

**Protecting an Endangered Species while Harvesting Its Prey in a
General Equilibrium Ecosystem Model**

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ABSTRACT

Because endangered species are in predator/prey, competitive, and other relationships with many species sharing their habitat, efficient conservation requires simultaneously considering the needs of many species. Therefore, understanding ecological relationships is an important part of designing endangered species policies. Equally important is to understand how human activity affects these other species and indirectly affects endangered species. This paper offers an integrated ecological/economic model that tracks both ecological relationships and human activities. The model is applied to an Alaskan marine ecosystem in which fish are harvested and Steller sea lions are endangered. Results illustrate the tradeoff between harvested fish and endangered sea lions.

I. INTRODUCTION

Biodiversity is essential for human existence, yet there is growing evidence cited in popular and scientific publications about the decline of biodiversity within ecosystems owing to increasing per capita resource consumption of increasing numbers of people.¹ Our incomplete understanding of both the interactions among the species that comprise ecosystems, and of how the ecosystems themselves interface with the economies contained within them, complicates policies aimed at biodiversity preservation.

Policies to preserve specific endangered species are a high profile component of preserving biodiversity generally. Because endangered species are in predator/prey, mutualistic, competitive, and other ecological relationships with many other species that share their habitat, landscape conservation that simultaneously considers the needs of many species can be an efficient means of protecting endangered species (Beissinger and Perrine 2001). Therefore, understanding ecological relationships is an important part of designing endangered species policies (Hayward et al. 2001). Equally important is to understand how human activity affects these other species and, thereby, indirectly affects endangered species. Indirect affects have been labeled ecosystem externalities and not accounting for them creates inefficiencies (Crocker and Tschirhart 1992). This paper offers a new integrated ecological/economic approach that can track both ecological relationships and ecosystem externalities.

Other authors have developed multi-species (usually two species) bioeconomic models that recognize predator-prey or mutualistic relationships between the species and in which one or both species are harvested (E.g.s, Quirk and Smith 1970; Clark 1976; Hannesson 1983; Conrad and Adu-Asamoah 1986; Flaaten 1991; Conrad and Salas 1993; Flaaten and Stollery 1996; Stroebele and Wacker 1995; and Wacker 1999). Extensions of these methods to include non-

consumptive values of stocks other than that harvested are developed in Ragozin and Brown (1985), Wilen and Brown (1986), and Tu and Wilman (1992). In a specific application to a predator-prey system where the prey is harvested and the predator is an endangered species, Kaplan and Smith (2000) further extend the above literature to include a general constraint on the endangered species' population.

We also constrain the endangered species population by incorporating a simple recovery plan. However, our model is in discrete time in keeping with biological reproduction, and we use a new general equilibrium ecosystem model (GEEM) to trace how harvesting the prey species impacts an endangered predator species, in addition to tracing the impacts on other species in the ecosystem that interact with the predator and prey. GEEM is a simulation model and like ecological models it contains dynamic population updating. But unlike ecological models, the updating uses general equilibrium calculations of individual plant and animal optimization problems whose solutions are aggregated to species levels, similar to how computable general equilibrium (CGE) economic models start with individual consumer and firm demands and supplies and aggregate them to market levels. By tracking populations other than the prey and predator, our approach is a step toward ecosystem-based management in which the importance of non-target species is recognized and preserving biodiversity is a goal (MRAG 2000).

GEEM differs from extant ecological models in that it combines individual behavior with ecosystem wide outcomes. It also differs from extant bioeconomic models because it can include any number of species in predator-prey and resource competition relationships. Like economic CGE models, GEEM relies on simulation and does not yield analytical solutions found in renewable resource optimal control models with few species. But also like CGE models that rely on micro foundations of individual consumer and firm behavior to drive the macro outcomes, the

individual behavior in GEEM appeals to the micro principle that plant and animal success depends on their efficient energy utilization, and this drives the ecological macro outcomes (i.e., population changes). In other words, population increase depends on individuals' abilities to convert energy into offspring (Schoener 1986).

