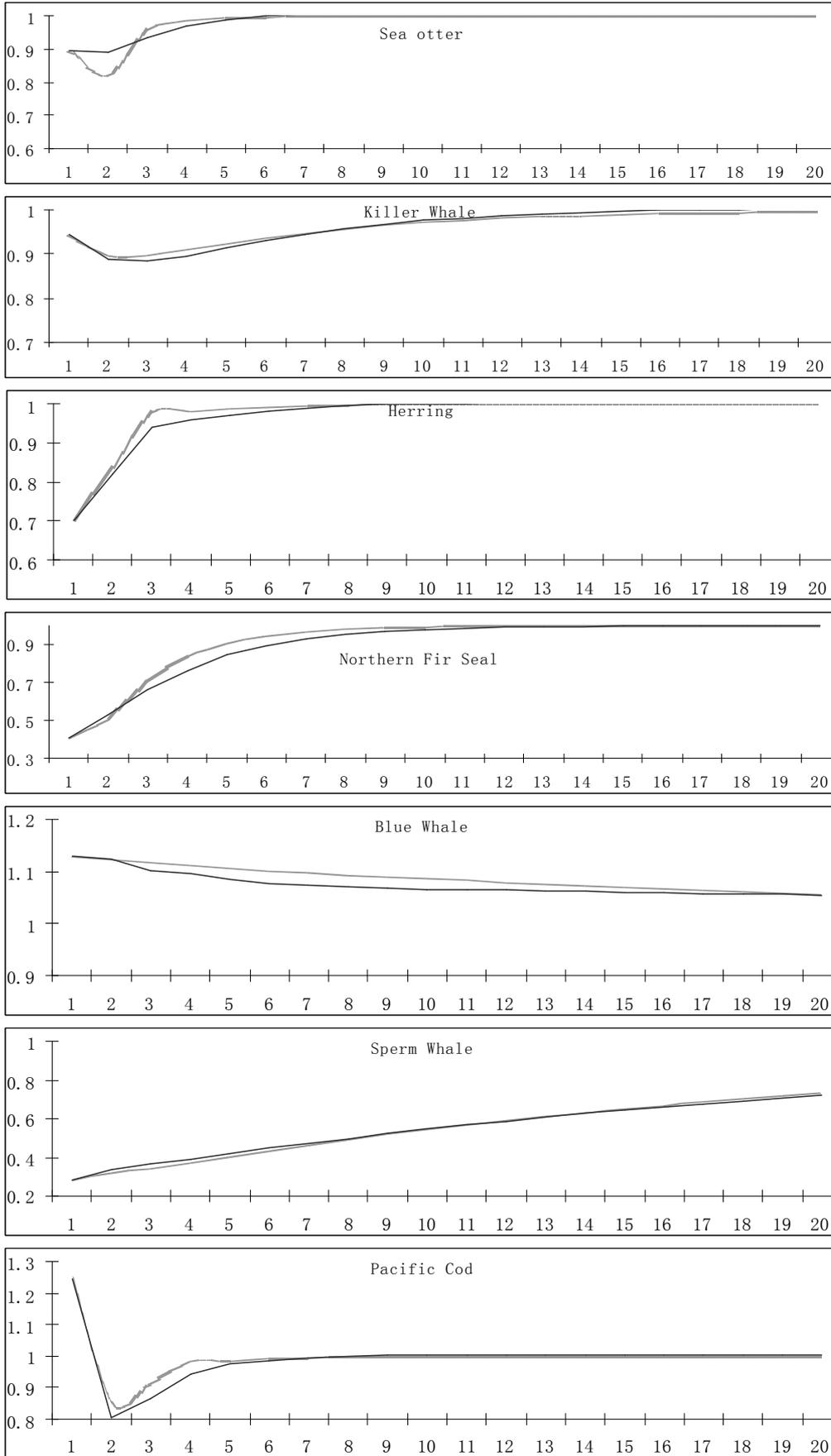
**Table 6: The R-GEEM Matrix—Linear Model**

	$N_1^t$	$N_2^t$	$N_3^t$	$N_4^t$	$N_5^t$	$N_6^t$	$N_7^t$	$N_8^t$	$N_9^t$	$N_{10}^t$	$N_{11}^t$	$N_{12}^t$	$N_{13}^t$
$C_i$	0.39	0.49	0.90	0.20	0.41	0.11	0.10	0.02	0.19	0.05	-0.01	0.01	0.06
$N_1^{t-1}$	0.62	0.49	0.00	0.21	-0.01	0.06	-0.01	0.02	0.20	0.05	0.04	0.01	0.10
$N_2^{t-1}$	-0.01	-0.02	-0.01	0.44	0.01	0.13	-0.03	0.05	0.41	0.10	-0.02	0.00	0.22
$N_3^{t-1}$	0.00	0.00	0.04	0.00	0.41	0.00	0.10	0.02	-0.02	-0.01	0.00	0.01	0.00
$N_4^{t-1}$	0.00	0.01	0.01	0.12	0.01	0.24	-0.01	0.09	0.01	0.16	0.01	0.02	0.41
$N_5^{t-1}$	0.02	0.01	0.01	0.00	0.16	0.00	0.20	0.01	0.00	0.02	-0.01	-0.03	0.00
$N_6^{t-1}$	-0.01	0.00	0.00	0.02	-0.03	0.50	0.00	0.02	0.00	-0.01	0.01	0.01	0.00
$N_7^{t-1}$	0.00	-0.01	0.01	0.01	0.00	-0.03	0.58	0.01	-0.01	0.00	-0.02	0.00	0.00
$N_8^{t-1}$	0.00	0.00	-0.03	-0.01	0.00	-0.02	-0.01	0.81	0.00	-0.02	0.03	-0.03	0.00
$N_9^{t-1}$	0.00	0.01	0.00	0.00	-0.01	0.00	-0.01	-0.01	0.18	0.02	0.02	0.01	0.00
$N_{10}^{t-1}$	-0.01	0.01	0.00	0.00	-0.01	0.02	0.00	0.01	0.00	0.60	-0.01	0.00	0.02
$N_{11}^{t-1}$	0.00	-0.02	-0.01	0.00	0.03	0.00	-0.01	0.03	-0.03	0.00	0.95	-0.01	0.00
$N_{12}^{t-1}$	-0.01	-0.01	0.00	-0.01	0.00	0.00	-0.02	0.01	0.00	0.00	0.00	0.95	-0.02
$N_{13}^{t-1}$	-0.01	-0.01	0.00	0.01	0.00	0.02	0.01	-0.03	0.00	0.01	0.01	0.02	0.16
$N_1^{t-2}$	0.01	0.01	0.00	0.03	0.01	0.00	0.03	0.01	-0.02	0.00	0.01	0.00	0.00
$N_2^{t-2}$	0.01	-0.02	0.00	-0.01	-0.01	-0.03	0.02	0.01	-0.02	-0.01	-0.01	-0.01	0.01
$N_3^{t-2}$	-0.02	-0.01	-0.02	0.00	0.01	0.02	0.00	-0.01	0.01	0.00	-0.01	0.01	0.00
$N_4^{t-2}$	0.00	0.00	0.00	0.02	0.03	0.01	0.01	-0.02	0.00	0.01	0.00	0.01	0.02
$N_5^{t-2}$	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01
$N_6^{t-2}$	0.01	-0.01	-0.01	-0.02	0.01	0.00	0.00	0.00	0.01	0.01	-0.01	-0.01	0.00
$N_7^{t-2}$	0.00	0.01	-0.01	0.00	0.01	-0.01	0.04	0.01	0.01	-0.01	0.01	0.00	0.01
$N_8^{t-2}$	0.00	0.00	0.02	0.00	0.00	0.02	-0.02	0.00	0.00	-0.02	-0.04	0.02	-0.02
$N_9^{t-2}$	0.00	0.00	-0.01	-0.01	0.02	-0.01	0.00	0.00	0.00	0.03	0.01	0.00	0.01
$N_{10}^{t-2}$	0.00	0.00	-0.01	0.02	0.00	-0.01	0.01	0.00	0.00	0.02	0.02	-0.01	-0.01
$N_{11}^{t-2}$	0.00	0.01	0.00	0.00	-0.03	0.00	0.02	-0.02	0.03	0.00	-0.01	0.03	0.00
$N_{12}^{t-2}$	0.01	0.01	0.00	0.02	0.00	0.00	0.02	-0.01	0.00	0.01	-0.01	0.01	0.02
$N_{13}^{t-2}$	0.00	0.01	0.00	-0.02	-0.01	0.01	0.00	0.00	-0.01	-0.01	0.01	0.00	0.00
$N_1^{t-3}$	-0.02	0.01	0.01	-0.01	-0.02	0.02	-0.01	0.00	0.02	0.01	-0.01	-0.01	0.00
$N_2^{t-3}$	0.01	0.00	0.01	-0.01	0.00	-0.02	0.02	0.02	0.00	-0.02	0.00	0.01	0.00
$N_3^{t-3}$	0.00	0.00	0.02	0.01	0.00	0.00	0.00	-0.01	0.01	-0.02	0.01	0.01	-0.01
$N_4^{t-3}$	0.00	-0.01	0.02	0.00	0.00	0.00	-0.01	0.01	0.00	0.01	0.00	0.00	0.01
$N_5^{t-3}$	0.00	0.00	-0.01	0.01	-0.01	0.00	0.00	0.01	0.00	0.00	-0.01	0.01	0.00
$N_6^{t-3}$	-0.02	0.01	-0.01	0.00	0.00	0.00	0.00	-0.01	0.00	0.00	0.00	0.00	0.00
$N_7^{t-3}$	0.00	0.00	0.00	0.00	-0.01	0.00	0.00	0.00	0.00	0.01	0.00	-0.01	-0.01
$N_8^{t-3}$	0.01	-0.01	0.01	0.00	0.00	0.00	0.02	0.00	0.00	0.03	0.00	-0.01	0.03
$N_9^{t-3}$	0.02	0.01	0.02	0.01	0.00	0.00	-0.01	-0.01	0.00	0.00	0.01	-0.01	-0.02
$N_{10}^{t-3}$	0.00	0.00	0.01	0.00	0.02	-0.01	-0.01	-0.01	0.02	-0.01	0.00	0.01	-0.01
$N_{11}^{t-3}$	0.01	0.00	0.01	0.01	-0.01	0.00	-0.01	-0.01	0.00	0.00	0.02	-0.02	0.00
$N_{12}^{t-3}$	-0.01	0.01	0.00	0.00	0.00	0.00	-0.01	-0.01	0.00	-0.01	0.01	0.00	0.00
$N_{13}^{t-3}$	0.00	0.01	-0.02	0.01	0.00	-0.01	-0.01	0.01	0.00	0.00	0.01	0.00	0.02

