

Harvesting in an Eight Species Ecosystem*

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Abstract

The theory for a general equilibrium ecosystem model that can include large number of interacting species is presented. Features include: 1) individual plants and animals are assumed to behave *as if* they are maximizing their net energy intake, 2) short and long-run equilibriums are obtained, 3) species' population adjustments depend on individual net energies. The theory is applied using simulations of an eight-species Alaskan marine ecosystem for which a "natural" equilibrium is calculated. Humans are introduced by adding a regulated open access fishery that harvests one of the species. Fishing impacts the fish population as well as the populations of other species, including Stellar sea lions, an endangered species. The sensitivity of fish and non-fish species populations to harvesting are calculated.

Keywords: ecosystems and economics, bioeconomic harvesting, multispecies ecosystem

There exists a growing sense among resource scientists that scientific effort should be directed at multiples species, community and ecosystem approaches. (van Kooten and Bulte, 2000, p. 217)

I Introduction

In the promising field of bioeconomics, perhaps nowhere have biology and economics been integrated more closely than in fishery models. Following the work of Gordon (1954), economists have made liberal use of the biology inherent in the familiar Schaefer curve to describe optimal harvesting of fish and other species under a variety of economic conditions.¹ In addition, the biology has been extended to allow for harvesting multiple species that are in mutualistic or predator-prey relationships (egs. Quirk and Smith, 1970; Clark, 1976; Hannesson, 1983; Ragozin and Brown, 1985; Conrad and Adu-Asamoah, 1986; Wilen and Brown, 1986; Flaaten, 1991; Flaaten and Stollery, 1996; Stroebele and Wacker, 1995; and Wacker, 1999).

The latter advance is important because in reality a harvested species is always in one or more predator-prey relationships with other species that, in turn, are in still other predator-prey relationships. The ecosystem to which the harvested species belongs is a complex web of numerous interacting species, many of which may affect and be affected by harvesting decisions. Because ecosystems provide indispensable human services (Heal, 2000), understanding these affects can improve natural resource management. However, as pointed out by Munro and Scott (1985):

“Modeling these interactions in the real world proves to be a daunting undertaking.

Indeed, more often than not, the undertaking proves to be impossible.” (p. 646)

This paper offers a new approach that permits large numbers of interacting species in a bioeconomic model of harvesting. The approach employs a general equilibrium model of an ecosystem that resembles a general equilibrium model of an economy (Tschirhart, 2000).

¹ See Munro and Scott (1985) for a synopsis.

In the next section the features of the general equilibrium (GE) model are discussed and the concepts of short-run and long-run equilibrium are presented. Section III provides a simulation of an Alaskan marine food web comprising marine plants, zooplankton, sea urchins, fish and mammals. Then in Section IV humans are introduced into the model through their harvesting choices. Section V is a brief conclusion.

II The GE Model of an Ecosystem

II.A Features of the GE Approach

Before presenting the GE ecosystem model, five features that distinguish it from other bioeconomic approaches are summarized:

- 1) *Nonhuman individuals are assumed to behave rationally.* Rational behavior, of course, is a cornerstone in models about human economic behavior, although it is less frequently exploited in biology. But Lotka (1925) stated: “greater efficiency in utilizing energy...must work to the advantage of a species talented in that direction.” (p. 357) Lotka’s observation suggests that successful individuals behave *as if* they maximize their net energy intake.²
- 2) *Many species interact in complex food webs.* Economic GE models may comprise large numbers of consumers and firms (in many industries) interacting in many markets. Similarly, the ecosystem GE model may comprise large numbers of plants and animals (in many species) interacting in many predator-prey relationships, or biomass markets.
- 3) *Short and Long-run equilibriums are pertinent.* Short-run equilibrium is defined as a state wherein individuals are maximizing their net energies and the maximum energies may be nonnegative; however, there are biological market forces that drive these net energies to zero in long-run equilibrium. Long-run stability depends on plant and animal life spans and other

² Whether energy is an appropriate objective is subject to debate, and other objectives such as emergy (Mejer and Jorgensen, 1979) or ascendancy (Ulanowicz, 1980) have been proposed. Energy maximization has its roots in Lotka (1922), was formalized in a manner similar to that used here by Hannon (1973, 1976, 1979), and according to Herendeen (1991) has been the most frequently chosen maximand. The net energy objective function used below has been referred to as “the quantity which natural selection requires every animal to maximize. (Pennycuik, 1979)

parameters specific to individuals.

4) *Population adjustments depend on net energies.* In population biology models, plant and animal populations adjust according to population growth functions with lumped parameters that are meant to capture characteristics of entire species or interactions between entire species. An example used often in economics is the single-species logistic growth function. The difference here is that the parameters in the growth functions are individual characteristics and individual net energies; thus, micro behavior is linked to macro outcomes.

5) *The model uses familiar economic concepts.* The ecosystem is modeled as if each species is an industry. Where industries are comprised of firms, species are comprised of individuals. Where firms are assumed to maximize profit, predators are assumed to maximize net energy intake. Firms respond to input price signals to substitute across inputs, predators respond to energy prices signals to substitute across biomass from alternative prey. Physiological functions govern species' transformations of captured (input) energy into predation and respiration (output) energy, similar to the way firms' production functions transform inputs into outputs.

II.B The GE Model³

B.1 Maximizing Behavior

The ecosystem contains m (non human) species divided into plants (autotrophs) that are indexed $1, \dots, p$, and animals (heterotrophs) that are indexed $p+1, \dots, m$. All plants “prey” on the sun by producing biomass that they use to fix solar energy. The plant's biomass production is referred to as their demand for biomass, and there is one biomass market in which all plants participate. The animals may prey on plants and other animals, and they are arranged such that individuals in higher numbered species may prey on individuals in lower numbered species, but not vice versa. If an animal in species $i > p$ preys on an individuals in species j , $j = 1, \dots, i-1$, then

³ More detail of the model can be found in Tschirhart (2000, 2002) and Pethig and Tschirhart (2001).

species i is said to demand biomass from species j , which supplies biomass. The transfer of biomass is said to take place in an ecosystem market, and if there are m species in total and one plant market, then the maximum number of markets is

$$1 + (m - p)p + \sum_{i=p+2}^m (i - p - 1) \quad (1)$$

where the first one refers to the plant market, the second term is the maximum number of markets in which animals prey on plants, and the last term is the maximum number of markets in which animals prey on animals. In a real food web the actual number of markets will be considerably less than in (1).

Each individual is assumed to behave as if it is a net energy maximizer where net energy is the difference between energy inflows and outflows. All energy in the ecosystem originates with the sun, indexed by 0, is fixed by plants, and ends up either stored by the plants and animals or flows to the atmosphere via plant and animal respiration.

Animals

A general expression for the net energy of a representative animal individual from species i , $i = p+1, \dots, m$ is given by:

$$R_i = \sum_{j=1}^{i-1} [e_j u_{ij} - e_{ij}] x_{ij} - \sum_{k=i+1}^m e_i u_{ik} y_{ik} - f^i \left(\sum_{j=1}^{i-1} x_{ij} \right) - \beta_i \quad (2)$$

where the e terms are in energy units per biomass units (e.g., kcalories/kilograms (kcal/kg)) and the x and y are biomass flows (e.g., kgs/year (kg/y)). Thus R_i is in power units (e.g., Watts).

The first term on the right side of (2) is the inflow of energy from individuals of other species (including plants) to species i . The e_j is the energy (heat content) embodied in a unit of biomass from a member of species j , e_{ij} is the energy the member of species i must spend to locate and capture a unit of biomass of species j , and x_{ij} is the biomass transferred from the member of species j to the member of species i . Predators are often unsuccessful in locating and

capturing prey, and the $u_{ij} < 1$ reflects this reality by allowing less than the full amount of embodied energy to flow to the predator. In the simulations, u_{ij} is a function of e_{ij} to indicate that the greater is the energy spent on locating and capturing prey, the greater are the number of unsuccessful attempts.

The second term is the outflow of energy to animals of species k that prey on i . The e_i is the embodied energy in a unit of biomass from an animal of species i , and y_{ik} is the biomass supplied by i to k . Again, the u_{ik} term reflects lack of success in predation, although here from the prey's perspective. The third and fourth terms in (2) represent respiration which is energy lost by the individual to the atmosphere. Following Gurney and Nisbet (1998), respiration is divided into two parts, the variable respiration, $f^i(\cdot)$, which depends on energy intake and which includes feces, reproduction, defending territory, etc. Assuming differentiability,

$$\frac{\partial f^i(\cdot)}{\partial x_{ij}} > 0, \text{ for } i = p+1, \dots, m, j = 1, \dots, m, j < i \quad (3)$$

The second part of respiration, β_i , is resting metabolic rate and it is independent of energy intake.

Both $f^i(\cdot)$, and β_i are measured in Watts.

The embodied energy terms, e_i , are constants and assumed to be invariant. The energies spent in predation, the e_{ij} , are the energy prices. As in economic GE models, the prices play a central role in the maximization process, because an individual's choice of prey will depend on the relative energy prices it pays.⁴ Also, individuals are assumed to be price takers: they have no control over the price paid to capture prey, because each is only one among many individuals in

⁴ Prey preference has been examined elsewhere (See Gutierrez (1996) for a summary.) and predators are assumed to prefer one prey over another according to indices based on relative densities of the prey species. The model presented here is behaviorally more fundamental in that a predator's choices do not depend on its taking an inventory of available prey species to determine densities; instead, a predator's choices depend on how much energy will be lost in locating and capturing one prey versus another. Of course, the energy prices the predator must pay likely depends on densities, but densities are accounted for in the GE model through the equilibrium conditions involving many species, and not in the individuals' maximization problems. Analogously, in a competitive economic model a firm demands inputs from other firms based on prices, and not on how many suppliers there are of the input.

a predator species capturing only one of many individuals in a prey species. However, within the ecosystem the prices are endogenous, being determined in the biomass markets by demand and supply interactions explained below.

In maximizing (2), the individual would prefer to supply zero biomass ($y_{ik} = 0$) to other individuals since outflows reduce net energy. However, an individual can supply zero biomass only if it demands zero biomass in the sense that to capture prey biomass the individual risks being captured by other predator individuals, and the more biomass an individual captures the more it is exposed and the more biomass it supplies to predators.⁵ Because individuals are subject to predation risk, the biomass they supply can be written as a function of their demand:

$$y_{ik} = y_{ik} \left(\sum_{j=1}^{i-1} x_{ij} \right), \text{ for } i = p, \dots, m, \quad (4)$$

(Note that this representation is similar to, but in reverse from, a firm whose supply of output determines its demand for inputs.) Assuming differentiability of (4):

$$\frac{\partial y_{ik}(\cdot)}{\partial x_{ij}} > 0, \text{ for } i, j = 1, \dots, m-1, k = p+1, \dots, m, j < i < k \quad (5)$$

A problem of interpretation arises in the maximization problem, because once an animal is successfully preyed upon, it is gone. No further maximization takes place for this member. To avoid this discrete, zero/one issue, the maximization problem is assumed to represent the ‘average’ member of the species. Thus, when the animal is captured it does not lose its entire biomass, but rather it loses biomass equal to the mean loss over all members of its species.⁶

The representative animal in species i , $i = p, \dots, m$, behaves as if it maximizes expression (2) over all its demands, x_{ij} , $j = 0, \dots, i-1$. The necessary first-order condition for a maximum is:

⁵ This tradeoff between foraging gains and losses is called predation risk (See, e.g., Lima and Dik, 1990).