The next section provides ecological background and motivates the economic problem wherein harvesting of one species is constrained by a recovery plan to increase the population of an endangered species that preys on the harvested species. Section III introduces GEEM and its supporting ecological theory. Section IV presents the ecological data and uses it to simulate the relationship between harvesting and steady state species' populations. Specific impacts of harvesting on the endangered species are presented in Section V and Section VI is a brief conclusion.

II. MOTIVATING THE ECONOMIC PROBLEM

II.A Ecological Background

GEEM will be applied to a marine ecosystem that connects Alaska's Aleutian Islands (AI) with the Eastern Bering Sea (EBS). The ecosystem is represented by the food web in Figure 1. In the EBS, various species of phytoplankton are aggregated into a single species called phytoplankton and they are the plants in the EBS that compete for light.² 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 receive all their energy from the sun that is the source of all energy flowing through the ecosystem. Various species of zooplankton are aggregated into a single species that feeds on phytoplankton. Pollock are a groundfish in the EBS that feed on zooplankton and support an important fishery. This fishery provides a link between GEEM and economic activity. 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. Pollock is the harvested species in the model, and the Steller sea lion is the species whose population is subject to a recovery program.

****Insert Figure 1 Here****

Steller sea lions range across the Northern Pacific from Japan to California although the populations around Alaska have been declining steadily since the 1960s when, in our study area, they numbered as high as 180,000 (SEIS 2001). The causes of the decline are not fully understood, but several hypotheses have emerged. Prior to 1990 possible factors contributing to the decline included commercial harvesting, entanglement in fishing gear, subsistence hunting, intentional shooting, and nutritional stress owing to the decline of Pacific herring that are an energy rich prey species. Since 1990 possible factors contributing to the continued decline include nutritional stress owing to commercial harvesting of prey species, particularly pollock, increased predation by killer whales, and a climate regime shift causing warmer ocean temperatures.

The National Marine Fisheries Service (NMFS) in 1990 listed the Steller sea lion as threatened under the Endangered Species Act (ESA). In 1992 a recovery plan was completed that divided the sea lions into a western population that was downgraded to endangered, and an eastern population that remained threatened. A number of fisheries management practices were put into place in the 1990s to mitigate the impact of pollock harvesting on the sea lions, although in 2000 the NMFS issued a Biological Opinion maintaining that commercial fishing jeopardized sea lion recovery and called for measures that would adversely impact the commercial fishing industry. However, the North Pacific Fishery Management Council did not adopt the conclusions of the Biological Opinion and issued a call for two more scientific reviews that are now ongoing.

The NMFS in 2001 issued a Supplemental Environmental Impact Statement (SEIS) containing five alternative management strategies that call for varying degrees of catch limits and no fishing zones to protect both the sea lions and the fisheries. SEIS states: “Evaluation of the effects of fisheries removals of Groundfish on Steller sea lions require models that ultimately could relate fish biomass removed directly to changes in sea lion fecundity and survival.....such a model does not currently exist.” (pp. 4-4) Because GEEM can connect harvesting to sea lion populations, it can be used to draw inferences about the contribution of commercial pollock harvests on the sea lion decline.

II.B Commercial Harvesting

To motivate the economic problem, we extend a discrete time model from Hartwick and Olewiler (1998, hereafter HO) in which a benevolent government chooses how much to harvest a single species in order to maximize social net benefits. The sun, phytoplankton, kelp, zooplankton, pollock, Steller sea lion, urchin, otter and killer whale are indexed 0-8, respectively. Let $U(H^t)$ be the benefit derived from harvested pollock in period t , H^t , and let $C(H^t, N_4^t)$ be the cost of harvesting in period t that depends on the harvest and on the pollock stock or population, N_4^t . Given an initial stock, N_4^0 , the problem is to choose a vector of harvests, $H = (H^0, H^1, \dots, H^t, \dots)$, and populations, $N_4 = (N_4^0, N_4^1, \dots, N_4^t, \dots)$, to

$$\text{maximize} \quad \sum_{t=0}^{\infty} \frac{1}{(1+r)^t} [U(H^t) - C(H^t, N_4^t)] \quad (1)$$

where r is the rate of return on investment in the economy.