# Appendix 11

----- GEEM    \_\_\_\_\_ R-GEEM





**Figure 10: GEEM v.s R-GEEM Dynamics**

**Appendix 12**  
**Table 9a: Q-test for single species (L=1)**

Shock Distribution		Model			
		Linear Model		Quadratic Model	
		Q Statistics	Reject <b>H0</b> at 95% ?	Q Statistics	Reject <b>H0</b> at 95% ?
N(0,0.1)	Species 1	4.27E-11	NO	1.57E-11	NO
	Species 2	2.28E-08	NO	9.56E-10	NO
	Species 3	4.46E-08	NO	8.23E-08	NO
	Species 4	3.44E-08	NO	2.75E-10	NO
	Species 5	1.32E-08	NO	1.63E-09	NO
	Species 6	3.86E-09	NO	1.26E-08	NO
	Species 7	3.49E-09	NO	2.98E-10	NO
	Species 8	1.96E-09	NO	2.95E-08	NO
	Species 9	1.32E-09	NO	1.12E-08	NO
	Species 10	3.37E-09	NO	2.35E-10	NO
	Species 11	3.12E-12	NO	7.61E-10	NO
	Species 12	4.72E-08	NO	1.68E-08	NO
	Species 13	5.12E-08	NO	2.18E-09	NO
N(0,0.3)	Species 1	1.06E-08	NO	1.27E-08	NO
	Species 2	8.61E-08	NO	1.50E-07	NO
	Species 3	4.73E-08	NO	3.52E-10	NO
	Species 4	6.24E-07	NO	1.83E-06	NO
	Species 5	1.78E-07	NO	6.71E-07	NO
	Species 6	1.16E-07	NO	2.11E-08	NO
	Species 7	3.19E-07	NO	4.32E-07	NO
	Species 8	1.34E-07	NO	8.13E-09	NO
	Species 9	5.11E-07	NO	3.48E-11	NO
	Species 10	2.92E-07	NO	1.12E-07	NO
	Species 11	7.34E-08	NO	5.92E-08	NO
	Species 12	5.19E-08	NO	2.48E-08	NO
	Species 13	9.42E-09	NO	1.71E-07	NO
N(0,0.5)	Species 1	9.96E-07	NO	2.70E-06	NO
	Species 2	2.81E-09	NO	1.84E-06	NO
	Species 3	2.75E-06	NO	9.32E-06	NO
	Species 4	5.31E-06	NO	1.37E-05	NO
	Species 5	2.86E-08	NO	4.20E-16	NO
	Species 6	2.49E-08	NO	1.25E-16	NO
	Species 7	1.94E-09	NO	1.30E-06	NO
	Species 8	3.72E-09	NO	5.45E-14	NO
	Species 9	5.73E-07	NO	5.04E-07	NO
	Species 10	1.45E-06	NO	4.88E-07	NO
	Species 11	2.80E-07	NO	8.91E-19	NO
	Species 12	1.97E-07	NO	5.66E-08	NO
	Species 13	1.43E-06	NO	1.65E-12	NO

Note: The critical value of  $\chi^2$  (1) at p=0.05 is 3.84.

**Table 9b: Q-test for single species (L=3)**

Shock Distribution		Model			
		Linear Model		Quadratic Model	
		Q Statistics	Reject <b>H0</b> at 95% ?	Q Statistics	Reject <b>H0</b> at 95% ?
N(0,0.1)	Species 1	1.67E-03	NO	9.03E-04	NO
	Species 2	8.01E-04	NO	9.51E-05	NO
	Species 3	1.37E-04	NO	6.05E-05	NO
	Species 4	1.21E-04	NO	2.23E-05	NO
	Species 5	4.62E-04	NO	8.97E-04	NO
	Species 6	4.99E-04	NO	4.77E-04	NO
	Species 7	5.93E-04	NO	2.92E-04	NO
	Species 8	4.12E-03	NO	1.46E-03	NO
	Species 9	6.88E-04	NO	4.81E-05	NO
	Species 10	5.57E-04	NO	1.58E-03	NO
	Species 11	2.32E-03	NO	1.78E-04	NO
	Species 12	1.33E-03	NO	2.73E-03	NO
	Species 13	1.27E-04	NO	2.09E-04	NO
N(0,0.3)	Species 1	2.79E-03	NO	1.21E-03	NO
	Species 2	2.26E-04	NO	9.67E-04	NO
	Species 3	2.31E-04	NO	2.17E-04	NO
	Species 4	1.26E-04	NO	2.86E-04	NO
	Species 5	4.53E-04	NO	5.34E-04	NO
	Species 6	1.95E-04	NO	5.63E-04	NO
	Species 7	8.54E-04	NO	1.12E-03	NO
	Species 8	3.66E-04	NO	3.73E-05	NO
	Species 9	1.44E-04	NO	3.74E-04	NO
	Species 10	4.17E-05	NO	3.74E-03	NO
	Species 11	3.14E-03	NO	1.52E-03	NO
	Species 12	1.63E-04	NO	9.26E-04	NO
	Species 13	7.02E-04	NO	1.35E-05	NO
N(0,0.5)	Species 1	1.28E-03	NO	1.11E-03	NO
	Species 2	2.41E-03	NO	2.25E-04	NO
	Species 3	6.13E-05	NO	4.44E-04	NO
	Species 4	1.58E-03	NO	9.50E-04	NO
	Species 5	3.54E-04	NO	2.11E-12	NO
	Species 6	1.46E-04	NO	1.48E-12	NO
	Species 7	5.53E-04	NO	1.83E-04	NO
	Species 8	2.35E-04	NO	1.10E-09	NO
	Species 9	5.14E-04	NO	1.23E-03	NO
	Species 10	4.48E-04	NO	9.67E-04	NO
	Species 11	2.69E-04	NO	7.91E-12	NO
	Species 12	8.11E-04	NO	2.80E-04	NO
	Species 13	9.41E-04	NO	2.29E-04	NO

Note: The critical value of  $\chi^2$  (3) at p=0.05 is 7.81.

**Table 9c: Q-test for single species (L=5)**

Shock Distribution		Model			
		Linear Model		Quadratic Model	
		Q Statistics	Reject <b>H0</b> at 95% ?	Q Statistics	Reject <b>H0</b> at 95% ?
N(0,0.1)	Species 1	9.78E-04	NO	1.61E-03	NO
	Species 2	2.07E-03	NO	2.45E-03	NO
	Species 3	4.55E-03	NO	9.54E-04	NO
	Species 4	2.06E-03	NO	1.82E-03	NO
	Species 5	7.18E-03	NO	2.25E-04	NO
	Species 6	1.96E-03	NO	1.39E-03	NO
	Species 7	1.94E-03	NO	1.54E-03	NO
	Species 8	9.46E-04	NO	4.68E-03	NO
	Species 9	1.42E-03	NO	3.09E-03	NO
	Species 10	3.39E-04	NO	3.56E-03	NO
	Species 11	1.58E-03	NO	1.01E-03	NO
	Species 12	2.87E-03	NO	3.08E-03	NO
	Species 13	2.30E-03	NO	3.85E-03	NO
N(0,0.3)	Species 1	9.15E-04	NO	2.49E-03	NO
	Species 2	3.52E-03	NO	1.26E-03	NO
	Species 3	1.48E-03	NO	2.75E-03	NO
	Species 4	3.56E-03	NO	2.78E-03	NO
	Species 5	1.03E-03	NO	3.27E-03	NO
	Species 6	1.14E-03	NO	1.79E-03	NO
	Species 7	2.77E-03	NO	2.81E-03	NO
	Species 8	1.74E-03	NO	4.24E-03	NO
	Species 9	1.08E-03	NO	3.89E-03	NO
	Species 10	7.89E-04	NO	9.59E-04	NO
	Species 11	3.83E-03	NO	3.49E-03	NO
	Species 12	1.51E-03	NO	7.48E-03	NO
	Species 13	5.22E-03	NO	1.48E-03	NO
N(0,0.5)	Species 1	3.28E-03	NO	2.27E-03	NO
	Species 2	1.72E-03	NO	2.99E-03	NO
	Species 3	3.31E-03	NO	3.47E-03	NO
	Species 4	2.30E-03	NO	1.31E-03	NO
	Species 5	1.59E-03	NO	-3.20E-03	NO
	Species 6	1.21E-03	NO	-2.12E-02	NO
	Species 7	8.56E-04	NO	4.16E-03	NO
	Species 8	4.84E-04	NO	4.15E-04	NO
	Species 9	6.33E-04	NO	2.07E-03	NO
	Species 10	1.81E-03	NO	1.09E-03	NO
	Species 11	1.76E-03	NO	1.79E-02	NO
	Species 12	2.71E-03	NO	2.21E-03	NO
	Species 13	2.14E-03	NO	2.11E-03	NO

Note: The critical value of  $\chi^2$  (5) at p=0.05 is 11.07.

**Table 9d: Q-test for single species (L=10)**

Shock Distribution		Model			
		Linear Model		Quadratic Model	
		Q Statistics	Reject <b>H0</b> at 95% ?	Q Statistics	Reject <b>H0</b> at 95% ?
N(0,0.1)	Species 1	0.03	NO	0.03	NO
	Species 2	0.01	NO	0.01	NO
	Species 3	0.02	NO	0.02	NO
	Species 4	0.01	NO	0.02	NO
	Species 5	0.03	NO	0.03	NO
	Species 6	0.01	NO	0.01	NO
	Species 7	0.02	NO	0.02	NO
	Species 8	0.01	NO	0.01	NO
	Species 9	0.02	NO	0.02	NO
	Species 10	0.02	NO	0.01	NO
	Species 11	0.01	NO	0.01	NO
	Species 12	0.02	NO	0.03	NO
	Species 13	0.02	NO	0.02	NO
N(0,0.3)	Species 1	0.01	NO	0.01	NO
	Species 2	0.02	NO	0.02	NO
	Species 3	0.01	NO	0.01	NO
	Species 4	0.03	NO	0.02	NO
	Species 5	0.02	NO	0.01	NO
	Species 6	0.02	NO	0.01	NO
	Species 7	0.02	NO	0.01	NO
	Species 8	0.01	NO	0.01	NO
	Species 9	0.01	NO	0.01	NO
	Species 10	0.02	NO	0.01	NO
	Species 11	0.03	NO	0.01	NO
	Species 12	0.01	NO	0.01	NO
	Species 13	0.02	NO	0.02	NO
N(0,0.5)	Species 1	0.04	NO	1.05	NO
	Species 2	0.06	NO	1.02	NO
	Species 3	0.02	NO	0.21	NO
	Species 4	0.07	NO	1.04	NO
	Species 5	0.02	NO	0.96	NO
	Species 6	0.06	NO	0.98	NO
	Species 7	0.02	NO	0.02	NO
	Species 8	0.06	NO	1.18	NO
	Species 9	0.05	NO	1.03	NO
	Species 10	0.05	NO	1.03	NO
	Species 11	0.03	NO	0.99	NO
	Species 12	0.03	NO	1.01	NO
	Species 13	0.05	NO	1.04	NO

Note: The critical value of  $\chi^2$  (10) at p=0.05 is 18.30.