⁶ For example, if the species population consisted of 100 fish and 5 were captured by sea lions, then the biomass supplied from each representative ‘average’ fish would be 0.05.

$$[e_j u_{ij} - e_{ij}] - \sum_{k=i+1}^m e_i u_{ik} \frac{\partial y_{ik}}{\partial x_{ij}} - \frac{\partial f^i}{\partial x_{ij}} = 0, \text{ for } j = 1, \dots, i-1 \quad (6)$$

Conditions (6) states that the animal maximizes net energy by setting the marginal energy received from predation on species j (the first term in (6)) equal to the marginal energy lost to predation by species k , where the loss is a result of being preyed upon (second term), plus marginal respiration (third term). Expressions (6) also lays out the conditions for predator substitution between prey species in terms of marginal rates of substitution equaling energy price ratios.⁷

Assuming second-order sufficient conditions for a maximum are satisfied,⁸ the first-order conditions can be solved for the x_{ij} as functions of the energy prices to yield i 's demands:

$$x_{ij}(\mathbf{e}_i) \equiv x_{ij}(e_{i1}, \dots, e_{i,i-1}), \text{ for } j = 1, \dots, i-1 \quad (7)$$

where the boldface $\mathbf{e}_i = (e_{i1}, \dots, e_{i,i-1})$ is a vector of energy prices. Substituting these demands into the y_{ik} yields the representative animal i 's supplies:

$$y_{ik}(\mathbf{x}_i(\mathbf{e}_i)) \equiv y_{ik}(x_{i1}(e_{i1}, \dots, e_{i,i-1}), \dots, x_{i,i-1}(e_{i1}, \dots, e_{i,i-1})), \text{ for } k = i+1, \dots, m \quad (8)$$

where the boldface $\mathbf{x}_i = (x_{i1}, \dots, x_{i,i-1})$ is a vector of demands.

Using standard comparative static analysis, the effect of price changes on the animals' optimum demands can be determined. Of particular interest is that demands are downward sloping and supplies are upward sloping; that is, as the energy price the animal pays to capture prey increases (decreases), the demand for the prey decreases (increases), and the supply of the prey increases (decreases):

$$\frac{\partial x_{ij}}{\partial e_{ij}} < 0 \quad \text{and} \quad \frac{\partial y_{ji}}{\partial e_{ij}} > 0 \quad (9)$$

for all $i = p, \dots, m$ and $j < i$.

⁷ For details at the species level, see Hannon (1976) or Crocker and Tschirhart (1992), and at the individual level see Tschirhart (2000).

⁸ The second-order conditions place bounds on parameters in the variable respiration functions (Tschirhart, 2000).

Plants

A general expression for the net energy of a representative plant individual from species i is given by:

$$R_i = [e_{i0} - e_0] x_{i0} - \sum_{k=p+1}^m e_i u_{ik} y_{ik} - f^i(x_{i0}) - \beta_i \quad (10)$$

The first term on the right side of (10) is the incoming energy from the sun. The e_{i0} ($\text{kcal kg}^{-1} \text{y}^{-1}$), which is a constant but different across species, is the solar energy fixed for each unit of biomass, x_{i0} (kg), that the plant in species i produces from photosynthesis. The e_0 is the energy price spent to fix e_{i0} , and all plants are assumed to face the same energy price that is determined in the solar/plant market as explained below.⁹ The remaining terms in (10) are similar to those in the animal objective function. (Note that predation risk applies to plants as well. For example, a plant must produce leaves to fix energy, and the leaves are then exposed to predators. Plants utilize myriad weapons to discourage predators, and producing the weapons also consumes energy.) The first-order condition for maximizing (10) is also similar to the animal first-order condition, and inverting the conditions yields the plant demands:

$$x_{i0} \equiv x_{i0}(e_0), \text{ for } i = 1, \dots, p \quad (11)$$

that can be substituted into the y terms to obtain the plants' supplies to animals.

B.2 Short-Run and Long-run Equilibrium

The short run is that time over which the populations of all species are constant. In a short-run equilibrium, demand equals supply in every biomass market and a representative individual and its species may have negative, zero or positive net energy at the maximum. Nonzero net energy leads to long run changes, however. Positive (negative) net energy is

⁹ A distinction between plants and animals is that for the former the energy terms, e , are flows and the biomass terms, x , are not flows, and for the latter the energy terms are not flows and the biomass terms are flows. The distinction is made because plants compete for exposure to light or physical space, and it is convenient to represent the plant choice variable, x , as occupying space.

associated with greater (lesser) fitness and an increasing (decreasing) population, and populations adjust toward a long-run equilibrium in which all individuals have zero net energy and the short-run equilibrium conditions hold. (The analogy in a perfectly competitive economic model is that the number of firms in an industry changes according to whether profits are positive or negative.)

Consider first the short run. To find a set of prices that equates each demand with its associated supply, an equilibrium equation is needed for each price. The market equilibrium conditions involving animals are constructed by equating the sum of all the predator animals' demands with the sum of all the prey animals' or plants' supplies. Because each animal in (2) is assumed to be a representative individual from that species, all animals in each species are identical; therefore, to obtain the demand and supply sums, multiply the representative individual's demands and supplies by the population of the species. Let N_i be the population of species i , then the equilibrium conditions are:

$$N_i x_{ij}(\mathbf{e}_i) = N_j y_{ji}(\mathbf{x}_j(\mathbf{e}_j)) \quad (12)$$

for $i = p, \dots, m$ and $j = 1, \dots, i-1$. There is one condition for each market, and the maximum number of markets is given by the second and third terms in (1). The left side of (12) is the total demand of species i for species j , and the right side is the total supply of species j to species i .

The plant market wherein primary producers prey on the sun works as follows. The sun's supply is assumed to be limitless which is consistent with primary producers fixing only a small fraction of the solar energy striking their surface. However, the physical space occupied by the plants in the ecosystem is finite and equal to A which is measured in biomass units but can be converted to units of area as well. If the plants do not fill A then there is no competition for sunlight and the energy price they pay is zero (i.e., $e_0 = 0$). This is labeled the noncompetitive state of plant growth (See Tschirhart, 2002). In the competitive state the plants have reproduced

and/or grown larger to fill A , and the energy price is positive because plants must now compete for sunlight. In this paper only the competitive state is considered so that $e_0 > 0$ and the plant market clearing condition is:

$$\sum_{i=1}^p N_i x_{i0}(e_0) = \tau A \quad (13)$$

where τ is a congestion parameter.

Finding a set of energy prices that yields a short-run equilibrium is a matter of simultaneously solving the first-order conditions from (2) and (10) and the equilibrium conditions from (12) and (13) for the demands and the energy prices. There is a first-order condition for each demand and a market clearing condition for each price, so the number of equations equals the number of variables. Theoretical conditions on the functional forms of the net energy functions that guarantee a solution exists are not explored here, although in the simulations below solutions are found for specific parameters.

A system in short-run equilibrium moves toward long-run equilibrium through adjustments in the populations that will move the species toward zero net energy. For instance, suppose an animal species has positive net energy and its population increases. This increase lowers the energy price predators must pay to capture the species' members, because the species is more plentiful. Predators' demands for the species will increase by (9), the species' supply to predators will increase by (9), and net energy will decrease. In addition, the price paid by members of the species for their prey will increase as there is more intra-species competition when the species' population grows. This price movement will also reduce the species' net energy as the species demands less prey, a result that follows by applying the envelope theorem to (2). For a species with negative net energy in short-run equilibrium, the prices move in the opposite directions, and again the species moves toward zero net energy.

The update equations are derived as follows. Consider population changes for species i that, for simplicity, is assumed to be a top predator. (A top predator is simpler to work with because there are no predation terms in (2).) In steady-state it must be the case that births equals deaths. Moreover, if s_i is the lifespan of the representative individual, then the total number of births and deaths must be N_i/s_i . Dividing the totals by N_i yields the per capita birth and death rates:

$$1/s_i \tag{14}$$

The logic behind (14) is that in a steady state each individual over its lifetime must replace itself exactly once. If the individual lives s_i periods, then on average in each period it reproduces $1/s_i^{th}$ of itself.

Now consider the i^{th} species, $i = 1, \dots, m$, with maximum net energy function given by $R_i(x_{ij}; N^t) = R_i(\cdot)$ which is obtained by substituting the optimum demands as functions of energy prices into objective functions (2) or (10). N^t is a vector of all species' populations and it appears in $R_i(\cdot)$ to indicate that net energies in time period t depend on populations in time period t . In the steady state $R_i(x_{ij}; N^t) = R_i(\cdot) = 0$. Reproduction requires energy and, by the definitions of the terms in the individual's objective function, that energy must be contained in the variable respiration, or the third term on the right side of (2). Let \hat{V}_i be the steady-state variable respiration, and let $\rho \hat{V}_i$ be the proportion of this variable respiration devoted to reproduction. Thus, in steady state the energy given by $\rho \hat{V}_i$ yields a per capita birth rate of $1/s_i$. Next, suppose the species is not in steady state and that $R_i(\cdot) > 0$ and variable respiration is V_i . Assuming that the proportion of $R_i(\cdot)$ that is available for reproduction is the same as the proportion of variable respiration available for reproduction, the energy now available for reproduction is $\rho [R_i(\cdot) + V_i$

]. Finally, assuming that reproduction is linear in available energy, then it follows that if $\rho\hat{V}_i$ yields a per capita birth rate $1/s_i$, then $\rho[R_i(\cdot) + V_i]$ yields a per capita birth rate of:

$$(1/s_i) [R_i(\cdot) + V_i] / \hat{V}_i . \quad (15)$$

The change in population is obtained by multiplying the population by the difference between the birth and death rates, where it seems reasonable to assume the latter rate is independent of energy available for reproduction. Therefore, using (15), the population adjustment equation is

$$\begin{aligned} N_i^{t+1} &= N_i^t + N_i^t \left[\frac{R_i(\cdot) + V_i}{s_i \hat{V}_i} - \frac{1}{s_i} \right] \\ &= N_i^t + N_i^t \frac{1}{s_i} \left[\frac{R_i(\cdot) + V_i}{\hat{V}_i} - 1 \right] \end{aligned} \quad (16)$$

Expression (16) reduces to the steady state if $R_i(\cdot) = 0$ (in which case $V_i = \hat{V}_i$), because the bracketed term is zero. Alternatively, $R_i(\cdot) > (<) 0$ implies that $V_i > (<) \hat{V}_i$, in which case population increases (decreases).¹⁰

If the species is not a top predator and is prey for another species, then in steady state the births must equal the deaths *plus* any individuals lost to predation. This complication yields a population adjustment equation given by (17) (Tschirhart, 2001).

$$N_i^{t+1} = N_i^t + N_i^t \left[p + \frac{(1-p)^s}{s} \right] \left[\frac{R_i(\cdot) + V_i}{\hat{V}_i} - 1 \right] \quad (17)$$

where $p = \frac{y_{ik}}{w_i}$ is the predation rate, or the biomass lost to predation divided by the weight of the

individual, w_i , which when multiplied by the population gives the number of individuals lost to predation.

¹⁰ That the sign of R_i determines whether respiration is greater or less than steady-state respiration follows from applying the envelope theorem to the maximization problem.

Before leaving the population adjustment equations, compare (17) to other population models that start with a set of difference or differential equations, one equation for each species. The simplest example of these models, and the one usually employed in economic models that address ecology, uses the well-known Verhulst-Pearl logistic equation which in discrete time is:

$$N_i^{t+1} = N_i^t + g_{si} N_i^t [1 - N_i^t / K_i^t] \quad (18)$$

In (18), g_{si} is the intrinsic growth rate and K is the carrying capacity. More sophisticated ecological models have more species in either predator/prey or mutualistic relationships;¹¹ however, the equations often contain lumped parameters (i.e., g and K in (18)) that do not vary over time. Yet in real ecosystems species i 's carrying capacity and growth rate will depend on the density of other species. Some authors address this dependence by introducing stochastic growth rates or stock uncertainty (e.g., Reed, 1979; Pindyck, 1984; Clark and Kirkwood, 1986). As an alternative to introducing stochasticity, update equation (17) explains at least some of the randomness in growth and stocks because p , $R_i(\cdot)$ and V_i depend on all other populations and on predation. Moreover, p , $R_i(\cdot)$ and V_i are species dependent and they change period-to-period depending on the demand and supply interactions among all species.^{12,13}

III Simulation of An Alaskan Marine Ecosystem

III.1 Equations and Variables A marine ecosystem that links Alaska's Aleutian Islands

¹¹ Gutierrez (1996, Chpt. 5) surveys models in which the ratio of prey eaten per predator is a function of the prey population. Whether the ratio is linear, strictly concave or strictly convex in the prey population defines the prey's "functional response." The term $\sum_{j=1}^{i-1} [e_j u_{ij} - e_{ij}] x_{ij}$ in (2) is similar to functional response in that it gives the

biomass of prey eaten per the representative predator. However, in our model this functional response is optimally chosen each period in response to energy prices, making the above term more in line with optimal foraging theory.
¹² Species dependency is consistent with Deacon (1989) who points out that population adjustment should vary across species.