The objective function, (1), implies that only the benefit associated with the harvesting industry is being considered. Alternatively, the predator population could be included in the benefits function, because the stock of this species must yield some payoff to humans otherwise

there would be no recovery plan. The payoffs might be in the form of existence value, recreational or scientific observation, recognizing that the species might occupy an important niche in the ecosystem, or upholding ethical and moral principles. Including the population in the benefit function would suggest the government knows the monetary benefits attached to the various payoffs; however, measuring the benefits of threatened or endangered species is difficult. Adopting a cost-effective goal such as reaching a specific population by a set date is more realistic (Brown and Shogren 1998). Omitting the predator population from the benefit function does not alter the main points made below.³

Maximization is subject to population growth functions and constraints for a Steller sea lion recovery program. With respect to the growth functions, the eight species are in a food web and changes in any one species population can potentially impact all other species. Accordingly, let the growth function for species j be written as:

$$G_j(N_1^t, \dots, N_8^t) = G_j(\bar{N}^t), \quad j = 1, \dots, 8 \quad (2)$$

where \bar{N}^t is the vector of all species populations in period t . The population update equations for all species except pollock are:

$$N_j^{t+1} = N_j^t + G_j(\bar{N}^t), \quad j = 1, \dots, 8, \quad j \neq 4, \quad (3)$$

and the update equation for pollock has harvest subtracted from growth:

$$N_4^{t+1} = N_4^t + G_4(\bar{N}^t) - H^t \quad t = 0, \dots, \infty \quad (4)$$

Steller sea lion recovery is characterized by the following constraints:

$$G_5(\bar{N}^t) \geq \frac{1}{T-t} [\tilde{N}_5 - N_5^t] \quad t = 1, \dots, T-1 \quad (5)$$

$$G_5(\bar{N}^t) \geq 0 \quad t = T, \dots, \quad (6)$$

Constraint (5) stipulates that the predator population must move toward the safe minimum population, \tilde{N}_5 , in increments no less than $\frac{1}{T-t}$ of the remaining gap between the safe minimum and the t^{th} period's populations. Once the safe minimum population is reached in period T , constraint (10) ensures that the population never falls below the safe minimum.⁴

The government chooses vectors of harvests and harvested species populations to maximize (1) subject to (3)-(6). (In practice, GEEM would provide the biology part of the problem given by constraints (3)-(6).) Constraints (3) and (4) can be substituted into the objective function,⁵ to form the Lagrange expression:

$$L(N_4) = \sum_{t=0}^{\infty} \frac{1}{(1+r)^t} [U(N_4^t - N_4^{t+1} + G_4(Y^t)) - C(N_4^t - N_4^{t+1} + G_4(Y^t), N_4^t)] + \sum_{t=1}^{T-1} \frac{\lambda^t}{(1+r)^t} [[T-t]G_5(\bar{N}^t) - \tilde{N}_5 + N_5^t] + \sum_{t=T-1}^{\infty} \frac{\lambda^t}{(1+r)^t} G_5(\bar{N}^t) \quad (7)$$

where $Y^t = N_1^{t+1} - G_1(\bar{N}^t), \dots, N_3^{t+1} - G_3(\bar{N}^t), N_4^t, N_5^{t+1} - G_5(\bar{N}^t), \dots, N_8^{t+1} - G_8(\bar{N}^t)$. The

Lagrange multipliers, λ^t , are discounted because they are period-by-period shadow prices on the minimum viable population. Thus, λ^{t+1} is a shadow price of the minimum viable population in period $t+1$, and relative to the net benefits in period t , it is discounted by $1/(1+r)$ to give its present value in period t . (Discounting the multiplier follows Conrad 1999, 11.)

For any period t , using the Kuhn-Tucker condition with respect to N_4^t , and assuming $N_4^t > 0$ at the optimum, yields the condition:

$$\begin{aligned}
 & \frac{[U_{H^{t+1}} - C_{H^{t+1}}] - [U_{H^t} - C_{H^t}]}{U_{H^t} - C_{H^t}} - \frac{C_{N^{t+1}}}{U_{H^t} - C_{H^t}} + \frac{\lambda^t \tau G_{5N_4^t}}{U_{H^t} - C_{H^t}} \\
 & + \frac{U_{H^{t+1}} - C_{H^{t+1}}}{U_{H^t} - C_{H^t}} [-G_{4N_1^t} G_{1N_4^t} - \dots - G_{4N_3^t} G_{3N_4^t} + G_{4N_4^t} - G_{4N_5^t} G_{5N_4^t} - \dots - G_{4N_8^t} G_{8N_4^t}] = r
 \end{aligned} \tag{8}$$

where $\tau = T - t - 1$, for $t = 0, \dots, T-2$ and $\tau = 1$, for $t > T-2$. Subscripts on U and C in (8) denote partial derivatives, and equations (3), (4) and (8) determine the time paths for the harvests and populations that maximize net benefits.