## Appendix 13

**Table 10: The R-GEEM Matrix – Quadratic Model**

	$N_1^t$	$N_2^t$	$N_3^t$	$N_4^t$	$N_5^t$	$N_6^t$	$N_7^t$	$N_8^t$	$N_9^t$	$N_{10}^t$	$N_{11}^t$	$N_{12}^t$	$N_{13}^t$
$C_i$	0.85	1.87	1.34	0.93	0.98	0.93	0.75	0.46	0.50	0.46	0.10	-0.10	0.36
$N_1^{t-1}$	0.18	0.28	-0.08	0.40	-0.01	0.11	0.03	0.05	0.31	0.04	0.00	0.02	0.19
$N_2^{t-1}$	0.01	-1.95	0.01	0.45	-0.04	-0.13	-0.01	0.04	0.53	0.13	-0.08	0.01	0.29
$N_3^{t-1}$	0.00	-0.03	-1.12	0.13	0.30	0.01	0.16	0.01	-0.19	-0.03	-0.01	0.07	-0.02
$N_4^{t-1}$	-0.04	0.00	0.22	-0.83	-0.06	0.06	0.02	0.08	-0.08	0.20	-0.12	0.01	0.40
$N_5^{t-1}$	-0.01	0.03	-0.28	0.00	-0.70	0.03	0.21	0.03	0.03	0.02	0.02	-0.40	0.06
$N_6^{t-1}$	-0.16	-0.01	0.14	-0.36	0.34	-0.71	0.14	0.07	-0.12	-0.12	0.02	0.01	-0.01
$N_7^{t-1}$	0.01	0.01	0.03	0.00	0.03	-0.49	0.26	0.02	-0.03	0.03	0.08	0.03	0.01
$N_8^{t-1}$	0.00	0.05	0.00	0.01	-0.04	0.07	-0.02	0.55	-0.02	0.22	0.25	0.49	-0.10
$N_9^{t-1}$	0.08	-0.08	-0.01	0.03	0.03	0.08	0.06	-0.29	-0.74	0.01	0.43	0.19	0.00
$N_{10}^{t-1}$	-0.03	-0.04	0.00	-0.01	-0.08	-0.12	0.02	-0.02	0.11	-0.31	-0.02	0.01	0.04
$N_{11}^{t-1}$	-0.24	0.05	-0.06	-0.01	-0.09	0.00	0.01	0.18	-0.26	0.13	0.92	0.07	0.00
$N_{12}^{t-1}$	-0.01	-0.20	-0.02	-0.15	-0.02	0.00	-0.28	0.05	0.00	-0.02	0.02	0.95	-0.05
$N_{13}^{t-1}$	0.08	0.06	0.10	-0.04	-0.02	0.02	0.07	-0.03	0.10	-0.04	-0.22	0.03	-0.75
$N_1^{t-2}$	-0.06	0.43	0.14	-0.21	-0.03	0.09	0.03	-0.03	0.25	-0.03	0.32	-0.05	-0.03
$N_2^{t-2}$	0.06	-0.10	-0.09	-0.03	-0.31	0.34	-0.26	0.05	-0.08	0.02	-0.09	0.27	0.05
$N_3^{t-2}$	0.01	-0.05	0.17	-0.04	0.06	-0.11	0.00	0.02	-0.05	-0.09	0.11	0.05	0.04
$N_4^{t-2}$	-0.03	-0.02	-0.12	0.08	0.25	-0.20	-0.11	-0.36	0.10	-0.02	0.05	0.18	0.13
$N_5^{t-2}$	0.03	0.00	0.02	-0.01	0.08	-0.04	-0.08	-0.15	0.00	0.00	0.05	0.01	0.10
$N_6^{t-2}$	0.05	-0.10	-0.09	0.20	-0.09	0.12	-0.02	-0.05	-0.11	0.00	-0.01	-0.12	0.07
$N_7^{t-2}$	0.02	-0.12	0.00	0.02	-0.09	-0.48	-0.27	-0.10	0.02	-0.03	-0.02	0.01	0.05
$N_8^{t-2}$	-0.06	0.09	0.09	-0.01	0.10	-0.07	-0.14	0.19	0.01	-0.34	-0.11	-0.32	0.02
$N_9^{t-2}$	0.10	0.01	-0.01	0.05	0.15	-0.11	-0.05	0.10	-0.07	0.43	-0.10	0.11	0.08
$N_{10}^{t-2}$	-0.02	-0.04	-0.12	0.21	0.01	0.07	-0.32	-0.10	-0.03	0.08	0.15	0.00	0.03
$N_{11}^{t-2}$	0.09	-0.06	0.02	0.33	0.08	-0.04	-0.20	-0.16	0.38	-0.06	0.08	-0.34	-0.01
$N_{12}^{t-2}$	-0.04	0.14	0.00	0.17	0.00	0.22	0.18	0.02	0.01	0.12	-0.02	-0.03	0.10
$N_{13}^{t-2}$	0.04	-0.18	0.10	-0.31	0.06	0.02	0.00	-0.08	0.07	-0.03	-0.06	0.00	0.08
$N_1^{t-3}$	0.07	0.02	-0.19	0.35	-0.10	0.07	0.07	0.03	0.08	-0.04	-0.16	-0.07	0.19
$N_2^{t-3}$	-0.02	-0.14	0.02	0.15	-0.09	0.07	0.40	-0.24	-0.06	-0.03	0.08	-0.07	0.02
$N_3^{t-3}$	-0.11	-0.07	0.25	0.02	0.01	0.07	-0.07	0.21	0.03	-0.31	-0.03	-0.06	-0.03
$N_4^{t-3}$	-0.09	-0.50	-0.03	0.03	-0.09	0.07	-0.08	0.06	0.00	0.39	-0.07	0.03	0.05
$N_5^{t-3}$	-0.03	0.04	-0.04	-0.16	-0.03	-0.03	-0.04	-0.17	-0.01	-0.02	-0.32	-0.05	-0.04
$N_6^{t-3}$	-0.39	-0.01	-0.07	-0.05	-0.04	-0.03	-0.01	-0.08	0.10	0.00	0.01	-0.19	-0.08
$N_7^{t-3}$	0.00	0.05	-0.06	0.05	-0.09	0.39	-0.32	0.13	0.03	-0.09	-0.17	0.07	-0.02
$N_8^{t-3}$	-0.01	-0.06	-0.05	0.04	-0.08	0.02	0.06	-0.11	-0.01	0.00	-0.01	-0.06	-0.13
$N_9^{t-3}$	-0.02	0.13	0.02	-0.13	0.03	0.14	-0.10	0.02	0.03	-0.05	-0.04	0.09	-0.14
$N_{10}^{t-3}$	0.00	0.00	0.06	-0.22	0.11	-0.12	-0.02	0.17	0.04	-0.11	-0.14	-0.05	-0.18
$N_{11}^{t-3}$	0.10	0.07	0.05	-0.32	-0.04	0.04	0.19	-0.02	-0.22	-0.06	-0.03	0.22	-0.02
$N_{12}^{t-3}$	0.06	0.10	0.03	-0.05	0.06	-0.29	0.02	-0.13	-0.01	-0.02	-0.01	0.00	-0.06
$N_{13}^{t-3}$	0.07	-0.04	0.17	-0.46	-0.08	0.12	0.05	0.15	0.03	0.19	0.02	0.10	0.02
$(N_1^{t-1})^2$	0.22	0.10	0.04	-0.09	0.00	-0.02	-0.02	-0.02	-0.05	0.00	0.02	-0.01	-0.04
$(N_2^{t-1})^2$	-0.01	0.97	-0.01	-0.01	0.02	0.14	-0.01	0.00	-0.06	-0.01	0.03	0.00	-0.04
$(N_3^{t-1})^2$	0.00	0.01	0.59	-0.07	0.06	-0.01	-0.03	0.00	0.09	0.01	0.01	-0.03	0.01
$(N_4^{t-1})^2$	0.02	0.00	-0.11	0.47	0.03	0.09	-0.02	0.00	0.04	-0.02	0.06	0.01	0.00
$(N_5^{t-1})^2$	0.02	-0.01	0.15	0.00	0.44	-0.01	-0.01	-0.02	-0.01	0.00	-0.01	0.19	-0.03