¹³ For the case of one plant species, holding all other plant populations fixed, reduced form equations can be obtained for steady-state population, biomass and energy (Tschirhart, 2002):

$$\hat{N}_i = \left(\frac{r_i}{\beta_i} \right)^{0.5} [A - \sum_{i \neq j} x_{j0} N_j] \quad \hat{x}_i = \left(\frac{\beta_i}{r_i} \right)^{0.5} \quad \hat{e}_0 = e_i - 2(r_i \beta_i)^{0.5}$$

(AI) with the Eastern Bering Sea (EBS) is used to illustrate the model. The ecosystem is represented by the food web in Figure 1. There are two plant markets. In the EBS, various species of phytoplankton are aggregated into a single species called phytoplankton and they are the plants in the EBS.¹⁴ A kelp forest comprises the plants in the AI, where kelp is an aggregation of various species of brown and red algae. The phytoplankton and kelp are the sources of all energy that flows through the ecosystem. Various species of zooplankton are aggregated into a single species that feeds on phytoplankton. Pollock are an important ground fish in the EBS and they feed on zooplankton. Steller sea lions, an endangered pinniped species, feed on the Pollock, while killer whales feed on the sea lions. Killer whales also feed on sea otter that in turn feed on various species of sea urchin that in turn feed on the kelp. There are many other species that interact with these eight species in the EBS and the AI that are not included in the model, and more will be said about their omission below.

From (2), the net energies of a representative individual of phytoplankton, kelp, zooplankton, pollock, Steller sea lion, urchin, otter and killer whale, indexed 1-8, respectively, are given by (19)-(26), respectively:

$$R_1 = [e_{01} - e_{10}]x_{10} - e_1 d_{31} x_{10}^5 - r_1 x_{10}^2 - \beta_1 \quad (19)$$

$$R_2 = [e_{02} - e_{20}]x_{20} - e_2 [1 - te_{62}]d_{62} x_{20}^5 - r_2 x_{20}^2 - \beta_2 \quad (20)$$

$$R_3 = [e_1 - e_{31}]x_{31} - e_3 [1 - te_{43}]d_{34} x_{31}^5 - r_3 x_{31}^2 - \beta_3 \quad (21)$$

$$R_4 = [e_3 [1 - te_{43}] - e_{43}]x_{43} - e_4 [1 - te_{54}]d_{45} x_{43}^5 - r_4 x_{43}^2 - \beta_4 \quad (22)$$

$$R_5 = [e_4 [1 - te_{54}] - e_{54}]x_{54} - e_5 [1 - te_{85}]d_{58} x_{54}^5 - r_5 x_{54}^2 - \beta_5 \quad (23)$$

$$R_6 = [e_2 [1 - te_{62}] - e_{62}]x_{62} - e_6 [1 - te_{76}]d_{67} x_{62}^5 - r_6 x_{62}^2 - \beta_6 \quad (24)$$

¹⁴ Aggregating species in food webs is common practice in ecological modeling (Solow and Beet, 1998).

$$R_7 = [e_6[1-te_{76}] - e_{76}]x_{76} - e_7[1-te_{87}]d_{78}x_{62}^5 - r_6x_{62}^2 - \beta_6 \quad (25)$$

$$R_8 = [e_5[1-te_{85}] - e_{85}]x_{85} + [e_7[1-te_{87}] - e_{87}]x_{87} - r_8x_{85}^2 - r_8x_{87}^2 - \beta_8 \quad (26)$$

The terms in (19)-(26) containing d_{ij} predation parameters are the supply functions:

$y_{ik} = d_{ik}x_{ij}^5$ in which the i th species is supplying biomass to the k th species, and demanding biomass from the j th species. The terms containing the r_i parameters are the variable portions of respiration in (2) and (10): i.e., $f^i(\cdot) = r_ix_{ij}^2$. The exponent value on the x_{ij} in the supply functions ensures that an increase (decrease) in the population of a prey species lowers (raises) the energy price paid by the predator species to capture the prey, and the exponent value on x_{ij} in the variable respiration function satisfies the second-order sufficient conditions for a maximum (Tschirhart, 2000). For the killer whales, variable respiration is divided into two parts, which allows for differences in the prices whales must pay in equilibrium for otters and pinnepeds. The terms containing t are the u_{ij} terms in (2) and (10) (i.e., $u_{ik} = I - te_{ki}$) and they represent energy not transferred owing to unsuccessful hunting attempts.¹⁵

A short-run equilibrium is obtained by solving for eighteen variables: nine demands (x_{ij}) including the two biomasses of the two plants and the seven biomass flows for the six animals (two flows for the killer whales), and the nine prices including two paid by plants (e_{i0}) and seven paid by animals (e_{ij}). Nine equations are obtained from setting the derivatives of (19)–(26) with respect to the demands equal to zero, and the other nine equations are the equilibrium conditions:

¹⁵ Suppose predator j makes n attempts at locating and capturing prey k , and s attempts are successful and u are not, $s+u = n$. The energy to the predator is $[se_k - ne_{jk}] = [ne_k - ue_k - ne_{jk}]$ and from the prey is $[se_k + ne_{esc}] = [ne_k - ue_k + ne_{esc}]$ where e_{esc} is energy spent escaping capture which is ignored in this paper so that $e_{esc}=0$. Success in locating and capturing prey is assumed to be a function of how much energy is spent on these activities; for example, a lynx that spends little energy locating and/or capturing a hare is enjoying successful hunts. The function is assumed to take the simple form $u(e_{jk}) = ne_{jk}$ where t is chosen to ensure $u < n$. Substituting ne_{jk} for u above, the energy to the predator becomes $[ne_k - nte_{jk}e_k - ne_{jk}]$ and from the prey becomes $[ne_k - nte_{jk}e_k]$. Dividing both terms by n to put the energy on a per unit of biomass basis yields the net price terms in (19)–(26).

$$N_3x_{31} = N_1d_{13}x_{10}^5 \quad (27) \quad N_6x_{62} = N_2d_{26}x_{20}^5 \quad (28)$$

$$N_4x_{43} = N_3d_{34}x_{31}^5 \quad (29) \quad N_7x_{76} = N_6d_{67}x_{62}^5 \quad (30)$$

$$N_5x_{54} = N_4d_{45}x_{43}^5 \quad (31) \quad N_8x_{87} = N_7d_{78}x_{76}^5 \quad (32)$$

$$N_8x_{85} = N_5d_{58}x_{54}^5 \quad (33)$$

$$N_1x_{10} = \tau_1A_1 \quad (34) \quad N_2x_{20} = \tau_2A_2 \quad (35)$$

Conditions (27)-(33) are from (12) and conditions (34) and (35) are from (13). In the latter two conditions the subscripts 1 and 2 on the right sides refer to the EBS and the AI, respectively.

The procedure for running the simulations is in two steps: 1) start with fixed populations for the eight species and use the above eighteen equations to solve for the demands (x_{ij}) and prices (e_{ij}), and 2) use the demands and prices to adjust the populations according to (16) for killer whales and (17) for the other species then go back to step one. Each set of two steps comprises a time period. If the populations converge over time then a steady state is obtained.

III.2 Data The initial simulations are run sans harvesting by humans. There is no single study that contains the data needed to run simulations; however, by consulting a variety of ecological studies of the Alaskan and other ecosystems, a data set was constructed. The parameter values and the variables used to construct the parameters are listed in Table 1. All data are from around 1980. The notes for Table 1 contain the data sources and comments on parameter construction.

To understand some of the issues involved in assembling the data, consider the Steller sea lions. In 1980 the population of sea lions was 125,000 (no distinction is made between adults and juveniles). To make the magnitude of the population more manageable, which becomes very important for the species such as zooplankton with very large numbers, the population was divided by the square kilometers of surface area of the EBS (1,300,000) to obtain the population

per square kilometer (0.096154).

The biomass flow or demand of the sea lions was taken from experiments in which the daily caloric requirement of sea lions was measured. The caloric value was converted to a biomass flow by dividing it by the number of calories embodied in a kg of pollock. A complication arises, however, because in the wild sea lions are known to eat octopus and squid and other fish species besides pollock. Because only pollock are in the model, only the sea lion intake of pollock was reflected in their biomass demand. Using studies that estimate 76% of the sea lion diet in the wild is fish, of which 40% is pollock, yields the result of 1332 kg y⁻¹ of pollock.¹⁶ The sea lion demand and population (along with the demand and population for the killer whale) can be substituted into equilibrium condition (33) to obtain the predation parameter d_{78} . The resting metabolic rate was obtained from a formula relating a mammal's weight to its fixed respiration. Embodied energy e_7 is available in the ecological literature.

For a plant there are two additional parameters. Consider phytoplankton. A rough rule of thumb is that 10% of the energy taken at one trophic level is passed on to the next trophic level, although for marine communities a 20% transfer rule has been estimated. 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 $e_{01} = 15150 \text{ kcal kg}^{-1} \text{ yr}^{-1}$. The phytoplankton congestion parameter, τ_1 , was obtained by substituting the phytoplankton demand and population into (34). Because the population of phytoplankton was in the sextillions, the population was converted to population units where each unit is 1×10^{12} individuals. Furthermore, the populations were converted to unit km⁻² as described above for sea lions. All populations were converted to population units except for sea lions.

Finally, the variable respiration parameters r_i for all species were obtained through

¹⁶ This method whereby a predator's energy intake is confined to reflect only the prey included in the model was also used for killer whales. It was not necessary to confine the energy intake for the other predator species because they prey mostly on species included in the model. For example, urchin prey exclusively on kelp.

calibration. Assuming that in 1980 the ecosystem was in steady state, then all $R_i = 0$ and all species are maximizing their net energies. Therefore, the demands, populations and all parameters for all species, except the r_i parameters, were substituted into the nine first-order conditions and into (19)-(26) set to zero, and these seventeen equations were solved for the r_i and the e_{io} . The r_i were then used as the variable respiration parameters in simulating short-run equilibriums and they also were used to obtain the variable respirations in steady state as needed in the update equations (16) and (17).

III.3 Long-run Population Adjustments. All populations were adjusted according to (16) and (17) after each short-run equilibrium simulation. Each simulation and subsequent adjustment takes place in one period, and a period is assumed to be one year. Individuals are assumed to reproduce once per year, which is reasonable for all species except phytoplankton that can reproduce every few days and zooplankton that can reproduce every few weeks, and both of which may have lifespans less than one year. To adjust for the rapid turnover of the planktons, their weights in (17) were multiplied by 365 to put them on a daily basis, and the longevity term was redefined to be length of life divided by the number of times the individual reproduces over the life. (For nonplankton species this redefinition does not change s_i since they live more than one year and reproduce once per year.)

Population adjustment equations (16) and (17) contain the steady state variable respiration terms, \hat{V}_i , that are constructed from the r_i parameters. As populations are adjusted period after period these terms are constant. This raises the question: From what steady state are these variable respiration terms obtained? The convention adopted here was that the v_i were from the steady state in which there was no human intervention into the ecosystem, and we refer to this as the *natural* steady state. Of course, humans have been intervening in most ecosystems for thousands of years; thus this convention may need to be altered depending on the ecosystem

being examined and the problem being addressed. For the Alaskan example, the major human intervention in 1980 from which time the data are taken was commercial fishing. Specifically, about 16% of the pollock population was being harvested, mostly by Russian trawlers. Because the r_i and v_i are to represent the steady state in which there is no human intervention, yet they are obtained via a calibration using biomass demand and population data from 1980 when there was intervention, the following two step procedure is adopted: First, the calibration described in subsection III.2 was run with its seventeen equations in addition to equations (36) and (37).

$$N_4^t \left[p + \frac{(1-p)^{s_i}}{s} \right] \left[\frac{R_4(\hat{x}_{43}; N_4^t) + V_4}{\hat{V}_4} - 1 \right] = h \quad (36)$$

$$R_4(\hat{x}_{43}; N_4^t) = 0 \quad (37)$$

where $p = \frac{d_{45}x_{43}^5}{w_4}$ is described in (17). The purpose of adding (36) and (37) was to solve for the pollock variable respiration parameter and the pollock biomass demand in a natural steady state. Equation (36) sets the fish population growth from (17) on the left side with the harvest, h . (The harvest was about 1 billion kg in 1980. (NMFS, EBS Pollock Assessment)) The x_{43} in (36) is the observed biomass demand in 1980 when harvesting occurred and as shown in Table 1; but the biomass demand, \hat{x}_{43} , used to calculate the steady-state variable respiration, \hat{V}_4 , in (36) was solved for in the calibration. This latter biomass demand was then used in (37) which is the pollock net energy in steady state as if there was no harvesting, and (37) then yields the variable respiration parameter, \hat{r}_4 , as if there was no harvesting.