The first and second terms on the left side of (8) are the change in net benefits from period t to $t + 1$ and the stock externality, respectively. (See HO, 355). The third term on the left side of (8) follows from the endangered species recovery constraints. Applying the envelope theorem to (7) yields:

$$\frac{\partial L}{\partial \tilde{N}_5} = - \sum_{t=1}^{T-1} \frac{\lambda^t}{(1+r)^t} \tag{9}$$

indicating that Lagrange multipliers in each period up to period $T - 1$ are that period's contribution to the marginal lost net benefits in the harvesting industry (the shadow prices) from setting a safe minimum population. Thus, the third term gives lost net benefits in period t of moving toward the safe minimum population by increasing the pollock population via smaller harvests. For periods beyond $T - 1$, the third term is the marginal cost of maintaining the safe minimum population.⁶

The fourth term is the marginal stock effect, and it accounts for the interaction between the eight species. The bracketed term indicates how changes in the harvested pollock population affect directly the growth of the pollock, and affect indirectly the growth of the sea lion predator as well as the other six species through changes in the growth of the pollock population. In the standard single species bioeconomic fishery model, only the $G_{4N_4^t}$ term would be present in the

brackets. Finally, in a steady state where no populations are changing, which can only occur after the minimum viable sea lion population is attained, (8) reduces to:

$$\begin{aligned} & [-G_{4N_1^t} G_{1N_4^t} - \dots - G_{4N_3^t} G_{3N_4^t} + G_{4N_4^t} - G_{4N_5^t} G_{5N_4^t} - \dots - G_{4N_8^t} G_{8N_4^t}] \\ & - \frac{C_{N^{t+1}}}{U_{H^t} - C_{H^t}} + \frac{\lambda^t G_{5N_4^t}}{U_{H^t} - C_{H^t}} = r \end{aligned} \quad (10)$$

A major difficulty with implementing a recovery plan is the lack of information about both the growth functions, $G_j(\cdot)$, and how harvesting impacts steady-state populations via the first and third terms in (10). Nevertheless, because the seven non-harvested species may provide direct benefits/costs to humans, or be the source of ecosystem externalities if they provide indirect benefits/costs through their impacts on species providing direct benefits/costs, their inclusion in the model may be critical for formulating harvesting policies. In the remaining sections GEEM is used to determine growth relationships like those in the bracketed term in (10), and to show how a range of constant harvests impact steady-state populations for the eight Alaskan species. GEEM does not include the social net benefit optimization problem, and we will elaborate on this in section V.B.

III. THE ECOLOGICAL MODEL ⁷

GEEM is fundamentally different from the familiar Lotka-Volterra predator/prey models and their variations, from familiar resource competition models (e.g., Gurney and Nisbet 1998, chpt. 6), and from large simulation models (e.g., Christensen and Pauly 1992). First, its basic decision-making unit is an individual organism and not a species. Second, optimization is used: individuals maximize net energy intake, because natural selection requires plants and animals to use energy efficiently. Third, species population update equations are derived from individual behavior and linked to individual energy efficiency. Lumped parameters in the update equations

are thus avoided. GEEM does not account for spatial differences within the EBS and AI, nor does it include age-distributed populations, both of which would be useful extensions.