$(N_6^{t-1})^2$	0.07	0.01	-0.07	0.18	-0.18	0.59	-0.07	-0.02	0.06	0.05	-0.01	0.00	0.00
$(N_7^{t-1})^2$	0.00	-0.01	-0.01	0.00	-0.02	0.23	0.15	-0.01	0.01	-0.02	-0.05	-0.02	0.00
$(N_8^{t-1})^2$	0.00	-0.02	-0.01	-0.01	0.02	-0.04	0.01	0.13	0.01	-0.12	-0.11	-0.25	0.05
$(N_9^{t-1})^2$	-0.04	0.05	0.01	-0.02	-0.02	-0.04	-0.04	0.14	0.46	0.01	-0.21	-0.09	0.00
$(N_{10}^{t-1})^2$	0.01	0.02	0.00	0.00	0.04	0.07	-0.01	0.01	-0.06	0.46	0.01	0.00	-0.01
$(N_{11}^{t-1})^2$	0.12	-0.03	0.03	0.00	0.06	0.00	-0.01	-0.08	0.12	-0.07	0.01	-0.04	0.00
$(N_{12}^{t-1})^2$	0.00	0.09	0.01	0.07	0.01	0.00	0.13	-0.02	0.00	0.01	-0.01	0.00	0.02
$(N_{13}^{t-1})^2$	-0.05	-0.04	-0.05	0.02	0.01	0.00	-0.03	0.00	-0.05	0.02	0.12	0.00	0.46
$(N_1^{t-2})^2$	0.03	-0.21	-0.07	0.12	0.02	-0.05	0.00	0.02	-0.13	0.02	-0.15	0.03	0.01
$(N_2^{t-2})^2$	-0.02	0.04	0.04	0.01	0.15	-0.18	0.14	-0.02	0.03	-0.02	0.04	-0.14	-0.02
$(N_3^{t-2})^2$	-0.01	0.02	-0.10	0.02	-0.03	0.06	0.00	-0.01	0.03	0.05	-0.07	-0.02	-0.02
$(N_4^{t-2})^2$	0.01	0.01	0.06	-0.03	-0.11	0.11	0.06	0.17	-0.05	0.01	-0.03	-0.09	-0.06
$(N_5^{t-2})^2$	-0.02	0.00	0.00	0.00	-0.04	0.02	0.04	0.08	0.00	0.00	-0.03	-0.01	-0.04
$(N_6^{t-2})^2$	-0.02	0.04	0.04	-0.11	0.05	-0.06	0.01	0.03	0.06	0.00	0.00	0.05	-0.03
$(N_7^{t-2})^2$	-0.01	0.07	0.00	-0.01	0.05	0.23	0.15	0.05	-0.01	0.01	0.02	0.00	-0.02
$(N_8^{t-2})^2$	0.03	-0.04	-0.04	0.01	-0.05	0.05	0.06	-0.09	-0.01	0.16	0.03	0.17	-0.02
$(N_9^{t-2})^2$	-0.05	-0.01	0.00	-0.03	-0.06	0.05	0.03	-0.05	0.03	-0.20	0.05	-0.06	-0.03
$(N_{10}^{t-2})^2$	0.01	0.02	0.06	-0.10	-0.01	-0.04	0.17	0.05	0.01	-0.04	-0.07	-0.01	-0.02
$(N_{11}^{t-2})^2$	-0.05	0.04	-0.01	-0.17	-0.05	0.02	0.11	0.07	-0.18	0.03	-0.05	0.19	0.00
$(N_{12}^{t-2})^2$	0.03	-0.06	0.00	-0.07	0.00	-0.11	-0.08	-0.01	-0.01	-0.05	0.01	0.02	-0.04
$(N_{13}^{t-2})^2$	-0.02	0.09	-0.05	0.14	-0.03	0.00	0.00	0.04	-0.04	0.01	0.03	0.00	-0.05
$(N_1^{t-3})^2$	-0.04	0.00	0.10	-0.18	0.04	-0.03	-0.04	-0.01	-0.03	0.03	0.08	0.03	-0.09
$(N_2^{t-3})^2$	0.02	0.07	-0.01	-0.08	0.05	-0.04	-0.19	0.13	0.03	0.00	-0.04	0.04	-0.01
$(N_3^{t-3})^2$	0.06	0.04	-0.12	-0.01	-0.01	-0.04	0.03	-0.12	-0.02	0.15	0.02	0.03	0.01
$(N_4^{t-3})^2$	0.05	0.24	0.02	-0.01	0.04	-0.04	0.03	-0.03	0.00	-0.19	0.03	-0.01	-0.02
$(N_5^{t-3})^2$	0.01	-0.02	0.02	0.08	0.01	0.01	0.02	0.09	0.01	0.01	0.16	0.03	0.02
$(N_6^{t-3})^2$	0.18	0.01	0.03	0.02	0.02	0.02	0.00	0.03	-0.05	0.00	0.00	0.09	0.04
$(N_7^{t-3})^2$	0.00	-0.03	0.03	-0.02	0.04	-0.19	0.16	-0.06	-0.01	0.05	0.08	-0.04	0.00
$(N_8^{t-3})^2$	0.01	0.02	0.03	-0.02	0.04	-0.01	-0.02	0.06	0.01	0.01	0.00	0.02	0.08
$(N_9^{t-3})^2$	0.02	-0.06	0.00	0.07	-0.02	-0.07	0.05	-0.01	-0.02	0.02	0.02	-0.04	0.06
$(N_{10}^{t-3})^2$	0.00	0.00	-0.03	0.11	-0.04	0.06	0.01	-0.09	-0.01	0.05	0.07	0.03	0.09
$(N_{11}^{t-3})^2$	-0.05	-0.03	-0.02	0.16	0.02	-0.02	-0.10	0.00	0.11	0.03	0.03	-0.12	0.01
$(N_{12}^{t-3})^2$	-0.03	-0.04	-0.01	0.02	-0.03	0.14	-0.01	0.06	0.00	0.01	0.01	0.00	0.03
$(N_{13}^{t-3})^2$	-0.03	0.02	-0.09	0.24	0.04	-0.07	-0.03	-0.07	-0.01	-0.10	-0.01	-0.05	0.00

## Appendix 14

**Table 11: The R-GEEM Matrix Used in the Optimization Problem**

$C_i$	$N_1^t$	$N_2^t$	$N_3^t$	$N_4^t$	$N_5^t$	$N_6^t$	$N_7^t$	$N_8^t$	$N_9^t$	$N_{10}^t$	$N_{11}^t$	$N_{12}^t$	$N_{13}^t$
$C_i$	34.50	80.11	964.02	1.23	4.46	0.01	0.01	0.00	0.32	0.00	0.00	0.01	0.13
$N_1^{t-1}$	54.45	79.51	3.08	1.31	-0.06	0.01	0.00	0.00	0.34	0.00	0.00	0.00	0.23
$N_2^{t-1}$	-0.55	-2.73	-5.75	2.68	0.07	0.01	0.00	0.00	0.70	0.01	0.00	0.00	0.48
$N_3^{t-1}$	-0.19	0.52	43.91	-0.01	4.46	0.00	0.01	0.00	-0.03	0.00	0.00	0.01	0.00
$N_4^{t-1}$	-0.16	1.01	5.62	0.72	0.06	0.02	0.00	0.00	0.01	0.01	0.00	0.01	0.91
$N_5^{t-1}$	1.83	0.95	15.13	-0.02	1.77	0.00	0.01	0.00	0.00	0.00	0.00	-0.02	0.01
$N_6^{t-1}$	-0.60	0.16	4.74	0.11	-0.28	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$N_7^{t-1}$	0.10	-1.34	15.69	0.03	-0.01	0.00	0.03	0.00	-0.01	0.00	0.00	0.00	0.00
$N_8^{t-1}$	-0.32	0.59	-27.04	-0.03	-0.04	0.00	0.00	0.01	0.00	0.00	0.00	-0.02	0.01
$N_9^{t-1}$	0.35	2.17	-2.96	-0.02	-0.07	0.00	0.00	0.00	0.31	0.00	0.00	0.01	-0.01
$N_{10}^{t-1}$	-0.89	0.91	-4.33	-0.01	-0.06	0.00	0.00	0.00	-0.01	0.05	0.00	0.00	0.03
$N_{11}^{t-1}$	0.00	-2.74	-13.72	-0.01	0.35	0.00	0.00	0.00	-0.05	0.00	0.02	0.00	0.01
$N_{12}^{t-1}$	-0.49	-2.35	0.55	-0.09	-0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.60	-0.04
$N_{13}^{t-1}$	-1.03	-1.05	1.24	0.03	-0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.36
$N_1^{t-2}$	0.66	1.71	-3.31	0.16	0.08	0.00	0.00	0.00	-0.03	0.00	0.00	0.00	-0.01
$N_2^{t-2}$	0.61	-3.12	-2.55	-0.04	-0.12	0.00	0.00	0.00	-0.04	0.00	0.00	0.00	0.03
$N_3^{t-2}$	-1.50	-1.62	-21.25	-0.03	0.06	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00
$N_4^{t-2}$	0.23	-0.17	1.31	0.10	0.29	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.04
$N_5^{t-2}$	-0.21	0.33	12.89	0.00	0.04	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.02
$N_6^{t-2}$	0.75	-1.80	-5.49	-0.10	0.10	0.00	0.00	0.00	0.02	0.00	0.00	-0.01	0.01
$N_7^{t-2}$	-0.02	1.77	-7.39	-0.01	0.16	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.02
$N_8^{t-2}$	-0.42	0.77	16.57	0.03	-0.03	0.00	0.00	0.00	0.01	0.00	0.00	0.02	-0.04
$N_9^{t-2}$	0.06	-0.09	-6.13	-0.04	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
$N_{10}^{t-2}$	0.15	-0.48	-8.52	0.11	0.00	0.00	0.00	0.00	-0.01	0.00	0.00	0.00	-0.02
$N_{11}^{t-2}$	-0.44	2.20	4.86	-0.03	-0.28	0.00	0.00	0.00	0.05	0.00	0.00	0.02	0.00
$N_{12}^{t-2}$	0.71	0.97	-1.34	0.11	-0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04
$N_{13}^{t-2}$	-0.30	1.76	3.45	-0.13	-0.08	0.00	0.00	0.00	-0.01	0.00	0.00	0.00	0.00
$N_1^{t-3}$	-1.57	2.30	13.31	-0.06	-0.18	0.00	0.00	0.00	0.04	0.00	0.00	-0.01	0.00
$N_2^{t-3}$	0.74	-0.04	11.97	-0.06	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00
$N_3^{t-3}$	0.44	0.17	21.24	0.05	-0.04	0.00	0.00	0.00	0.01	0.00	0.00	0.00	-0.03
$N_4^{t-3}$	0.41	-2.00	24.85	-0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
$N_5^{t-3}$	-0.14	-0.08	-6.35	0.05	-0.06	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
$N_6^{t-3}$	-1.91	1.28	-9.08	-0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.01
$N_7^{t-3}$	-0.02	-0.31	3.05	0.00	-0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.03
$N_8^{t-3}$	0.85	-1.31	7.75	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	-0.01	0.06
$N_9^{t-3}$	1.60	1.36	25.22	0.06	0.01	0.00	0.00	0.00	-0.01	0.00	0.00	0.00	-0.04
$N_{10}^{t-3}$	0.27	0.43	9.22	0.00	0.17	0.00	0.00	0.00	0.03	0.00	0.00	0.00	-0.02
$N_{11}^{t-3}$	0.58	0.39	11.63	0.04	-0.09	0.00	0.00	0.00	0.00	0.00	0.00	-0.01	0.01
$N_{12}^{t-3}$	-0.62	1.15	-0.56	-0.02	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$N_{13}^{t-3}$	-0.20	1.12	-18.88	0.09	-0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05

## Appendix 15

Table 12: Engenvalues of the R-GEEM Matrix – Linear Model

0.96015  
0.953157  
0.804301  
0.653164  
0.631886  
0.588756 + 0.12519347i  
0.588756 - 0.12519347i  
0.187687 + 0.35321898i  
0.187687 - 0.35321898i  
0.401524  
-0.23803 + 0.19244838i  
-0.23803 - 0.19244838i  
-0.10833 + 0.29583954i  
-0.10833 - 0.29583954i  
0.228054 + 0.19395486i  
0.228054 - 0.19395486i  
0.298557 + 0.034420712i  
0.298557 - 0.034420712i  
-0.27164  
-0.08057 + 0.25262407i  
-0.08057 - 0.25262407i  
-0.18365 + 0.12530751i  
-0.18365 - 0.12530751i  
-0.18463 + 0.011385422i  
-0.18463 - 0.011385422i  
-0.03841 + 0.20923590i  
-0.03841 - 0.20923590i  
-0.10406 + 0.11449983i  
-0.10406 - 0.11449983i  
0.123631 + 0.17532901i  
0.123631 - 0.17532901i  
0.016214 + 0.14902065i  
0.016214 - 0.14902065i  
0.11368 + 0.10612205i  
0.11368 - 0.10612205i  
0.068991 + 0.054314410i  
0.068991 - 0.054314410i  
-0.04292  
0.191134

## Appendix 16

### The Estimation of Harvest Functions David Finnoff

Let:

$\pi_t^i$  = annual harvesting profits for  $i = \{pollock(species\ 4), cod(species\ 13)\}$

$N_t^i$  = populations

$h_t^i$  = annual harvests

$e_t^i$  = harvesting effort

$p^i$  = price of harvested fish

$c^i$  = per unit cost of harvesting effort

Annual profits are given by:

$$\pi_t^i = p^i h_t^i - c^i e_t^i$$

with harvest functions given by:

$$h_t^i = q^i (e_t^i)^{a^i} (N_t^i)^{b^i}$$

Writing annual profits in terms of harvests:

$$\pi_t^i = p^i h_t^i - c^i \left( \frac{h_t^i}{q^i (N_t^i)^{b^i}} \right)^{\frac{1}{a^i}}$$

For pollock, the application is to the “catcher processor” (CP) Bering Sea and Aleutian Island (BSAI) Walleye (Alaska) pollock (*Theragra chalcogramma*) fishery. The CP fleet consists of factory trawler vessels that both catch and process pollock. The fishery has been limited to domestic vessels and heavily regulated under the Eastern Bering Sea/Aleutian Island (BSAI) Fishery Management Plan (FMP) since 1991. The FMP regulates the fishery through total allowable catches, variable season lengths, permits and limited entry, gear restrictions, area restrictions, bycatch limits

and rates, and allocations (Witherell, 2001).