Second, all the parameters from the calibration are used in short-run equilibrium simulations and population adjustments until a new steady state with new biomass demands and populations is generated. The new demands and populations reflect the no harvesting assumption. Next, these new biomass demands and populations are used in a second calibration

to obtain the final variable respiration parameters used in all the results presented below.

III.4 Simulations

Figure 2 displays the populations of the eight species over fifteen years. Because the population magnitudes vary so widely, they are rescaled to fit in the Figure. The initial populations of the eight species were disturbed either up or down from their natural steady state values, and then at or before year 15 they returned to their steady states. Other sets of disturbances were carried out, and the populations converged to the steady state for every combination of disturbances of 50% or less. Convergence to a natural steady state also occurred for disturbances of some species as high as 75%. The simulations suggest some measure of stability, although general stability properties are left for further research.

Table 2 presents the second through fifth periods' short-run equilibrium values from Figure 2 for populations, demands, prices and net energies of the six animals. The values reflect the ecosystem market forces that drive the system to steady state. First, as dictated by the adjustment equations, the sign of the population change for any species between periods is opposite the sign of the net energy. Second, energy prices and biomass demands obey the law of demand. For example, the change from period two to three in the energy price pollock pay to consume zooplankton is $81.7 - 64.3 = 17.4$, and the change in pollock demand for zooplankton is opposite in sign and equal to $5460 - 6930 = -1470$. Third, the population changes determine movements in energy prices. For example, from period two to three, the pollock population decreases and sea lion population increases. Both of these population changes put upward pressure on the price sea lions pay to capture pollock, and there is a relatively large price increase from 137 to 358. Over the next two periods both pollock and sea lion populations decrease: the former puts upward pressure while the latter puts downward pressure on the sea lion price to capture pollock and the net results are relatively small decreases in prices from 358

to 351 to 336. The lower prices yield increased sea lion demands moving from 1127 to 1150 to 1210, and because pollock weigh 1 kg, this demand change means on average each sea lion takes $1210 - 1127 = 83$ more pollock annually.

A whale equates its marginal rate of substitution between sea lion and otter energy intake, calculated as the ratio of derivatives of the respiration functions in (26) to the ratio of marginal energies received from these prey. As relative energy prices change, whales substitute (or switch in ecological terminology) between their two prey species. This is not observable from the numbers in Table 2, because whale net energies are also changing over time. In moving between periods four and five, whale net energy is falling as they are demanding less of both sea lions and otter because the energy prices paid for both species are rising. The rising energy prices follow from greater intraspecific competition among whales owing to an increasing whale population. Between the periods a representative whale unit demands $648 - 559 = 89$ fewer sea lion units and $32.2 - 28.8 = 3.4$ fewer otter units. In non-adjusted figures these results imply that each whale consumed 4.45 fewer sea lions and 0.089 fewer otter per year. For the entire whale population this implies 4557 fewer sea lion and 91 fewer otter taken per year. These changes are not large partially because sea lion and otter together make up only about 10% of the whale diet.

IV. Introducing Humans

IV.1 Equations and Variables

Human harvesting of pollock in the EBS and AI now are added to the ecosystem model. The pollock fishery in the EBS and AI is a relatively recent phenomenon. The first notable exploitation of the fishery began in 1980, largely by foreign vessels in joint venture agreements. Since 1991 the fishery has been limited to domestic vessels and regulated under the Bering Sea/Aleutian Island (BSAI) Fishery Management Plan (FMP). The fishery is heavily regulated and classified as "Not Overfished" and as having "Above Target Biomass" and "Stable Stock

Size" (Witherell, 2000). Management methods have primarily focused on total allowable catches and variable length seasons.

Given the prevalence of regulation in the fishery we closely follow the model (and notation) of a regulated open access fishery presented in Homans and Wilen (1997), written hereafter as HW. HW modify Gordon's (1954) model of an open access fishery to incorporate the fact that since 1976 most fisheries exist under some manner of regulation. The "regulated open access equilibrium" introduced by HW depicts firms that exploit the fishery resource as entering and exiting until all long-run rents accruing to the unpaid resource are dissipated. The regulatory instruments described in HW are total allowable catch, TAC , and season length, T . We maintain this convention for the BSAI pollock fishery.

Seasons are continuous and assumed to start at the beginning of each year t . After the season ends, the remainder of the year is known as "between seasons". Within season, the initial pollock stock is assumed known by both the regulator and fishery participants. The cumulative harvests impact the reproductive stock, with all population dynamics occurring between seasons.

Seasonal cumulative industry harvests, H_t , are a function of fishery capacity, E_t (constant within seasons), each seasons' initial biomass, $N_4^{0,t}$, and T_t . Instantaneous harvests are given by a Schaffer harvest function,

$$H_t = qE_t N_4^{0,t} \quad (38)$$

with catchability coefficient q . Fishery rents, $PH_t - fE_t - vE_tT_t$, are exhausted when the value of cumulative harvests, given exvessel price P , equates the sum of fixed and variable costs, where f is per unit capacity cost and v is per unit capacity cost per unit time (variable effort is assumed to be uniformly applied over the season).

Given the fishery structure, the regulator chooses the TAC_t and T_t in two stages. In the first stage the regulator uses a linear decision rule to determine TAC_t . This "quota" is based on

the season's initial biomass, $N_4^{0,t}$ (equation (5) in HW):

$$TAC_t = a + bN_4^{0,t}. \quad (39)$$

A quota function of this form can be solved for a minimum level of biomass under which harvesting is permitted, N_4^{min} . In the second stage, if $N_4^{0,t} \geq N_4^{min}$ the regulator chooses T_t to achieve the TAC_t . The regulatory and industry behavior are jointly determined: T_t depends on the capacity of the fishing fleet, E_t , the TAC_t and $N_4^{0,t}$, while E_t depends on the TAC_t and T_t . T_t and E_t are determined simultaneously through the rent dissipation condition and the regulatory constraint on season length, given the requirement that H_t exhaust the TAC_t . For any season's initial fish population, the corresponding equations to HW's equations (4) and (7) are:

$$PN_4^{0,t}(1 - e^{-qE_t T_t}) - fE_t - vE_t T_t = 0 \quad (40a)$$

$$T_t = \frac{1}{qE_t} \ln\left[\frac{N_4^{0,t}}{N_4^{0,t} - TAC_t}\right] \quad (40b)$$

Introducing humans also requires modifying the ecosystem model. Given our assumptions on seasons, initial pollock stocks, and population dynamics occurring between seasons, the reproducing population is necessarily net of harvests. Affected ecosystem equations are equilibrium conditions (29) and (31) and the pollock population adjustment. In (29) and (31) the pollock population, N_4^t , is replaced with the residual reproducing population, $(N_4^{0,t} - H_t)$. Using (17), the pollock population adjustment equation becomes:

$$N_4^{0,t+1} = [N_4^{0,t} - H_t] \left[1 + \left[p + \frac{(1-p)^{s_i}}{s} \right] \left[\frac{R_4(\cdot) + \mathbf{v}_4}{\hat{\mathbf{v}}_4} - 1 \right] \right] \quad (18')$$

IV. 2 Data and Simulation

Applying HW's methods to the pollock fishery in the BSAI involved estimating parameters a , b , q , f , and v . Data were gathered for pollock populations, total allowable catches,

season lengths, measures of effort, actual harvests and exvessel prices. Most of the data were gathered from a variety of National Marine Fisheries Service (NMFS) sources. Biomass estimates, total allowable catches and actual catches are from Witherell (2000). We assumed the biomass estimates for the fishery are used by both the regulator and industry in their decisions..

Unfortunately, pollock data were limited to the years 1981-2000, and within these years, only since 1991 has the fishery been limited to domestic fleets, further restricting the explanatory power of the data¹⁷. For season lengths we collected closure reports from the NMFS¹⁸. Sorting over pollock by areas within the BSAI, we totaled days closed per year. The residual of yearly closures was assumed to be the season lengths in days per year. Seasons were assumed to be continuous within each year¹⁹.

Measures of effort in the fishery were constructed from annual NMFS Stock Assessment And Fishery Evaluation (SAFE) Reports, Kinoshita, et al. (1993, 94, 96) and Hiatt and Terry (2000). Trawlers are the dominant gear in the fishery. We used numbers of vessels as a proxy for seasonal capacity in the fishery²⁰. Similar to HW, we assumed a constant efficiency of effort across fishery participants,²¹ and that capacity costs were proportional to actual costs. Finally, exvessel prices were gathered from the same source, expressed in dollars per pound round weight, and they were deflated using the CPI with base year 1982²².

To obtain parameter estimates, HW estimated the biological growth equation independent of all other equations; but the parameters in our growth equation are taken from the calibrations

¹⁷ Reasonable data for the quota function over the years 1980 through 1999 exists. But, given the institutional change in the fishery, we are limited to using observations on the domestic fleet and seasons from 1991 through 1999.

¹⁸ <http://www.fakr.noaa.gov/sustainablefisheries/catchstats.htm>

¹⁹ In reality, seasons are fragmented throughout the year and heterogeneous over area. But, the additional complexity needed to add the notion of space and within season temporal distinction is beyond the scope of this paper.

²⁰ In constructing this measure we use aggregate numbers of vessels of the three major size classes: less than 60 feet, 60 to 125 feet and greater than 125. This neglects any economies of scale that maybe present in larger vessels, but allows us to construct a simple measure of effort from readily available data.

²¹ This is admittedly a strong assumption given the above footnote.

²² U.S. Department of Labor, Bureau of Labor Statistics. <ftp://ftp.bls.gov/pub/special.requests/cpi/cpi.txt>.

in Section III. HW also estimate (39) independently using ordinary least squares, and the same procedure is followed here. HW point out that capacity and season length are determined simultaneously; accordingly they estimate (40a) and (40b) jointly with the cross equation restriction of a constant catchability coefficient. Given the limited pollock data, attempts to follow the simultaneous equation estimation of HW proved unsuccessful. Therefore, we separately estimated equations (40a) and (40b)²³ (with additive errors assumed iid) by ordinary least squares. All estimations were performed with LIMDEP software, and results are displayed in Table 3.

Durbin-Watson statistics were used to test for the presence of autocorrelation. We corrected for first order autocorrelation found in the quota function. Parameter estimates are all of the expected sign and all but ν significant at the 0.1 level or better. Estimating the quota function presented difficulty due to fairly constant *TAC*'s since the fisheries inception (with relatively stable, large populations). A linear quota rule applied to the data for the BSAI did not yield a positive N_4^{min} . To expand the sample, data for quotas and biomass for the Gulf of Alaska (GOA) were appended to the BSAI data. In doing this we assumed the NMFS behaves identically in determining the *TAC* for both regions. Given the expanded dataset, several specifications of Equation (39) were estimated. A quota function with the natural logarithm of biomass gave the best fit.²⁴

In light of the variable definitions, magnitudes of the variables are reasonable. In the estimated quota function, the minimum exploitable biomass level was 875,807 metric tons, or 674 individuals per km². Fixed and variable costs were \$432,000 and \$2335, respectively. The catchability coefficient's magnitude is small due the relatively large size of our measure of variable effort in relation to seasonal catch.

²³ Through a linear transformation.