GEEM builds on the individual plant's and animal's net energy maximization problem. A general expression for the net energy flow through a representative animal from species i is given by:

$$R_i = \sum_{j=1}^{i-1} [e_j - e_{ij}] x_{ij} - \sum_{k=i+1}^m e_i [1 + t_i e_{ki}] y_{ik} - f^i \left(\sum_{j=1}^{i-1} x_{ij} \right) - \beta_i \quad (11)$$

where R_i is in power units (e.g., Watts or kilocalories/time) and is the animals objective function.⁸ The species are arranged so that members of species i prey on organisms in lower numbered species and are preyed on by members of higher numbered species. The first term on the right side of (11) is the inflow of energy from members of prey species (including plants) to the representative individual of species i . The e_j is the energy embodied in a unit of biomass (e.g., in kilocalories/kilogram) from a member of species j , e_{ij} is the energy the member of species i must spend to locate, capture and handle a unit of biomass of species j and is described below as the “energy price”, and x_{ij} is the biomass (in kilograms/time) transferred from the member of species j to the member of species i .

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 the representative individual of species i , and y_{ik} is the biomass supplied by i to k . The term in brackets is the energy the individual uses in attempts to avoid being preyed upon. It is assumed to be a linear function of the energy its predators use in capture attempts: the more energy predators expend, the more energy the individual expends escaping. In a sense, t_i is a tax on the individual because it loses energy above what it loses owing to being captured. This energy loss could include various strategies such as fish schooling to avoid capture by predators or plants producing chemicals that deter

grazers.

The third and fourth terms in (11) represent respiration that is energy lost to the atmosphere. Following Gurney and Nisbet (1998), respiration is divided into two parts. First, the $f^i(\cdot)$ that depends on energy intake and includes feces, reproduction, defending territory, etc.

Assuming differentiability,

$$\frac{\partial f^i(\cdot)}{\partial x_{ij}} > 0, \text{ for } i = p+1, \dots, m, j = 1, \dots, m, j < i \quad (12)$$

Second, the b_i is basal metabolism and it is independent of energy intake.

To apply (11) to the Alaskan animal species, write the net energies of a representative individual pollock and Steller sea lion as (13) and (14), respectively:

$$R_4 = [e_3 - e_{43}]x_{43} - e_4[1 + t_4 e_{54}]d_{45}x_{43}^\alpha - r_4 x_{43}^\gamma - \beta_4 \quad (13)$$

$$R_5 = [e_4 - e_{54}]x_{54} - e_5[1 + t_5 e_{85}]d_{58}x_{54}^\alpha - r_5 x_{54}^\gamma - \beta_5 \quad (14)$$

In (13), e_3 is the energy (heat content) embodied in a unit of biomass of zooplankton, e_{43} is the “energy price” or the energy lost to the atmosphere that the pollock must spend to locate, capture and handle a unit of biomass of zooplankton. The x_{43} is the biomass flow from the zooplankton to the pollock: it is the choice variable that the pollock maximizes over, and it represents the pollock’s ‘demand’ for zooplankton. The first term on the right side of (14) is similar to that in (13), except that the energy and biomass is flowing from pollock to the representative sea lion.

The second term on the right side of (13) ((14)) is the energy lost by the pollock (sea lion) to the sea lions (killer whales). Examining (13), the e_4 is the embodied energy in a unit of pollock biomass. The biomass supplied by the pollock to sea lions is assumed to be a function of the consumption of zooplankton by the pollock, and it is assumed to take the form $y_{45} = d_{45}x_{43}^\alpha$ where d_{45} is a constant. Pollock supply of biomass is a function of its demand for biomass

owing to predation risk.⁹ In maximizing (13), the pollock would prefer to supply zero biomass to the sea lions because outflows reduce net energy. However, a pollock can supply zero biomass only if it demands zero biomass from zooplankton in the sense that to capture zooplankton the pollock risks being captured by sea lions, and the more zooplankton a pollock captures the more it is exposed and the more biomass it supplies to sea lion. (Note that this representation is similar to, but in reverse from, a firm whose supply of output determines its demand for inputs.) The exponential functional form allows for computer solutions to the general equilibrium, and to obtain reasonable population dynamics it must be that $0 < \alpha < 1$ (Tschirhart 2000). For all species it is assumed that $\alpha = 0.5$.

The third and fourth terms in (13) represent respiration energy lost to the atmosphere, and variable respiration is assumed to take the form $r_4 x_{43}^\gamma$ where r_4 is a constant. Again, the exponential form allows for computer solutions and $\gamma > 1$ is consistent with second-order sufficient conditions for a maximum. For all species it is assumed that $\gamma = 2$.