Complicating the use of data from this fleet are the consequences of regulatory change in the fishery. Since 1999 the American Fisheries Act (AFA) has limited pollock fishery access to designated vessels and processors (and has included a buyout of some vessels) in order to eliminate the race for fish. These regulatory changes make the standard bioeconomic use of a single measure of effort problematic. For simplicity we define effort by the number of vessels participating in the fishery. In the period preceding the initiation of the AFA capacity limitation program, this single measure of effort can be expected to be a reasonable proxy. But, following the AFA this measure is fixed by regulation, perhaps losing its explanatory power. This makes only years of data before 1999 appropriate for use in the estimation.

The data for annual harvests  $h_t$  as given by the fleet's pollock catch in metric tons, harvesting effort  $e_t^4$  as given by the number of vessels in the fleet each year, and the prices per metric ton for pollock  $p_t$  come from the National Marine Fisheries Service (NMFS), the Alaska Department of Fish and Game (ADFG), and the U.S. Coast Guard (USCG) compiled by Terry Hiatt at the Alaska Fisheries Science Center.

The harvest function was estimated using a logarithmic transformation and OLS. Although only 5 years of data were available at the time of estimation the model displays a high goodness of fit with an  $R^2$  of 0.96 and estimates of the parameters as given below (with standard errors in parentheses):

Each of the estimated parameters of the harvest function is significantly different than zero above the 0.1 level of significance.

The price of harvested pollock  $p_t$  was estimated from a regression of observed harvests on  $e_t^4$  value (for the period of data used in the harvest function estimation). In this we assume revenues are generated only from sales and therefore

we forced the intercepts through zero. With all values converted to be in terms of 2000 dollars, the price of pollock was estimated to be  $p_4 = \$614$  per ton, with standard error of 33.9414, or significant at better than the 0.001 level (with an  $R^2 = 0.99$ ). Cost of effort  $c_4$  was similarly estimated from the rent exhaustion condition of the open access structure of the fishery over the data's time series. All costs are assumed to be attributable to the measure of effort and again we force the intercept through zero. The cost of pollock effort was estimated (in 2000 dollars) to be  $c_4 = \$7,368,806$  with standard error of 310342, and again significant at better than the 0.001 level (with an  $R^2 = 0.99$ ).

**Table 14: Parameters in the Pollock Harvest Function**

Parameter	Estimate	P-value
q4	4574.616 (0.9512)	0.0125
a4	0.2245 (0.0740)	0.0937
b4	0.2494 (0.0638)	0.0597

An identical procedure was followed for Pacific cod. To estimate the cod harvest function, we used a time series (1992-2000) of Eastern Bering Sea (EBS) catcher processor harvests, effort (given by the number of catcher processors processing Pacific cod) and cod biomass estimates gathered from Northern Economics Inc. and EDAW (2001), Northern Economics (2001) and National Marine Fisheries Service (2003). OLS regression of the logarithmically transformed data provided a high goodness of fit with an  $R^2=0.91$  and coefficient estimates as given below (with standard errors in parentheses):

While only the estimate of  $a_{13}$  is significantly different than zero above the 0.05 level of significance, given the lack of available data the estimated coefficients are employed in the simulations.

**Table 15: Parameters in the Cod Harvest Function**

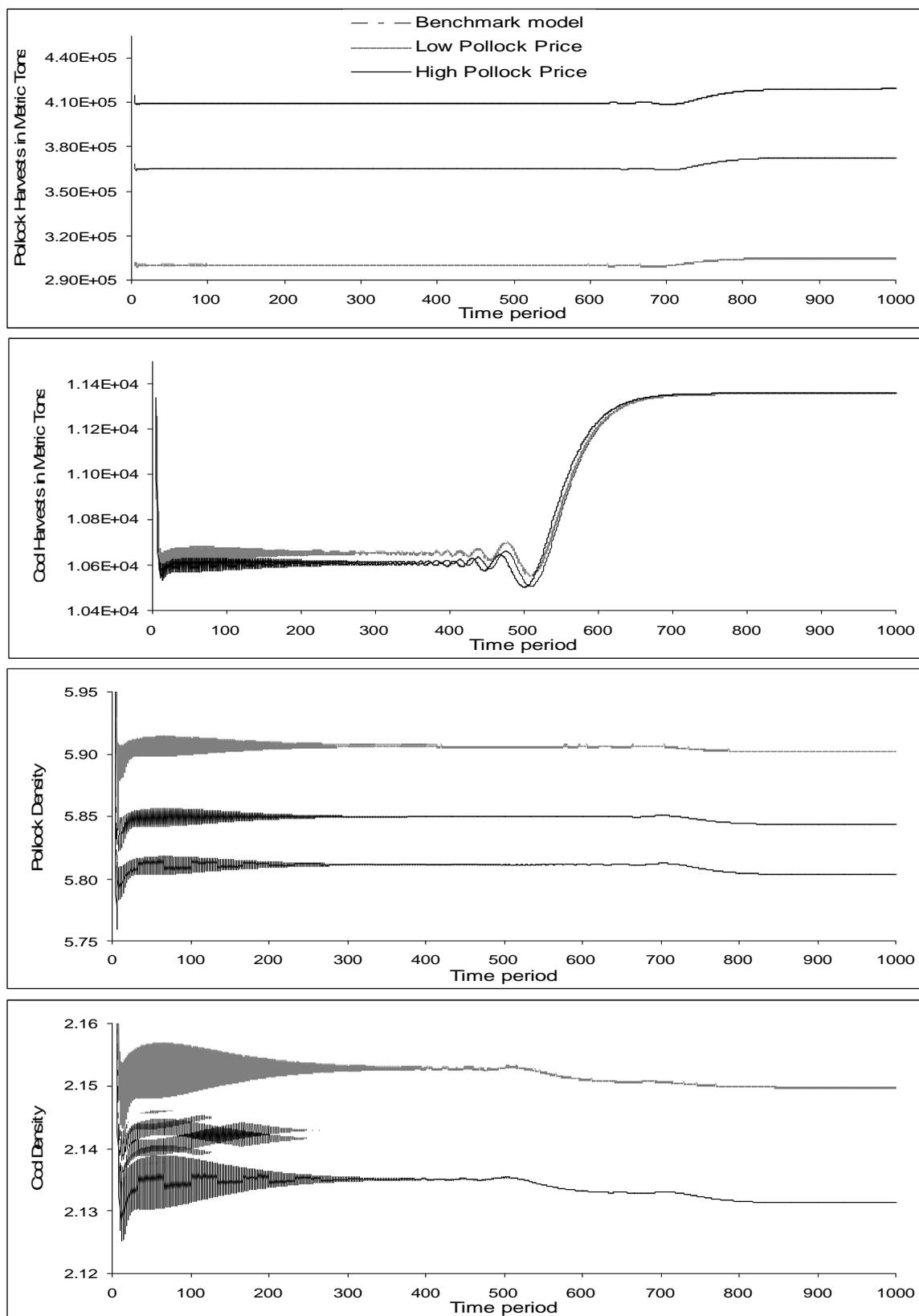
Parameter	Estimate	P-value
q13	4.2370 (5.7146)	0.8090
a13	0.6888 (0.2441)	0.0303
b13	0.4506 (0.4670)	0.3718

The price of cod p13 was estimated as for pollock from a regression of observed harvests on exvessel values. All values were expressed in 2000 dollars with price estimated to be  $p13 = \$489$  per ton, with standard error of 55.5308, or significant at better than the 0.001 level (with an  $R^2 = 0.91$ ). Cost of effort c13 was estimated from the rent exhaustion condition of the open access structure of the fishery over the data's time series. The cost of cod harvesting effort was estimated (in 2000 dollars) to be  $c13 = \$316,843$  with standard error of 33363, and again significant at better than the 0.001 level (with an  $R^2 = 0.92$ ).

In the simulations all monetary values were converted to be in terms of millions of 2000 dollars.

## Appendix 17

Figure 14a: Comparative Simulations of the Pollock Price



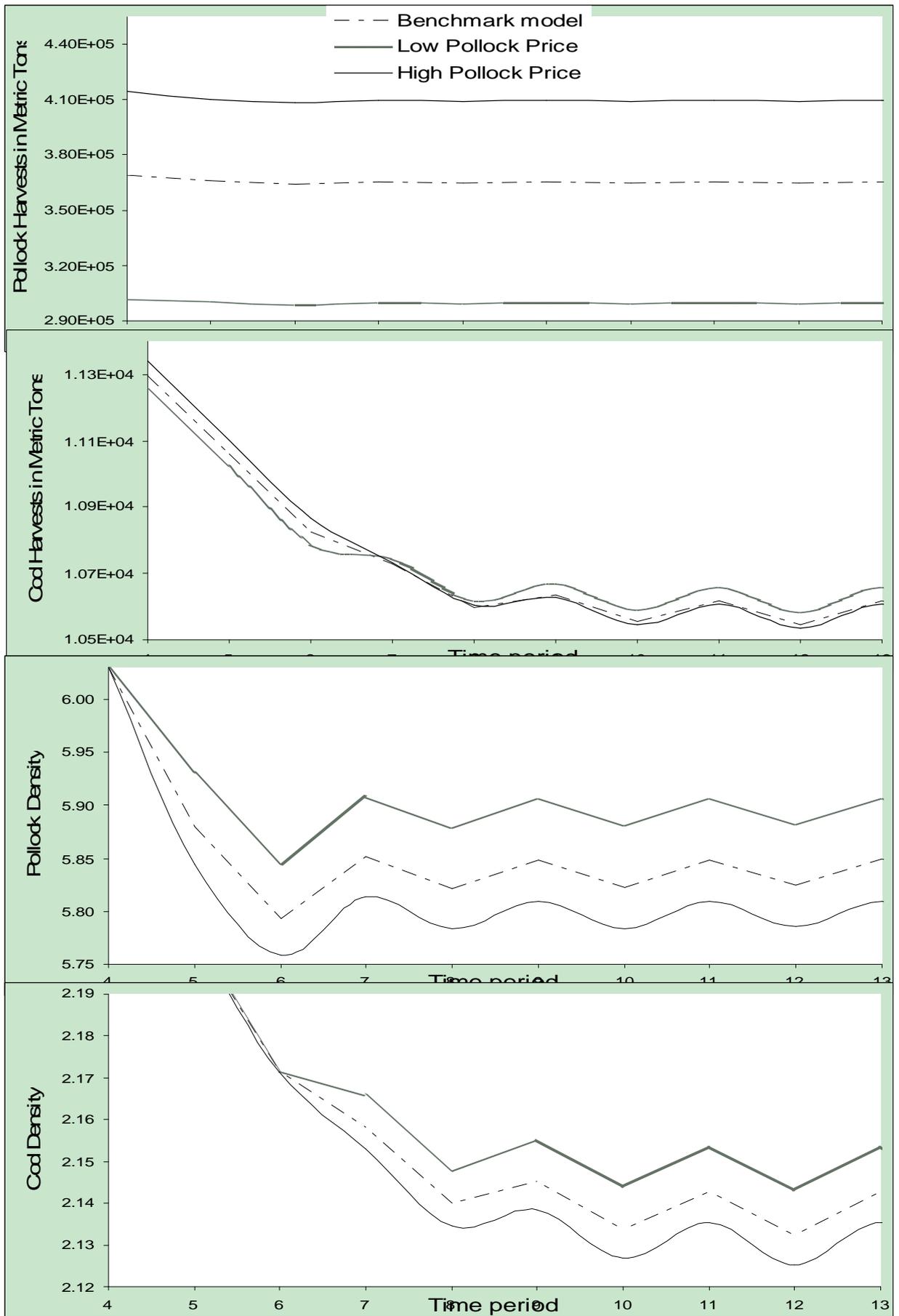


Figure 14b: Comparative Simulations of the Pollock Price (first 10 periods)