²⁴ Under this specification the quota function becomes $TAC_t = a + b(\ln[N_4^{o,t}])$

Combining the regulated fishery and ecosystem models requires reconciling ecological and human time scales.²⁵ All species reproductive time scales are on an annual basis, and a continuous fishing season occurs at the beginning of each year. All species reproduction occurs between seasons. The sequence of steps in the period-by-period simulations is: 1) for given beginning-of-the-year species' populations the regulator determines the year's quota; 2) using the quota and the beginning-of-the-year pollock population, fishery participants and the regulator simultaneously determine rent dissipating levels of effort and season length to harvest the quota (through a simultaneous solution of equations (40a) and (40b)); 3) with the pollock population reduced by the level of harvests, a short-run ecosystem equilibrium is calculated which yields energy prices and species' optimal demands and net energies; and 4) species' populations are updated using population update equations from (17). The steps are then repeated with the updated populations used for next year's beginning-of-the-year populations.

IV. 3 Simulation Results

The first simulation results presented in Figure 3 show the impacts of harvesting on the natural ecosystem. For five periods the populations are at their natural steady states shown in Figure 2, and then harvesting begins in period six. Again the population numbers are rescaled to fit on the same graph. The major population impacts are declines in the pre-harvested pollock (2.2%), declines in the Stellar sea lions that prey on pollock (7.6%), and declines in the killer whales that prey on sea lions (7.3%). We will have more to say about these percentages below. The impacts on the other species are too small to be picked up in the graph. A hypothesis put forth in Estes et al. (1998) is that declining sea lion populations have provided an incentive for whales to switch to otter as prey in the AI. Our results do show a very small decline in the otter population that is consistent with substitution by the whales from sea lions to otter as the energy

²⁵ We thank a referee for emphasizing this point.

price the whales pay for sea lions increases.

With respect to human actions, when harvesting is initiated there is a relative abundance of pollock. The fishery immediately hires a large capacity, forcing the regulator to limit the season length. As pollock decline capacity declines (3.2%) and season lengths increase (4.75%).

In the next two simulations that cover years 1980-2001, the harvesting model is initiated on 1980 fish populations when harvesting by Russian trawlers was ongoing. All species move to the steady-state values they attained when harvesting was initiated in the natural ecosystem in Figure 3, the difference being the steady state is reached in fewer periods than in Figure 3, because the starting populations were less than the natural steady state populations owing to ongoing harvesting.

The first simulation covering 1980-2001 is labeled the baseline model and it uses the species parameters described in Section III. As shown in Figure 4, the pollock population moves to a steady state before 1985, because the 1980 populations were already close to their steady-state values. As a sensitivity test that would introduce more oscillatory behavior, we ran a second simulation in which the lifespan of pollock was halved.²⁶ Lifespan enters the fish population adjustment equation given by (18') in a way similar to how the intrinsic growth rate enters the logistic growth function, and it is well known that larger intrinsic growth rates yield more oscillatory patterns. As expected, Figure 4 shows that when lifespan is halved the pollock population oscillates more and does not reach steady state until the late 1990s. Greater oscillations in the pollock population cause greater oscillations in fleet capacity and season length as shown in Figures 5 and 6 that cover 1986-2001. Comparing Figures 4-6 illustrates that peaks (valleys) in pollock populations correspond to peaks (valleys) in capacity and valleys (peaks) in season length.

²⁶ There is extensive evidence that fisheries cause changes in phenotypic evolution of fish including changes in growth rates, fecundity and age-at-sexual maturity (Law, 2000).

Actual populations, capacities and season lengths in Figures 4-6 are less stable than their predicted values. There are numerous ecological variables omitted in the model whose inclusion might explain some of the discrepancies. Consider three: 1) there are many other species in the BSAI marine ecosystems that interact with the eight species included here. For example, Pacific cod are prey for sea lions; moreover, cod also are harvested. 2) There is no age structure in the eight species as all individuals are assumed mature and identical. In fact, predator/prey relationships may depend on age; for example, juvenile sea lions eat smaller pollock than adult sea lions eat (Merrick and Calkins, 1995). 3) Environmental factors can impact some or all species. For example, seasonal and geographic changes in light and ocean temperatures impact phytoplankton populations, and being at the base of the food web such changes can impact all higher species.

Fishery managers confront uncertainties with respect to both ecosystem and economic variables at a time when they are being charged with identifying “the effects of fishing from an ecosystem perspective” (NMFS, Appendix D, p. 3). If uncertainty is considerable in this setting, the Precautionary Principle necessitates that managers take action before the uncertainty is resolved by establishing conservative *TACs* (Hanley et al., 1997). An important source of uncertainty is the interaction between the fish and other species. Knowing how fishing and fish stocks affect other species’ populations would reduce the uncertainty and allow managers to rely more on benefit/cost calculations than on the Precautionary Principle.

An advantage of the ecosystem general equilibrium approach for fisheries is that both the direct impact on the fish and the indirect impacts on other species can be tracked. In our framework, the direct impacts are determined by the magnitude of a and b in the quota function. We conducted a sensitivity test of the regulators choice over these parameters to develop relationships between *TAC* and species’ populations. Holding N_4^{min} constant we varied the level

of b by generating random draws from the uniform distribution, under bounds $\pm 50\%$ of the value of its estimated level. Given the randomly chosen b and N_4^{min} , a is determined. For each combination of a and b and the $TACs$ it yields, we reran the baseline simulation. $TACs$ were regressed against the steady-state populations of pollock, sea lions and whales to obtain elasticities of species populations to TAC . Results are in Table 4.

The pollock elasticity in Table 4 is the percent change in the steady-state population with respect to the percent change in the TAC . There are two pollock elasticities, one uses the pre-harvest populations, the other uses the post-harvest populations. The post-harvest elasticity is much greater because post-harvest populations vary more than pre-harvest populations. After the TAC is harvested, the population falls by the full amount of the harvest. But pre-harvest populations are determined by updating the post-harvest populations, and very different post-harvest populations tend to update to nearly the same pre-harvest populations, because smaller post-harvest populations grow more than larger post-harvest populations. This follows because smaller post-harvest populations are further from the natural steady-state population, and the energy price the pollock pay to capture zooplankton is relatively small while the energy price the sea lions pay to capture pollock is relatively large. Therefore, the pollock net energies will be relatively larger when the pollock population is relatively smaller, and the pollock will reproduce more. (In the model there is no time dimension within each period, so there is no sense of how long a population is in the pre or post-harvest stages. In reality, if the pre and post-harvests are defined by the season length and if we equate the season with pre-harvest, then longer seasons mean more time pre harvest and the more weight we would place on the pre-season elasticity.)²⁷

²⁷ The timing of pre and post-harvest underscores another feature of the general equilibrium approach. In standard fishery models each period is divided into two subperiods - pre and post-harvest. The post-harvest subperiod starts after harvest (H), and the pre-harvest subperiod starts after population updates, or reproduction (R). So over time the sequence is HR HR HR... In our model there is a third subperiod, the short-run equilibrium, or the feeding subperiod (F), when the net energy for each individual is determined. Therefore, timing can be HFR HFR HFR..., or

The sea lion and whale populations do not change from pre- to post-harvest; therefore, their elasticities do not change in Table 4. From a narrow, fisheries only perspective, the low pre-harvest pollock elasticity suggests that significantly more harvesting can be done without heavily impacting the pollock population. But from an ecosystem wide view, the elasticities for sea lions and whales suggest that harvesting's indirect effects on other species may be substantial. In effect, the sea lions and whales can place constraints on harvesting. Stellar sea lions were listed as an endangered species by the NMFS in 1990 and the NMFS has implemented several recovery plans (NMFS, Appendix D). These plans take into account fishing impacts on sea lion populations, and attempts have been made to determine correlations between pollock harvesting and sea lion populations, although results have been mixed and often statistically insignificant (Ferrero and Fritz, 1994). The general equilibrium ecosystem approach offers an alternative method to measure the impacts, a method that avoids estimating lumped parameters and instead builds on the individuals' behaviors and their interactions.

Killer whales are a high profile species and their existence value may be substantial. Killer whales also have both direct positive and negative economic values. People pay to view whales from shore, boats or cruise ships, and at the same time whales prey on fishery catches thereby lowering productivity. Knowing the sensitivity of whale populations to harvesting would help determine the impact of fisheries on these whale-based economic activities.

V Conclusion

Applying the simulation results to policy making for the BSAI fisheries would be premature. Although the model accounts for more of the ecosystem than other bioeconomic fishery models, it is still partial equilibrium and omits potentially important variables as pointed

HRF HRF HRF..... The model is set up above as HFR. HRF will yield smaller pre- and post-harvest populations because the fish are feeding while their population is larger than under HFR (they are feeding after the population reproduces); therefore, their net energies are smaller. When the reproduction occurs, each fish reproduces less owing to its smaller net energy. We do not investigate the differences between HRF vs. HFR in this paper.

out in the previous section. Clearly, more ecological research is needed in order to have confidence in the ecosystem calculations.

A fair question is whether moving from traditional bioeconomic models using aggregate measures to a model that tracks energy flows among individual plants and animals is really necessary for good policy making? But the same can be asked about computable GE models in economics. In the latter models, we are less concerned with individual consumer and firm variables than we are about prices and aggregate incomes. The advantage of the economic GE models is that the aggregate outcomes are based on individual behavior, and tracking that behavior is necessary to get the aggregate outcomes. The same applies to the GE ecosystem model: we are not concerned so much about the energy flow into a sea lion, but it is necessary to track that energy flow if the aggregate population results are to be founded in individual behavior.

Ecosystems provide humans with indispensable services, and virtually all economic activities impact ecosystems. As the general equilibrium approach to ecosystem modeling is improved through further research, it can be used to better understand the social value of the impacts.

References

- Clark, C. W., 1976. *Mathematical Bioeconomics: The Optimal Management of Renewable Resources*. 2nd ed. (1990) New York: Wiley.
- Clark, C. W. and G.P. Kirkwood. 1986. Optimal harvesting of an uncertain resource stock and the value of stock surveys. *Journal of Environmental Economics and Management*, **13**, 234-44.
- Conrad, J. M., and R. Adu-Asamoah, 1986. Single and multispecies systems: The program of tuna in the eastern tropical Atlantic, *Journal of Environmental Economics and Management*, **13**, 50-68.
- Costa, D. 1978. The sea otter: its interaction with man. *Oceanus*, 21, 24-30.
- Crocker, T.D. and J. Tschirhart, 1992. Ecosystems, externalities and economies. *Environmental and Resource Economics*, **2**, 551-567.
- Deacon, Robert T., 1989. An empirical model of fishery dynamics. *Journal of Environmental Economics and Management*, **16**, 167-83.
- Estes, J.A., Tinker, M.T., Williams, T.M., and D.F. Doak, 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282**, 473-6.
- Estes, J.A. and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: Generality and variation in a community ecological paradigm. *Ecological Monographs*, 65, 75-100.
- Ferrero, R.C. and L.W. Fritz. 1994. Comparisons of walleye pollock, *Theragra chalcogramma*, harvest to Stellar sea lion, *Eumetopias jubatus*, abundance in the Bering Sea and Gulf of Alaska. NMFS, Alaska Fisheries Science Center, NMFS-AFSC-43.
- Flaaten, O., 1991. Bioeconomics of sustainable harvest of competing species, *Journal of Environmental Economics and Management*, **20**, 163-180.
- Flaaten, O., and K. Stollery, 1996. The economic costs of biological predation, *Environmental and Resource Economics*, **8**, 75-95.
- Gordon, H.S., 1954. The economic theory of a common property resource: The fishery, *Journal of Political Economy*, **62**, 124-142.
- Gurney, W.S.C. and R.M. Nisbet. 1998. *Ecological Dynamics*. New York: Oxford University Press.
- Gutierrez, A.P. 1996. *Applied Population Ecology: A Supply-Demand Approach*. New York: John Wiley & Sons, Inc.
- Hanley, N., J.F. Shogren and B. White. 1997. *Environmental Economics in Theory and Practice*. New York: Oxford University Press.