In addition to (13) and (14), there is an objective function for each of the other six species. The plants are somewhat different in that they “prey” on the sun, they occupy a fixed area that dictates the supply of available solar energy, they are in resource competition for the solar energy, and their choice variable, x_{ij} , is biomass of the plant instead of a biomass flow as it is for animals (Tschirhart 2002). The embodied energy terms, e_i , and the metabolic rates, μ_i , for all species are constants.

The energies spent in predation, the e_{ij} , for both plants and animals are the energy prices. There is one price for each biomass transfer between a predator and prey species, and there are 9 transfers in total, one for each predator/prey relationship (including the two plant species “preying” on the sun), and two for the killer whales that prey on both otter and sea lion. As in

economic CGE models, the prices play a central role in each individual's maximization problem, because an individual's choice of prey will depend on the relative energy prices it pays.¹⁰ Also, individuals are assumed to be price takers: they have no control over the energy price paid to capture prey, because each is only one among many individuals in a predator species capturing one of many individuals in a prey species. However, within the ecosystem the prices are endogenous, being determined by demand and supply interactions explained below.

III.A Short Run Equilibrium

Time in the ecosystem is divided into the short run and the long run. In the short run the populations of all species are constant, and in a short-run equilibrium each plant and animal is maximizing its net energy, and aggregate demand equals aggregate supply between each predator and prey pair. A representative plant or animal and its species may have negative, zero or positive short-run net energy. Positive (negative) net energy is 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 competitive economy is the number of firms in an industry changes according to the sign of profits.)

To find a set of prices that equate demands and supplies, an equilibrium equation is needed for each price. For example, the equilibrium condition for pollock and sea lion is constructed by equating the sum of all the sea lion demands with the sum of all the pollock supplies. Because each pollock and sea lion is assumed to be a representative individual from their species, the equilibrium condition between sea lion and pollock can be written as:

$$N_5 x_{54} = N_4 d_{45} x_{43}^5 \tag{15}$$

The left side of (15) is the total sea lion demand for pollock from (14), and the right side is the total supply of pollock to sea lion from (13). In the case of plants preying on the sun, the equilibrium condition is similar except the supply depends on the physical space the plants occupy (Tschirhart 2002).

A short-run equilibrium is a matter of simultaneously solving eighteen equations for a set of nine energy prices and nine biomass demands. There are nine first-order conditions obtained from setting to zero the derivatives of the eight species objective functions with respect to their biomass demands (recall there are two derivatives for the killer whales since they prey on both otter and sea lion), and there are nine equilibrium clearing conditions similar to (15). The appendix shows the eighteen equations.

III.B Long-Run Adjustment

A system in short-run equilibrium moves toward long-run equilibrium through adjustment in the populations that will move the species toward zero net energy. For instance, suppose sea lions have positive net energy in a short-run equilibrium. Their population increases before the next short-run equilibrium is calculated with the updated populations for two reasons: First, in the next short-run calculations, the increased sea lion population lowers the energy price killer whales must pay to capture sea lions, because the sea lions are more plentiful. Killer whale demands for the sea lions increase (demands are downward sloping as in standard economic models), the sea lion supplies to killer whales increase, and sea lion net energy will decrease. Second, the price paid by sea lion for pollock increases as there is more intra-species competition when the sea lion population grows. This price movement will also reduce the sea lion net energy, as they demand less pollock. Thus, the initial positive net energy moves toward zero. 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 population update equations from (3) are derived as follows. Consider population changes for the killer whales whose objective function in (16) shows two prey species, sea lion and sea otter, two variable respiration terms, one for each prey, and no predation term because the whales are a top predator:

$$R_8 = [e_5 - e_{85}]x_{85} + [e_7 - e_{87}]x_{87} - r_8x_{85}^2 - r_8x_{87}^2 - \beta_8 \quad (16)$$

In steady-state it must be the case that births equals deaths. Moreover, if s_8 is the lifespan of the representative killer whale, then the total number of births and deaths must be N_8/s_8 . Dividing the totals by N_8 yields the per capita steady-state birth and death rates:

$$1/s_8 \quad (17)$$

Next consider the killer whale's maximum "indirect" net energy function given by $R_8(\bar{N}^t)$ which is obtained by substituting the whale optimum demands and equilibrium energy prices as functions of the eight species populations into (16). (Recall that $\bar{N}^t = (N_1^t, \dots, N_8^t)$.) In steady state, $R_8(\bar{N}^t) = 0$. 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.