### Appendix 18

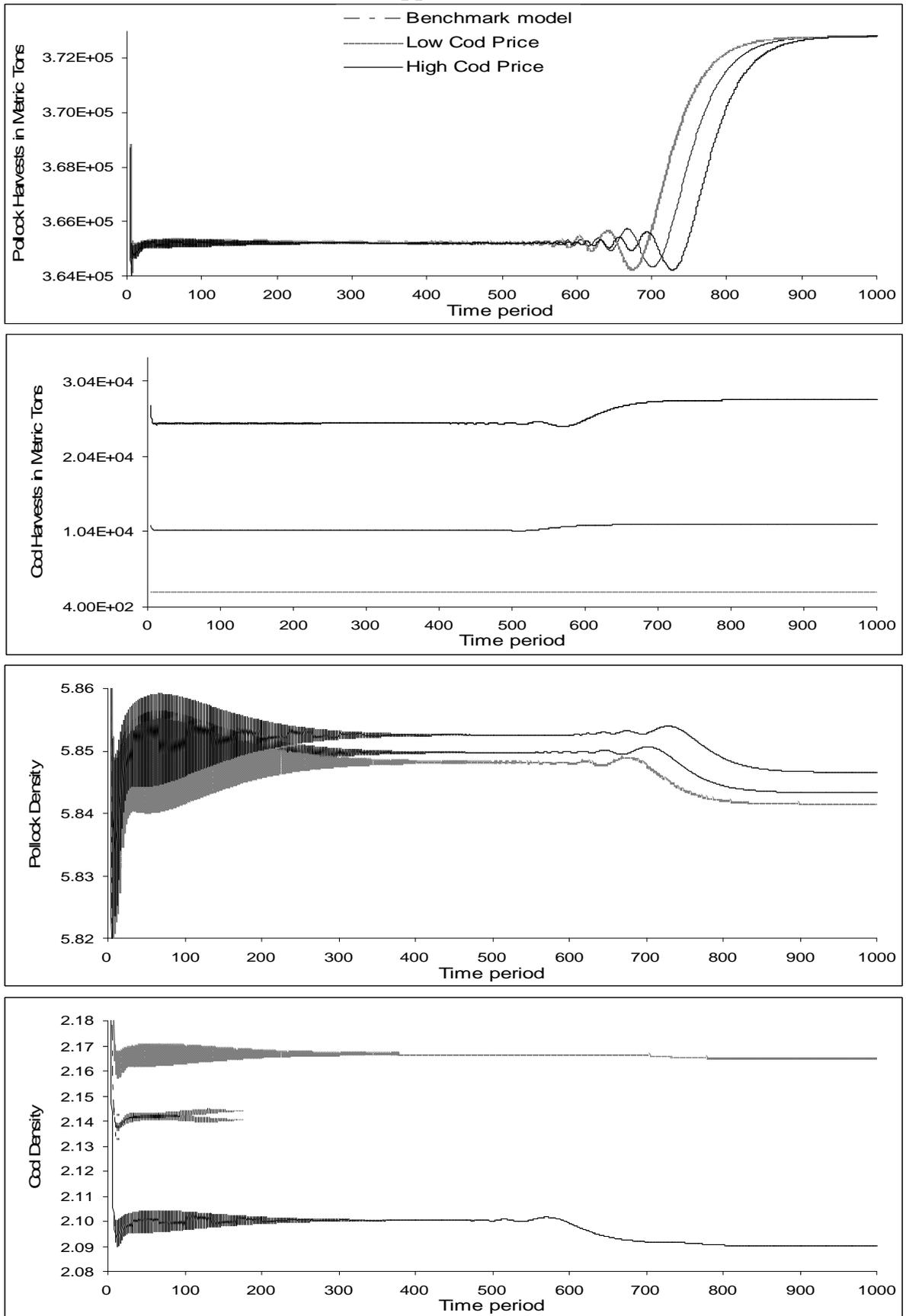


Figure 15a: Comparative Simulations of the Cod Price

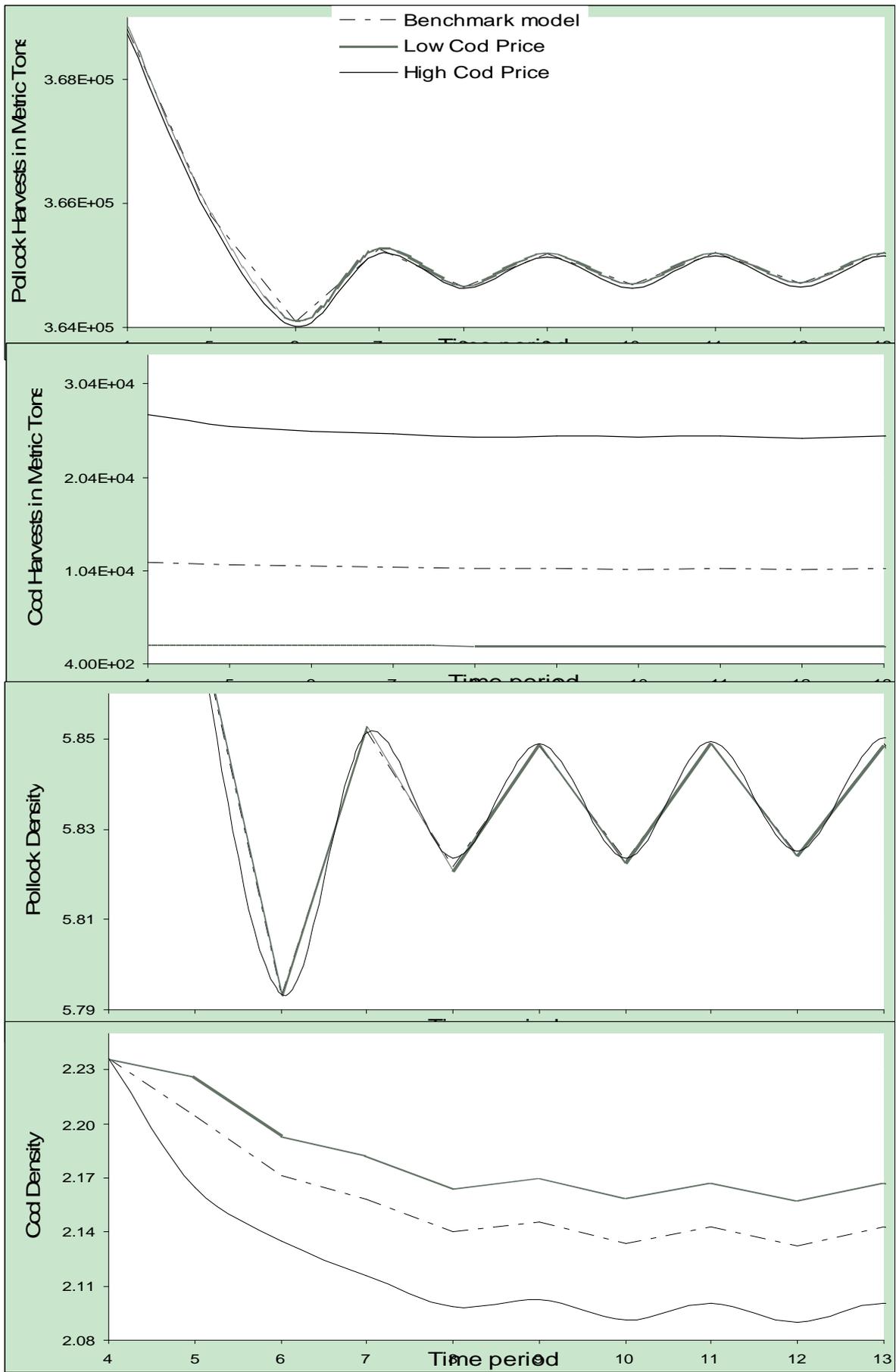


Figure 15b: Comparative Simulations of the Cod Price (first 10 harvesting periods)