- Hannesson, R., 1983. Optimal harvesting of ecologically interdependent fish species, *Journal of Environmental Economics and Management*, **10**, 329-345.
- Hannon, B., 1973. The structure of ecosystems. *Journal of Theoretical Biology* **41**, 535-546.
- Hannon, B., 1976. Marginal product pricing in the ecosystem. *Journal of Theoretical Biology* **56**, 253-267.
- Hannon, B., 1979. Total energy cost in ecosystems. *Journal of Theoretical Biology* **80**, 271-93.
- Heal, G. 2000. *Nature and the Marketplace*. Island Press: Washington, D.C.
- Herendeen, R., 1991. Do economic-like principles predict ecosystem behavior under changing resource constraints? In *Theoretical Studies Ecosystems: The Network Perspective*, eds. T. Burns and M. Higashi, 261-87, New York: Cambridge University Press.
- Hiatt, T., and J. Terry. 2000. Appendix C, Economic status of the groundfish fisheries off Alaska, 1999. *Stock Assessment and Fisheries Evaluation Report for the Groundfish Fisheries of Alaska and the Bering Sea/Aleutian Island Area*. National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, Washington.
- Holling, C.S., D.W.Schindler, B.W.Walker and Jonathan Roughgarden, 1995. "Biodiversity in the functioning of ecosystems: an ecological synthesis," in *Biodiversity Loss: Economic and Ecological Issues*, eds. C.Perrings, K.Maeler, C.Folke, C.S.Holling and B.Jansson, New York: Cambridge University Press.
- Homans, F.R., and J.E.Wilen, 1997. "A model of regulated open access resource use", *Journal of Environmental Economics and Management*, **32**, 1-21.
- Jefferson, T.A., P.J. Stacey and R.W. Baird. 1991. A review of killer whale interactions with other marine mammals: predation to co-existence. *Mammal Review*. 21: 151-180.
- Kerr, S.R. 1974. Theory of size distribution in ecological communities. *Journal Fisheries Research Board, Canada*. 34. 1859-62.
- Kinoshita, R. K, A. Grieg, J.D. Hastie, and J.M. Terry. 1993. Economic status of the groundfish fisheries off Alaska, 1992. *Stock Assessment and Fisheries Evaluation Report for the Groundfish Fisheries of Alaska and the Bering Sea/Aleutian Island Area*. National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, Washington.
- Kinoshita, R. K, A. Grieg, J.M. Terry. 1994. Economic status of the groundfish fisheries off Alaska, 1993. *Stock Assessment and Fisheries Evaluation Report for the Groundfish Fisheries of Alaska and the Bering Sea/Aleutian Island Area*. National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, Washington.

- Kinoshita, R. K., A. Grieg, D. Colpo, J.M Terry. 1996. Economic status of the groundfish fisheries off Alaska, 1995. *Stock Assessment and Fisheries Evaluation Report for the Groundfish Fisheries of Alaska and the Bering Sea/Aleutian Island Area*. National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, Washington.
- Kleiber, M. 1975. *The Fire of Life: An introduction to animal energetics*. Rev. ed. Huntington, NY: Robert E. Krieger Publishing Company.
- van Kooten, G.C. and E.H. Bulte. 2000. *The Economics of Nature*. Malden, Mass.: Blackwell Publishers.
- Law, R. 2000. Fishing, selection and phenotypic evolution. *ICES Journal of Marine Science*. 57: 659-668.
- Lembi, C.A. and J.R. Waaland. 1988. *Algae and Human Affairs*. Eds. Cambridge University Press: New York, 1988
- Lima, S.L. and L.M. Dik, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68, 619-640.
- Lotka, A.J., 1922. Contribution to the energetics of evolution. *Proceedings of the National Academy of Science U.S.A.* 8, 147-55.
- Lotka, A.J., 1925. *Elements of Physical Biology*, Baltimore: Williams and Wilkins Company.
- Mason, C.F. and S.M. Macdonald. 1986. *Otters: Ecology and Conservation*. New York: Cambridge University Press.
- Mejer, H.F. and S.E. Jorgensen. 1979. Energy and ecological buffer capacity. In: Jorgensen, S.E. (Ed.) *State of the Art of Ecological Modelling*, Conference Proceedings, International Society for Ecological Modelling, Copenhagen, 829-46.
- Merrick, R.L. and D.G. Calkins. 1995. Importance of juvenile walleye pollock in the diet of Gulf of Alaska sea lions. Unpublished manuscript. NMFS, National Marine Fisheries Laboratory, Seattle, Washington.
- Munro, G.R. and A. D. Scott, 1985. The economics of fisheries management, *Handbook of Natural Resource and Energy Economics*, A.V. Kneese and J.L.Sweeney, eds., Amsterdam: Elsevier Science Publishers.
- National Marine Fisheries Service, Stock Assessment and Fisheries Evaluation Document (SAFE), 2000. North Pacific Fisheries Management Council, Anchorage.
- National Marine Fisheries Service, Stock Assessment and Fisheries Evaluation Document (SAFE), 2000. EBS Walleye Pollock Stock Assessment. J.N. Ianelli, L. Fritz, T. Honkalehto, N. Williamson and G. Walters. 2000.

- National Marine Fisheries Service, Stock Assessment and Fisheries Evaluation Document (SAFE), 2000. Appendix D, Ecosystem considerations for 2001. 2000. Ed. Pat Livingston, North Pacific Fisheries Management Council, Anchorage.
- National Marine Fisheries Service. 1998. Stock Assessment and Fisheries Evaluation Document (SAFE), Appendix 2. Ed. Holowed, North Pacific Fisheries Management Council, Anchorage.
- Pauly, D. and V. Christensen. 1995. Primary production required to sustain global fisheries. *Nature*. March, v. 374: 255-57.
- Pennycuik, C.J. 1979. Energy costs of locomotion and the concept of "foraging radius." in *Serengeti: Dynamics of an Ecosystem*, ed. A.R.E. Sinclair and M. Norton-Griffiths, Chicago: University of Chicago Press.
- Pethig, R. and J. Tschirhart, 2001. "Micro foundations of biological growth." Working paper, University of Wyoming.
- Petipa, T.S., E.V. Pavlova and G.N. Mironov. 1970. The food web structure, utilization and transport of energy by trophic levels in the planktonic communities. In *Marine Food Chains*, ed. J.H. Steele, Edinburgh: Oliver & Boyd.
- Pindyck, R.S. 1984. Uncertainty in the Theory of Renewable Resource Markets. *Review of Economic Studies*. 51, 289-303.
- Quirk, J.P. and V.L. Smith, 1970. "Dynamic economic models of fishing," in A.D. Scott, ed., *Economics of Fisheries Management: A Symposium*, H. R. McMillan lectures in fisheries, 1969, University of British Columbia, Vancouver, pp. 3-32.
- Ragozin, D.L., and G Brown, 1985. Harvest policies and nonmarket valuation in a predator - prey system, *Journal of Environmental Economics and Management*, **12**, 155-168.
- Reed, W.J. 1979. Optimal escapement levels in stochastic and deterministic harvesting models. *Journal of Environmental Economics and Management*. **6**, 350-363.
- Rosen, D.A.S. and A. W. Trites, 2000. Pollock and the decline of Stellar sea lions: testing the junk-food hypothesis, *Canadian Journal of Zoology*. **78**, 1243-1250.
- Rosen, R. R., 1967. *Optimality Principles in Biology*, London: Butterworths.
- Solow, A.R. and A.R. Beet. 1998. On lumping species in food webs, *Ecology*, **79**, 2013-2018.
- Stroebele, W.J. and H. Wacker, 1995. The economics of harvesting predator-prey systems, *Journal of Economics*, **61**, 65-81.
- Trites, A. W. 1998. Stellar sea lions (*Eumetopias jubatus*): Causes for their decline and factors limiting their restoration, Marine Mammal Research Unit. UBC, Canada.

- Trites, A.W. and P.A. Larkin. 1996. Changes in the abundance of Stellar sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: how many were there? *Aquatic Mammals*, **22**, 153-66.
- Trites, A.W., V. Christensen and D. Pauly. 1997. Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. *Journal of the Northwest Atlantic Fisheries Society*. **22**: 173-187.
- Tschirhart, J., 2000. General equilibrium of an ecosystem. *Journal of Theoretical Biology*, **203**, March, 13-32.
- Tschirhart, J., 2001. "Population adjustments based on micro behavior," Working Paper, University of Wyoming, January.
- Tschirhart, J., 2002. Resource competition among plants: From optimizing individuals to community structure. *Ecological Modelling*, forthcoming.
- Ulanowicz, R.E. 1980. "An hypothesis on the development of natural communities," *Ecological Modeling* **85**, 223-45.
- Wacker, H., 1999. "Optimal harvesting of mutualistic ecological systems", *Resource and Energy Economics*, **21**, 89-102.
- Wilén, J., and G. Brown, 1986. "Optimal recovery paths for perturbations of trophic level bioeconomic systems", *Journal of Environmental Economics and Management*, **13**, 225-234.
- Witherell, D. 2000, Groundfish of the Bering sea and the Aleutian Islands area: Species profiles 2001, North Pacific Fisheries Management Council. December, Anchorage.

Table 1. Initial Variables and Parameters for the Marine Ecosystem

	Phytoplank.	Zooplank.	Pollock	Steller sea lion	Killer whale	Sea otter	Urchin	Kelp
Variables								
Populations	(i)	(ii)	(iii)	(iv)	(v)	(vi)	(vii)	(viii)
N_i^{\dagger}	87.6923 units km ⁻²	162.308 units km ⁻²	4.84615 units km ⁻²	0.096154 km ⁻²	0.007723 units km ⁻²	0.050631 units km ⁻²	10.7692 units km ⁻²	1076.92 units km ⁻²
	1 unit = 1x10 ¹² ind.	1 unit = 1x10 ⁹ ind.	1 unit = 1000 ind.	1 unit = 1 ind	1 unit = 0.1 ind.	1 unit = 100 ind.	1 unit = 1 x 10 ⁷ ind.	1 unit = 1x10 ⁴ ind
Biomass or biomass flow	(ix)	(x)	(xi)	(xii)	(xiii)	(xiv)	(xv)	(xvi)
x_{ij}	435.6 kg unit ⁻¹	1782.7 kg unit ⁻¹ y ⁻¹	9300. kg unit ⁻¹ y ⁻¹	1332. kg y ⁻¹	486.6 kg unit ⁻¹ y ⁻¹ (Steller) 28.3 kg unit ⁻¹ y ⁻¹ (otter)	255,500 kg unit ⁻¹ y ⁻¹	3,460. kg unit ⁻¹ y ⁻¹	1.05 x 10 ⁴ kg unit ⁻¹
Parameters								
Embodied energy e_i	(xvii) 400. kcal kg ⁻¹	(xviii) 559. kcal kg ⁻¹	(xix) 1108. kcal kg ⁻¹	(xx) 2000. kcal kg ⁻¹	(xxi) NA	(xxii) 1810 kcal kg ⁻¹	(xxiii) 717 kcal kg ⁻¹	(xxiv) 821 kcal kg ⁻¹
Light Absorption e_{0i}	(xxv) 15150. kcal kg ⁻¹ yr ⁻¹	(xxvi) NA	(xxvii) NA	(xxviii) NA	(xxix) NA	(xxx) NA	(xxxi) NA	(xxxii) 13.53 kcal kg ⁻¹ yr ⁻¹
Resting metabolic rate b_i	(xxxiii) 395948 kcal unit ⁻¹ yr ⁻¹	(xxxiv) 213924 kcal unit ⁻¹ yr ⁻¹	(xxxv) 1559610 kcal unit ⁻¹ yr ⁻¹	(xxxvi) 391134 kcal yr ⁻¹	(xxxvii) 1302283.5 kcal unit ⁻¹ yr ⁻¹	(xxxviii) 32193000 kcal unit ⁻¹ yr ⁻¹	(xxxix) 852198 kcal unit ⁻¹ yr ⁻¹	(xl) 21305 kcal unit ⁻¹ yr ⁻¹
Weight w_i	(xli) 435.6 kg unit ⁻¹	(xlii) 3.757 kg unit ⁻¹	(xliii) 1000 kg unit ⁻¹	(xliv) 200 kg	(xlv) 399.6 kg unit ⁻¹	(xlvi) 2800 kg. unit ⁻¹	(xlvii) 1x10 ⁵ kg unit ⁻¹	(xlviii) 1.05 x 10 ⁴ kg unit ⁻¹
Predation $d_{ij}^{\#}$	158.09306	6.57659	0.274052	2.67741	NA	.021365	20.4214	0.337661
Plant congestion $\tau_i^{\%}$.02938367	NA	NA	NA	NA	NA	NA	434.91
Var. Resp. $r_i^{\$}$ (kcal yr ⁻¹)	5.56456	0.085294	0.019220	0.234413	0.548144	4.9318x10 ⁻⁴	0.101000	3.19684x10 ⁻⁴

Table 1. Notes

NA – not applicable or not needed.