Let \hat{V}_8 be the steady-state variable respiration, and let $\rho \hat{V}_8$ be the proportion of this variable respiration devoted to reproduction. Thus, in steady state the energy given by $\rho \hat{V}_8$ yields a per capita birth rate of $1/s_8$. Next, suppose the whales are not in steady state and that $R_8(\bar{N}^t) > 0$ and variable respiration is V_8 . Assuming that the proportion of $R_8(\bar{N}^t)$ that is available for reproduction is the same as the proportion of variable respiration available for reproduction, the energy now available for reproduction is $[\rho R_8(\bar{N}^t) + \rho V_8]$. Finally, assuming that reproduction is

linear in available energy, then it follows that if $\rho \hat{V}_8$ yields a per capita birth rate $1/s_8$, then

$[R_8(\bar{N}^t) + V_{i8}]$ yields a per capita birth rate of:

$$(1/s_8) [R_8(\bar{N}^t) + V_8] / \hat{V}_8. \quad (18)$$

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 (18), the population adjustment equation is

$$N_8^{t+1} = N_8^t + N_8^t \left[\frac{R_8(\bar{N}^t) + V_8}{s_8 \hat{V}_8} - \frac{1}{s_8} \right] = N_8^t + N_8^t \frac{1}{s_8} \left[\frac{R_8(\bar{N}^t) + V_8}{\hat{V}_8} - 1 \right] \quad (19)$$

Expression (19) reduces to the steady state if $R_8(\bar{N}^t) = 0$ (in which case $V_8 = \hat{V}_8$), because the bracketed term is zero. Alternatively, $R_8(\bar{N}^t) > (<) 0$ implies that $V_8 > (<) \hat{V}_8$, in which case

population increases (decreases).¹¹ In (19), the term $\frac{1}{s_8} \left[\frac{R_8(\bar{N}^t) + V_8}{\hat{V}_8} - 1 \right]$ is

$G_8(N_1^t, \dots, N_8^t) - G_8(\bar{N}^t)$ from (2); thus, the individual's optimization problem in GEEM yields a specific form for the population growth function.

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 (20) (Tschirhart 2002a).

$$N_i^{t+1} = N_i^t + N_i^t \left[p + \frac{(1-p)^{s_i}}{s_i} \right] \left[\frac{R_i(\bar{N}^t) + V_i}{\hat{V}_i} - 1 \right] \quad (20)$$

where $p = \frac{d_{ij} x_{ik}^5}{w_i}$ is the predation rate, or the biomass supply to predator j divided by the weight of the individual, w_i , which when multiplied by the population gives the number of individuals lost to predation.

IV SIMULATIONS

IV.A Data

Ecological studies of the Alaskan and other ecosystems were used to compile a data set whose parameters and 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 explanations of parameter construction.

****Insert Table 1 Here****

To understand some of the issues involved in assembling the data, consider 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 units per square kilometer (0.096154). In addition, for all species except sea lions, the populations units were scaled further as defined in Table 1 for better computational precision.

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 60% is pollock, yields the result of 2663 kg y⁻¹ of pollock.¹² The sea lion demand and population (along with the demand and population for the killer whale) can be substituted into the equilibrium condition between sea lions and killer

whales to obtain the predation parameter d_{78} . The resting metabolic rate and embodied energy are explained in Table 1. Finally, the variable respiration parameters r_i for all species were obtained through calibration as explained below.

IV.B Long-run Population Adjustments

All populations were adjusted according to (19) and (20) after each short-run equilibrium calculation. Each calculation 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 (20) 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.