## Appendix 19

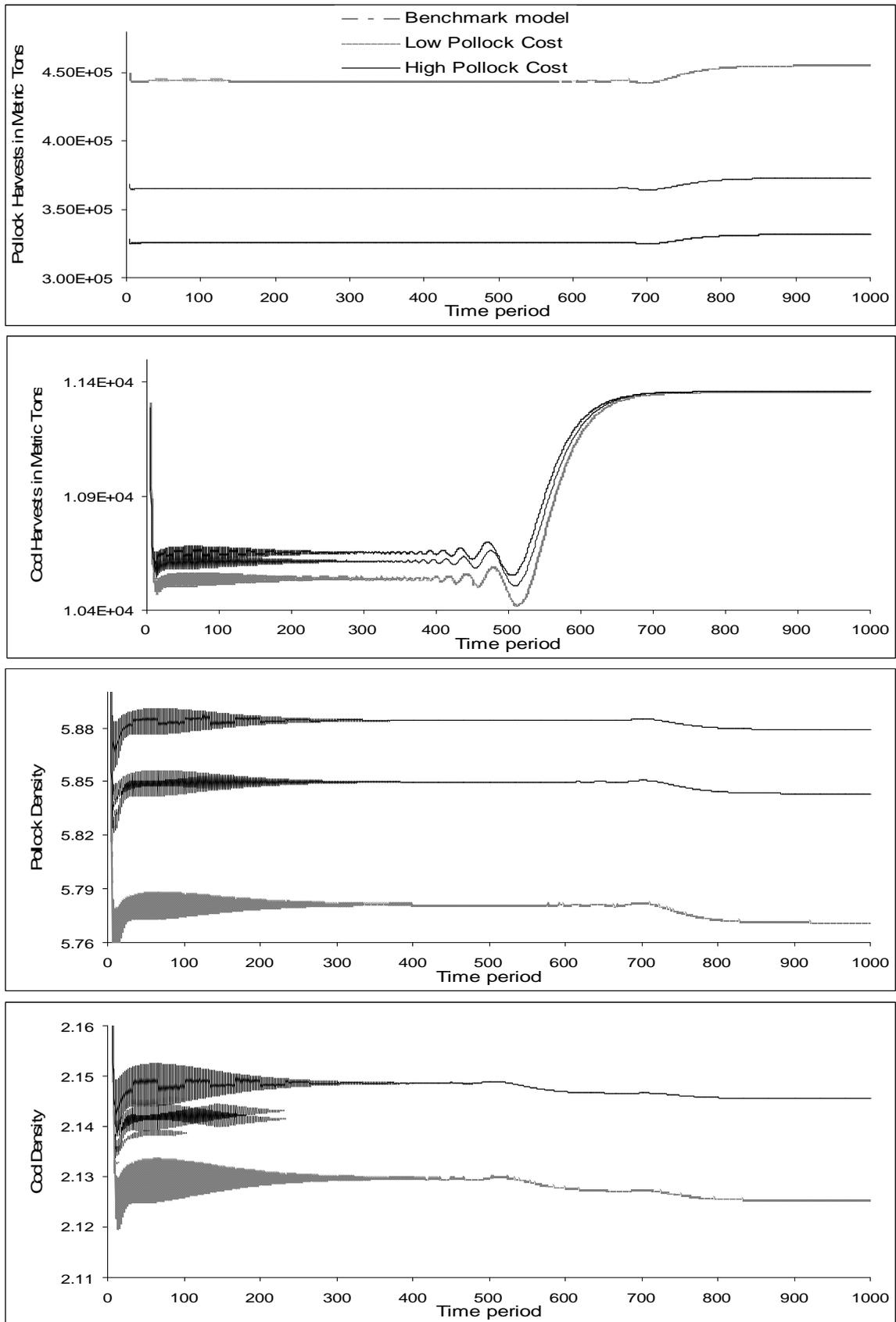


Figure 16a: Comparative Simulations of the Pollock Cost

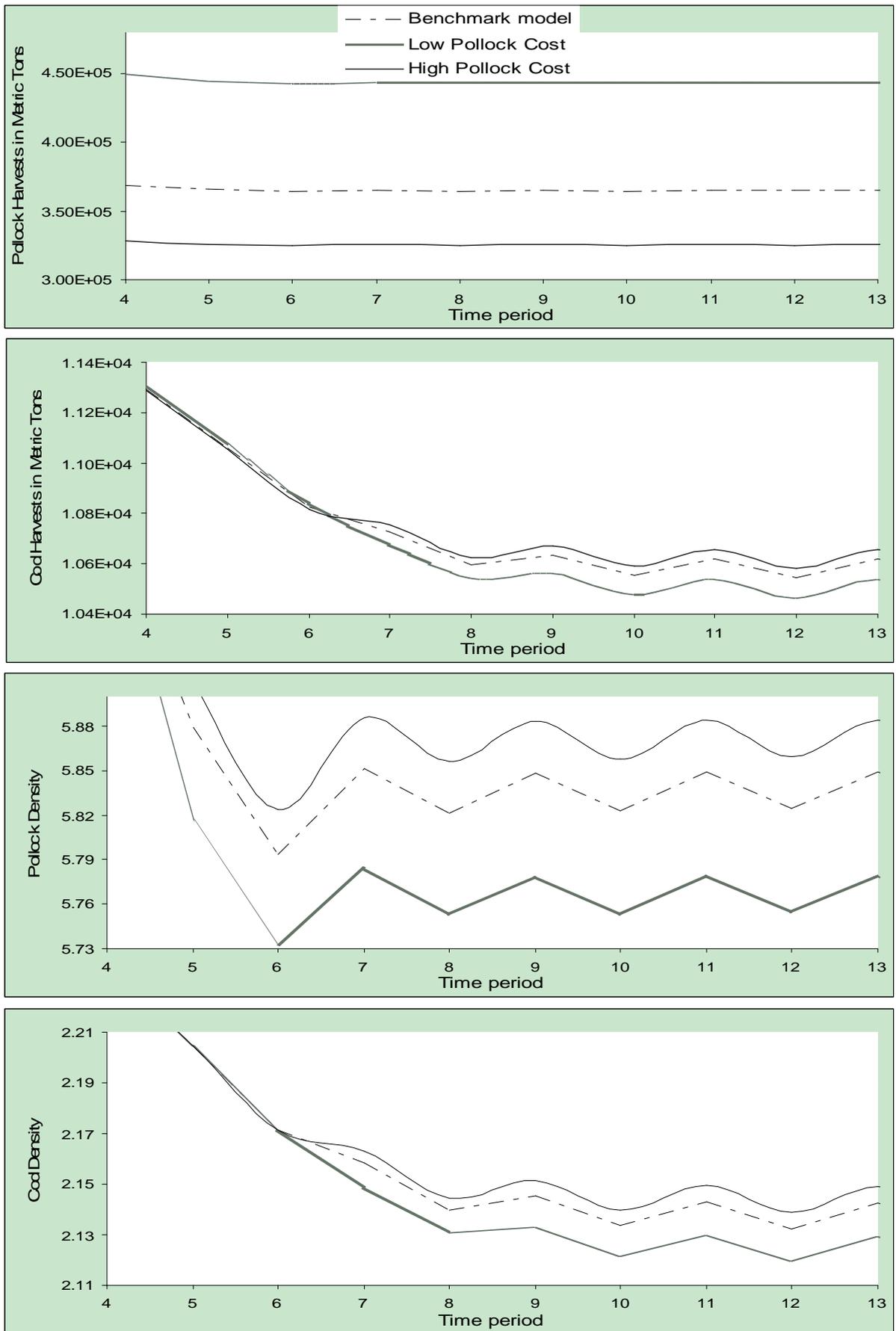


Figure 16b: Comparative Simulations of the Pollock Cost (first 10 periods)