[†] 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 $1.3 \times 10^6 \text{ km}^2$, the approximate area of the EBS, and nearshore populations are divided by $26,000 \text{ km}^2$, the approximate area along the Aleutian Islands.

- (i) 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.
- (ii) 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.
- (iii) Pollock estimates around 1980 are 6.3×10^9 kgs (Witherell, 2000). Assuming pollock are 1 kg on average, this is 6.3×10^9 individuals which converts to 6.3×10^6 population units. On a km^2 basis: $6.3 \times 10^6 \text{ units} / 1,300,000 \text{ km}^2 = 4.84615$. Recall, 1,300,000 is the ecosystem size in km^2 .
- (iv) The Stellar sea lion population was estimated to be 125,000 (Appendix D, 2000), and on a km^2 basis: $125,000 / 1,300,000 \text{ km}^2 = 0.096154$.
- (v) Based on 1024 individuals (Appendix D). 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.
- (vi) Based on 131,631 individuals extrapolated from Estes and Duggins (1995) estimates of populations in Aleutians island groups.
- (vii) Individuals from multiple sea urchin species at 153 randomly selected sites in the Aleutians (Estes and Duggins, 1995).
- (viii) Kelp density of multiple species is about 10% of urchin at the same 153 sites in the Aleutians (Estes and Duggins, 1995).
- (ix) A weighted average of phytoplankton species' body weights (4.35615×10^{-10} kg., Petipa et al., 1970, Table 1), in units of 1×10^{12} phytoplankton.
- (x) A weighted average of zooplankton species indicates an individual weighs 3.757×10^{-6} gm. and consumes 130% of its weight in phytoplankton per day (Petipa et al., 1970, Table 1). This yields a consumption of $1782.7 \text{ kg unit}^{-1} \text{ yr}^{-1}$.
- (xi) Trites et al. (1997) p. 186. Pollock eat mostly zooplankton (Witherell, 2000) and here they are assumed to eat only zooplankton.
- (xii) Based on Rosen and Trites (2000) and Appendix D, SAFE. From Appendix D, in 1990s Steller diet was 76% fish of which 40% was pollock. Therefore, of the 4380 kg/yr taken by an individual sea lion, the pollock consumption was $(.76) (.40) (4380) = 1332 \text{ kg/yr}$.
- (xiii) Killer whale prey includes sperm and baleen whales, pinnepeds, seabirds, fish, turtles, otter, and based on the stomach content of one whale, pigs; however, there is no consensus on the importance of any one prey (Jefferson et al., 1991). We assume that around 1980 the proportion of Steller sea lions in the killer whale diet was the same as the proportion of the Steller sea lion population in the sum of the populations of Steller sea lions, harbor seals, Northern fur seals and walrus in the EBS region as reported in

Trites et al. (1997). This amount is about 10% of the total diet (the total is based on the daily killer whale energy requirement (Estes et al., 1998)), and we also assume that otter made up 5% of the total. Estes et al. indicate killer whales did not consume significant numbers of otter until recently.

- (xiv) 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.
- (xv) Based on sea urchin growth rates (Estes and Duggins, 1995, Table 11).
- (xvi) Assumes prey biomass is 1.2 times predator biomass (Kerr, 1974), and using the kelp and urchin populations yields 1.05 kg per individual.
- (xvii) Weighted average of caloricity measures of three phytoplankton species groupings (Petipa et al., 1970, Table 7).
- (xviii) Weighted average of caloricity measures of three zooplankton species groupings (Petipa et al., 1970, Table 7).
- (xix) In a captive situation, the mean daily ration of pollock was 7.2kg d^{-1} which was in energy 33.39MJ d^{-1} (Rosen and Trites, 2000); therefore, the embodied energy in the daily ration is $(33.39\text{MJ d}^{-1})(1\text{Mcal}/4.184\text{MJ})(1000\text{kcal Mcal}^{-1})(1/7.2\text{kg}) = 1108\text{ kcal kg}^{-1}$.
- (xx) Estimated based on blubber content in a sea lion versus otter which have no blubber. (Costa, 1978) (See (xxii)).
- (xxi) Not needed because killer whales are at the top of the food web and are not prey.
- (xxii) Estes et al. (1998).
- (xxiii) Costa (1978).
- (xxiv) Lembi and Waalan (1988).
- (xxv) 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 (i), x_{10} from (ix), N_2 from (ii), x_{21} from (x) and e_1 is from (xvii)).
- (xxvi)-(xxxii) Not applicable because only plants photosynthesize.
- (xxxii) Using the 20% transfer rule (See (xxv).), equate 20% of the energy taken by kelp to the energy taken by urchin: $(20\%) N_8 x_{80} e_{08} = N_7 x_{78} e_8$ and solve to obtain $e_{08} = 13.53 \text{ kcal kg}^{-1} \text{ yr}^{-1}$. (Note N_8 is from (viii), x_{80} from (xvi), N_7 from (vii), x_{78} from (xv) and e_8 is from (xxiv)).
- (xxxiii) 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 $395,948 \text{ kcal yr}^{-1}$.
 - (xxxiv) An average of respiration as a % of body weight over multiple zooplankton species yields 30%. (Petipa et al., 1970, Table 2). Calculations are similar to (xxxiii).
- (xxxv) Pollock are assumed to follow the 30% estimate in (xxxiv).
- (xxxvi) For mammals, resting metabolic rate in kcal d^{-1} (M) is related to body weight (W) by the formula $M = 67.61W^{0.756} \pm 5\%$ (Kleiber, 1975). Using 200 kg as sea lion weight and extrapolating to one year yields $391,134 \text{ kcal yr}^{-1}$. The RMB used in the simulations is lowered by (76%)(40%) to reflect that sea lions are preying on more than just Pollock (See (xii).)

- (xxxvii) Use the formula from (xxxvi) and an average weight of 3996 kg. The RMB used in the simulations is lowered to 10% of this figure to reflect that killer whales are preying on more than just sea lions and otter (See (xiii)).
- (xxxviii) Use the formula from (xxxvi) and an average weight of 28 kg and a +5% because otter have high metabolic rates (Costa, 1978).
- (xxxix) Urchin are assumed to follow the 30% estimate in (xxxiv).
- (xl) Kelp are assumed to follow the 6% estimate in (xxxiii).
- (xli) Phytoplankton are plants; therefore, weight is given in (ix).
- (xlii) Average of multiple zooplankton herbivore species (Petipa et al., 1970, Table 1).
- (xliii) Average of adult and juvenile, both are taken by fisheries and Steller sea lions. (See (iii).)
- (xliv) Based on weights of immature sea lions in Rosen and Trites (2000).
- (xlv) Average of male and female adults is 3996 kg (Estes et al., 1998).
- (xlvi) Average of male and female adults is 28 kg (Costa, 1978).
- (xlvii) Urchins at six locations in the Aleutians averaged 8.76 gm each with a wide variance (Estes and Duggins, 1995, Table 2). We rounded to 10 gm.
- (xlviii) Kelp are plants; therefore, weight is given in (xvi).

[#] Calculated from the short-run equilibrium (i.e., market clearing) conditions using benchmark values for populations, biomasses and biomass flows (i.e., demands) from the first two table rows.

[%] 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.

^{\$} 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.

Table 2 – Animals sans Harvesting

period 2	zoo	pollock	urchins	sea lion	otters	whales	
						sea lion	otters
Populations	192.1	12.29	16.04	0.105	0.0649	0.0044	
Demands (xij)	1750	5460	2430	1866	249000	1104	62.8
Prices (eij)	46.2	81.7	40.6	137	347	395	914
Net Energies	8720	-892000	-554000	388000	-1660000	54000	

period 3	zoo	pollock	urchins	sea lion	otters	whales	
						sea lion	otters
Populations	192.2	9.45	12.94	0.151	0.0642	0.0062	
Demands (xij)	1670	6930	2940	1127	223000	872	41.6
Prices (eij)	54.1	64.3	22.9	358	366	521	926
Net Energies	-21600	-481000	-304000	-120000	-766000	288000	

period 4	zoo	pollock	urchins	sea lion	otters	whales	
						sea lion	otters
Populations	183.2	8.33	11.57	0.135	0.0612	0.0076	
Demands (xij)	1700	7590	3250	1150	220000	648	32.2
Prices (eij)	47.5	56.4	11.6	351	368	645	932
Net Energies	-18100	-264000	-125000	-104000	-8280000	101000	

period 5	zoo	pollock	urchins	sea lion	otters	whales	
						sea lion	otters
Populations	176.4	7.76	11.06	0.123	0.0580	0.0082	
Demands (xij)	1720	7890	3380	1210	226000	559	28.8
Prices (eij)	42.5	52.8	6.76	336	363	694	934
Net Energies	-13000	-159000	-44400	-73700	-6930000	41600	

Table 3. Parameter Estimates[#]

Parameter	Equation (39)	Equation (40a)	Equation (40b)
<i>a</i>	-6502115.654 (1097611.3)***		
<i>b</i>	475200.0879 (72931.371)***		
<i>f</i>		431725.25 (222615.3)*	
<i>v</i>		2332.5 (1347.36)	
<i>q</i>			0.535×10^{-5} $(.8877 \times 10^{-6})$ ***
ρ	0.80448 (.08436)***		
Durbin Watson	0.37487		
Adjusted R ²	0.7544	0.459	-0.8725 [%]

* = significant at the .1 level

** = significant at the .05 level

***= significant at the .001 level

[#] Standard errors in parentheses

[%] Linearized equation does not possess an intercept, allowing a non-positive adjusted R² (Pindyk and Rubinfeld, 1991, page 77).

Table 4. Population Elasticities

	pre harvest pop.	post harvest pop.
Species	Total Allowable Catch	Total Allowable Catch
Pollock	-0.011	-0.140
Sea Lion	-0.0710	-0.0710
Killer Whale	-0.0702	-0.0702