## Appendix 20

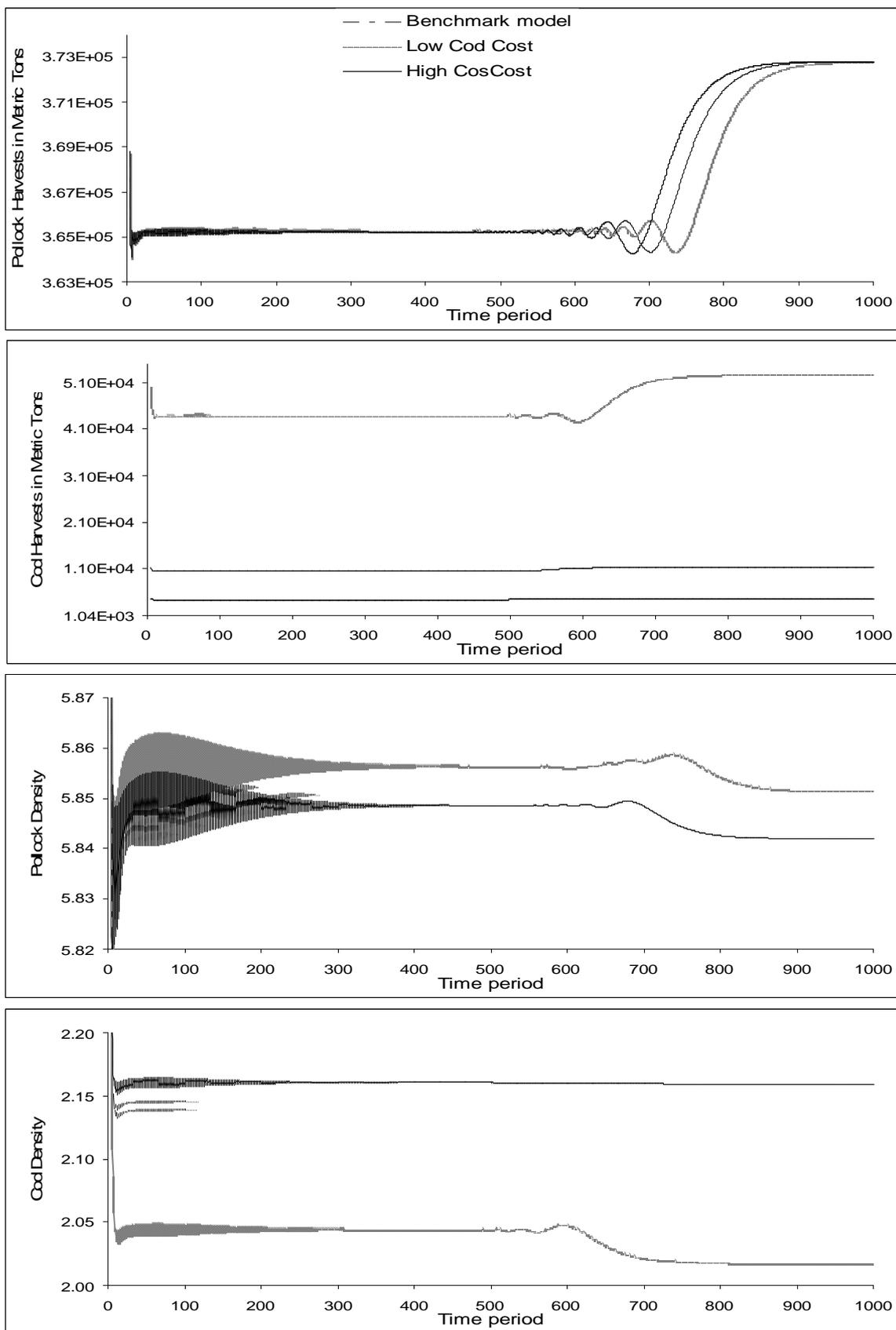


Figure 17a: Comparative Simulations of the Cod Cost

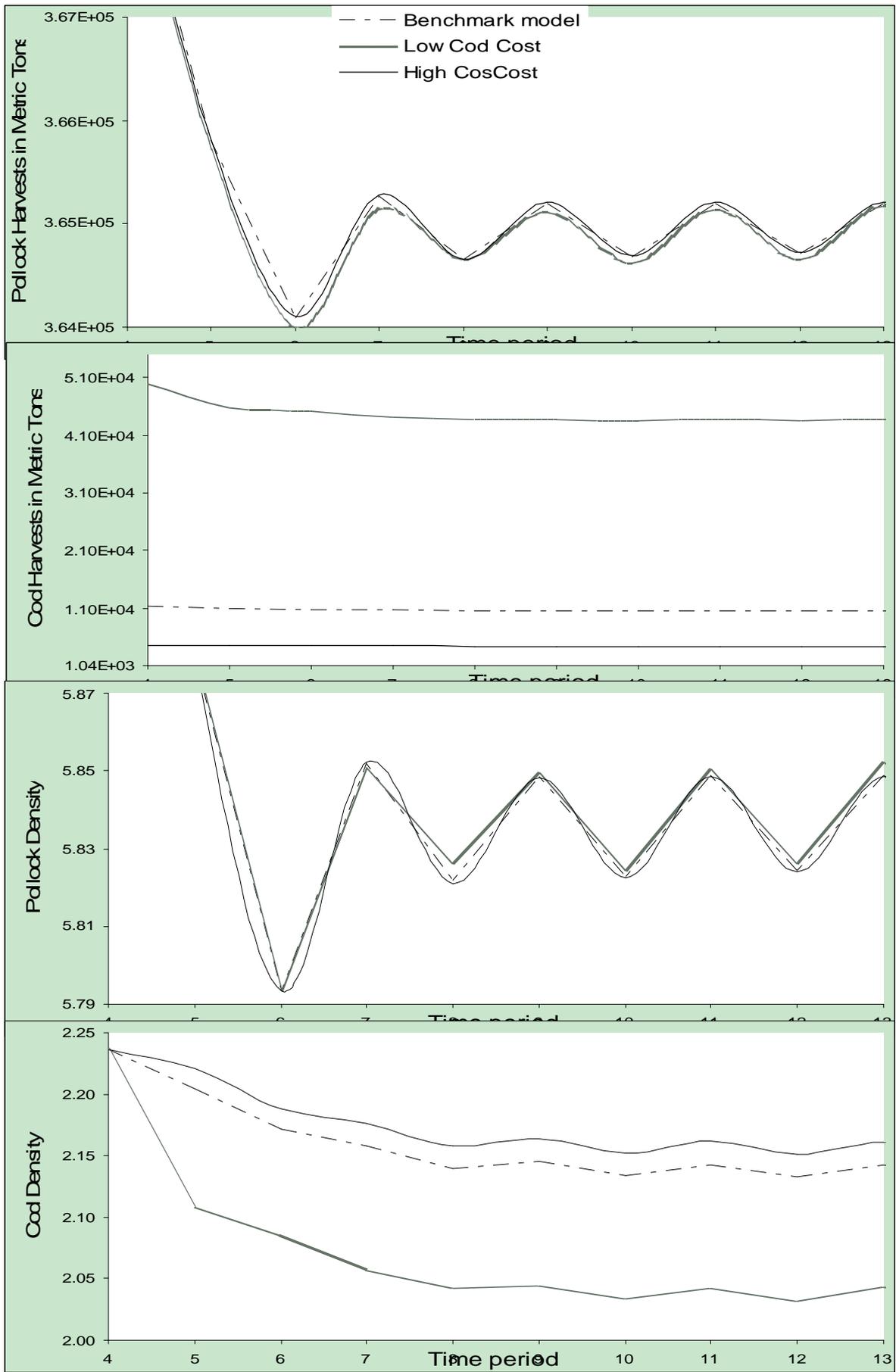


Figure 17b: Comparative Simulations of the Cod Cost (first 10 periods)

## Appendix 21

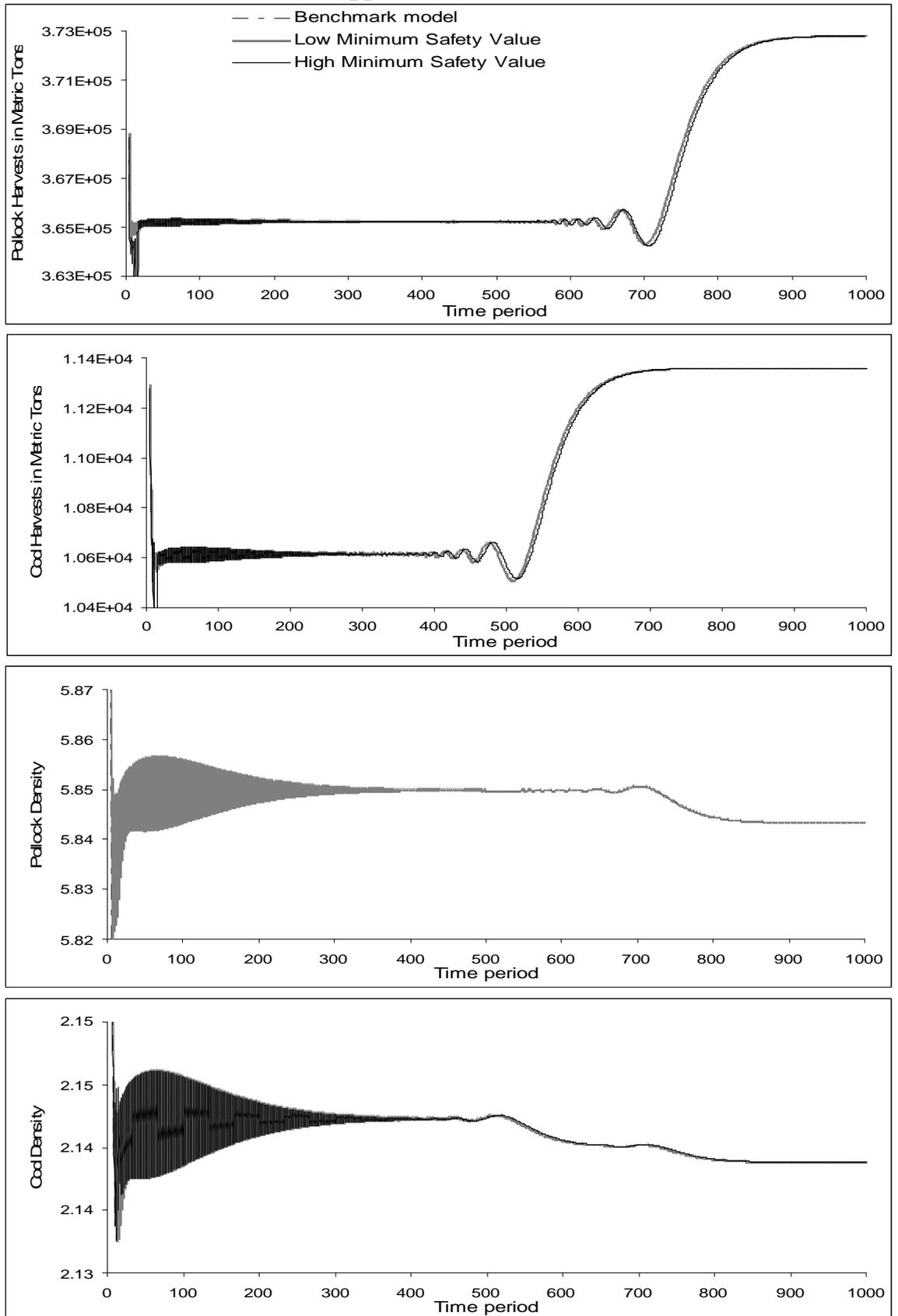


Figure 18a: Comparative Simulations of the Minimum Safety Values of Sea Lion

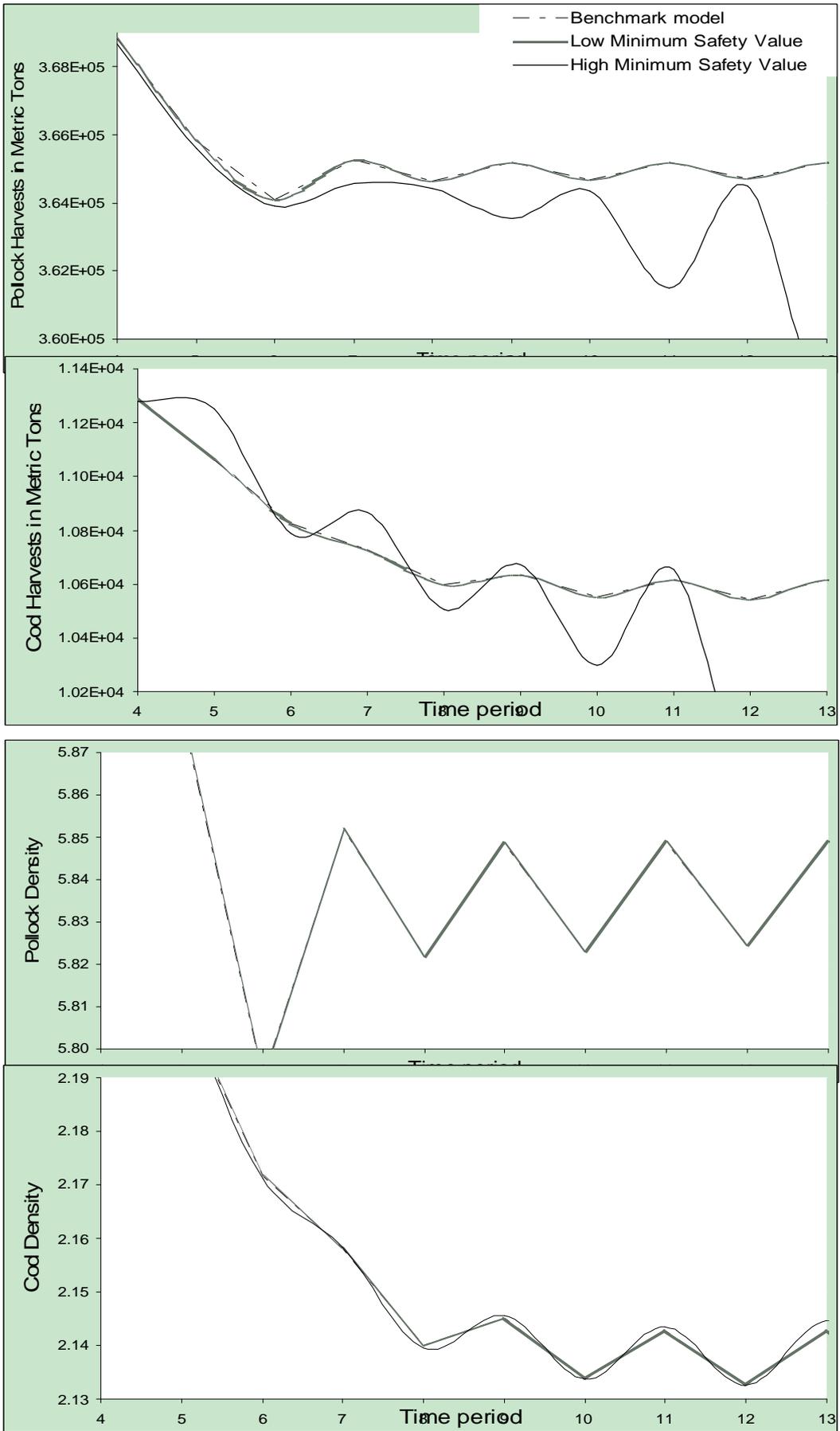


Figure 18b: Comparative Simulations of the Minimum Safety Values of Sea Lion (first 10 periods)

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