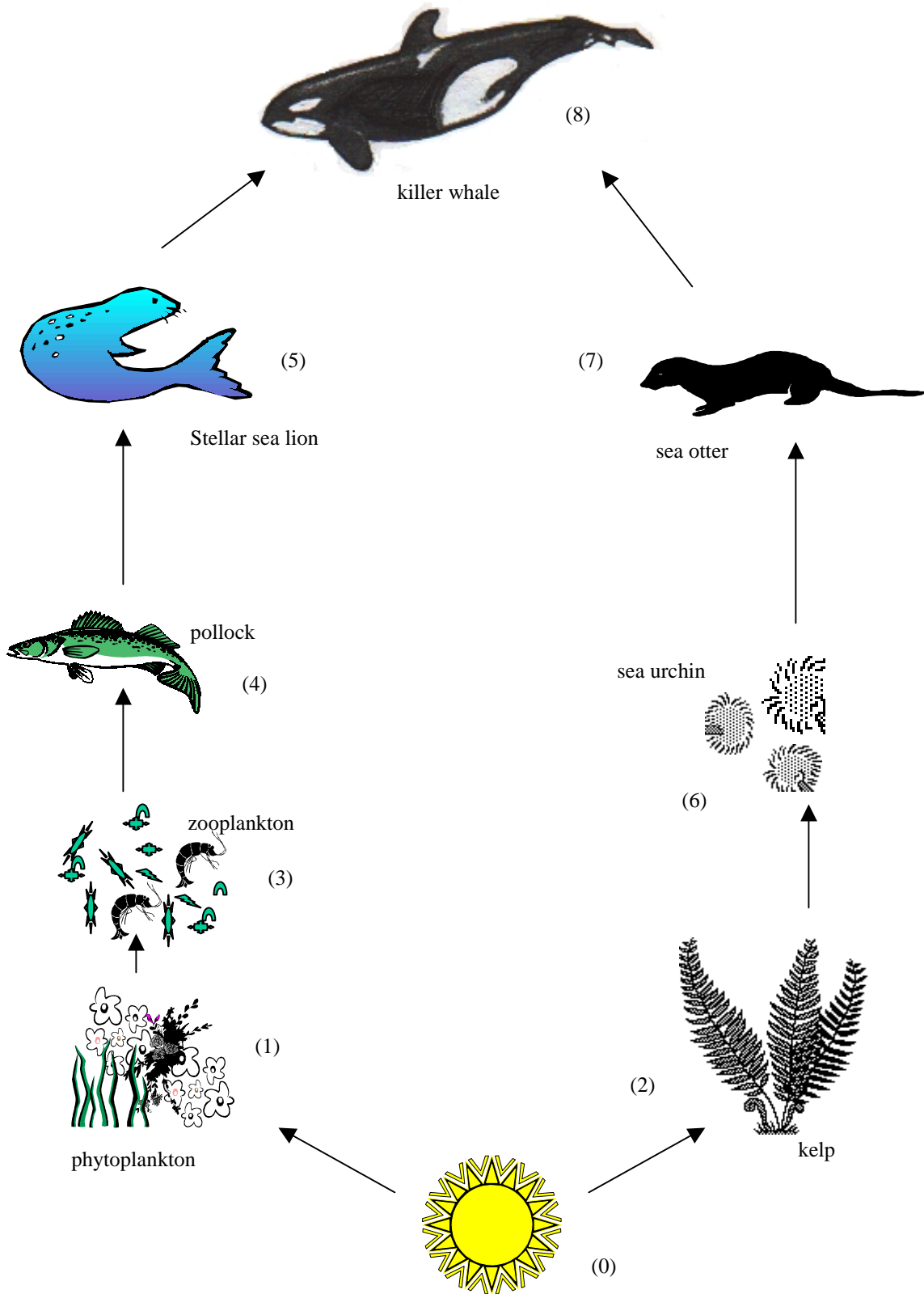


Figure 1 - Food Web
(index #)

Figure 3 - Harvesting on a Natural Ecosystem

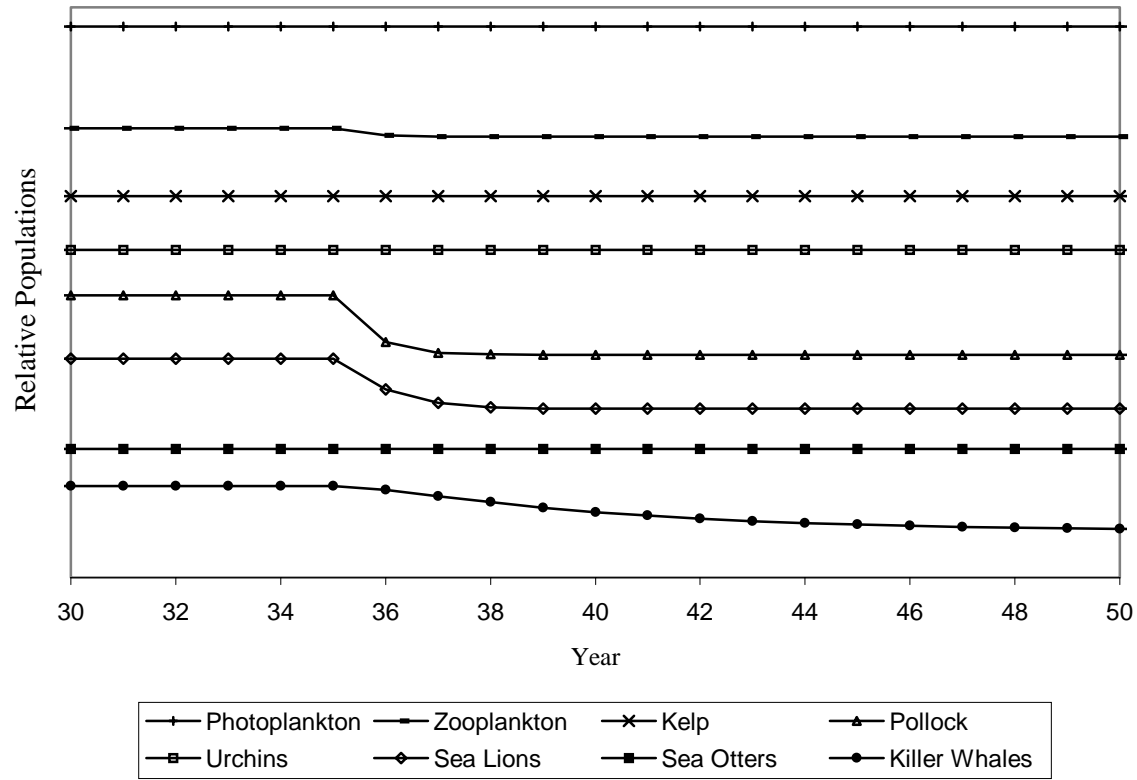


Figure 4 - Pollock Populations

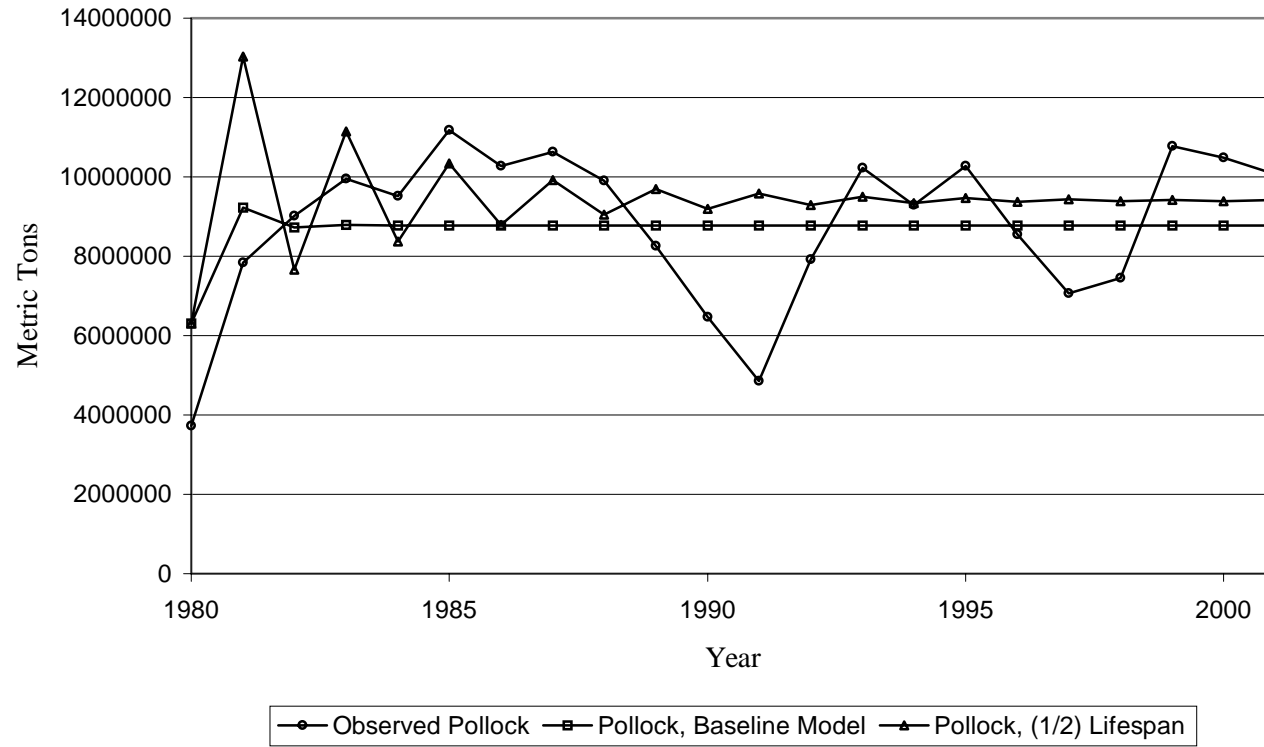


Figure 5 - Effort

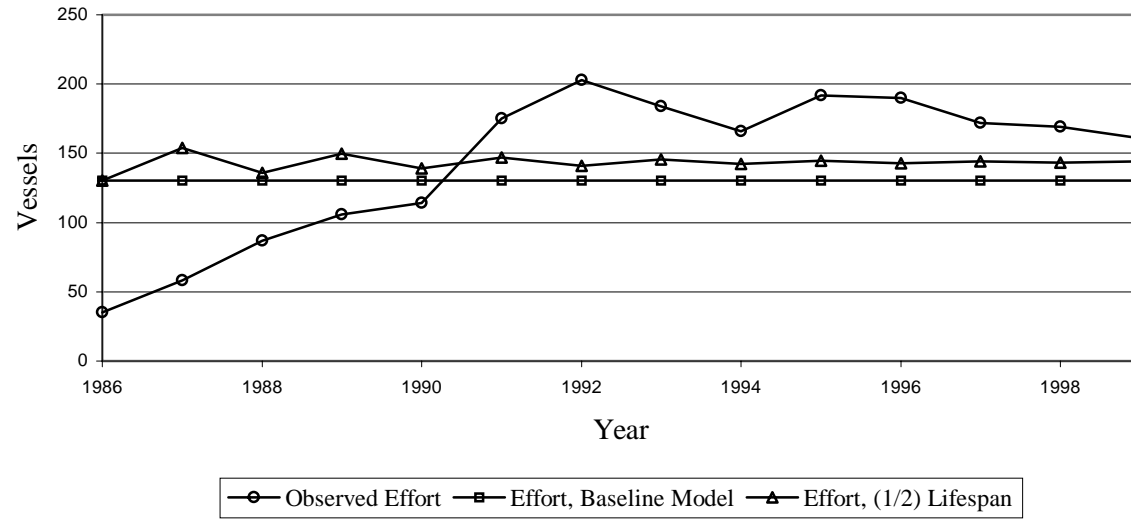
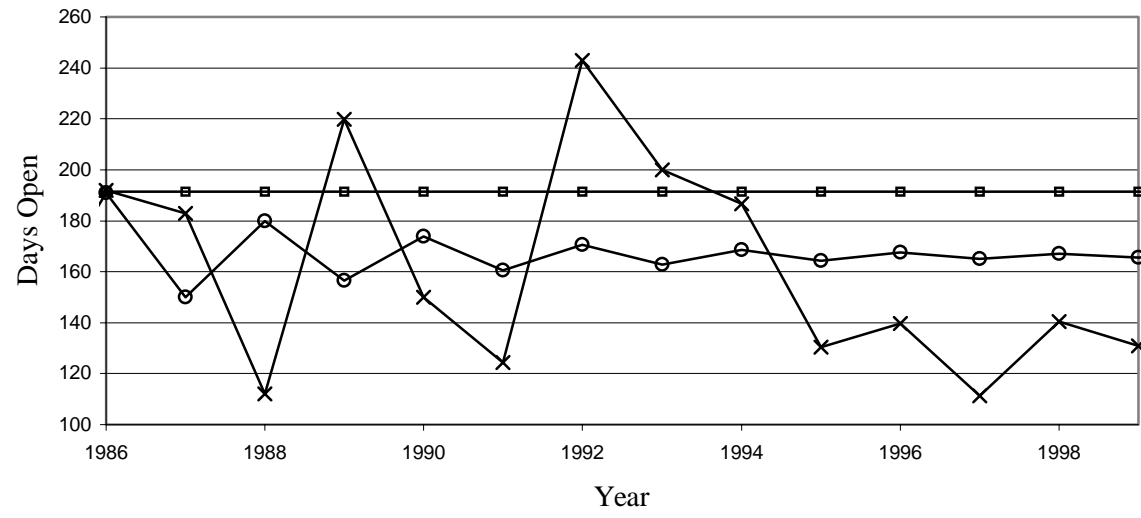


Figure 6 - Seasons



—x— Observed Seasons —■— Seasons, Baseline Model —○— Seasons, (1/2) Lifespan