Population adjustment equations (19) and (20) contain the constant steady-state variable respiration terms, \hat{V}_i , that contain the r_i parameters. But steady-states depend on harvests, so what harvests should be used to calibrate for the r_i to yield the \hat{V}_i ? The convention adopted here is that the \hat{V}_i are from the steady state in which there is no human intervention (harvest is zero), and we refer to this as the *natural* steady state. In 1980 from which time the data are taken, Russian trawlers were harvesting about 16% of the pollock population. (The harvest was about 1 billion kg in 1980 ($h = 0.769$ in adjusted population). (NMFS, EBS Pollock Assessment)) Because the r_i and \hat{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 demands, populations and all parameters for all species, except the r_i

parameters, are substituted into the nine first-order conditions and into the objective functions for all species except pollock and sea lions. These six objective functions are set to zero assuming that these six species are in steady state, and together with the first order conditions they provide fifteen equations. For pollock, equations (21) and (22) are added to the fifteen:

$$N_4^t \left[p + \frac{(1-p)^{s_4}}{s_4} \right] \left[\frac{R_4(x_{43}; N_4^t) + V_4}{\hat{V}_4} - 1 \right] = h \quad (21)$$

$$R_4(\hat{x}_{43}; N_4^t) = 0 \quad (22)$$

where $p = \frac{d_{45} x_{43}^5}{w_4}$ is described in (20). The purpose of adding (21) and (22) is to solve for the pollock variable respiration parameter and the pollock biomass demand in a natural steady state. Equation (21) sets the fish population growth on the left side (from (20)) with the 1980 harvest, h . The x_{43} in (21) 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 (21) was solved for in the calibration. This latter biomass demand was used in (22) which is the pollock net energy in steady state *as if there was no harvesting*, and (22) then yields the no-harvesting variable respiration parameter, \hat{r}_4 .

For the sea lions, their population in 1980 was in the midst of an ongoing decline starting in the 1960s, so they were not assumed to be in a steady state. The sea lion objective function was set to $-200,000$ which yielded a population decrease using the sea lion update equation approximately equal to the observed decrease from 1980 to 1981. The resulting eighteen equations are used to solve for the variable respiration parameters, r_i .

In the second step, 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 without (21) to obtain the final variable respiration parameters used in all the results presented below.

IV.C Simulations and Constant Harvests

Figure 2 displays the simulated population units of the eight species over a non-specific twenty-three years. Because the population unit magnitudes vary so widely, they are rescaled to fit in the Figure. The ecosystem is in a natural steady state (no human intervention) up to year 4 at which time constant pollock harvesting at 1980 levels ($h = 0.76$) commences as follows.¹³ With the populations set at their natural steady-state values, the harvest is subtracted from the pollock population, and then a short-run equilibrium is calculated. The short-run results are used in the update equations to obtain next period's populations, after which the harvest is again subtracted from the new pollock population. The new populations are then used in the next short-run calculation and the process is repeated until a steady state with the constant harvest is reached after about year 20.

****Insert Figure 2 Here****

Figure 2 shows that harvesting leads to lower pollock stocks. In turn, lower stocks mean less prey available for sea lions whose population decreases, and fewer sea lions mean less prey available for killer whales whose population also decreases. Alternatively, zooplankton benefit from fewer pollock and their population increases, and this results in a slight decrease in the phytoplankton population. On the other side of the food web, although killer whales substitute from sea lions to otter when the population of the former decreases, the switch is too small to

show up in the Figure. Consequently, there are only very small changes in the urchin and kelp populations as well.

The population movements after harvesting commences reflect the ecosystem forces that drive the system to steady state. The killer whales are particularly interesting because they exhibit switching behavior. In economic terms, a whale equates its marginal rate of substitution between sea lion and otter energy intake, calculated as the ratio of partial derivatives of the respiration functions with respect x_{85} and x_{87} , 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. Moving from the natural to the harvesting steady state in Figure 2, the killer whale population in real numbers falls from 1000 to 928. Also, because the sea lion population decreases, the energy price paid by a killer whale for sea lions increases and each whale demands 0.00556 fewer sea lions per year. Combining the population change with the demand change implies that annual killer whale predation drops from 19,462 to 18,056 sea lions.

Meanwhile, killer whales switch to more sea otter as the energy price for capturing otter decreases owing to less intraspecies competition for otter by the killer whales. After harvesting, each killer whale takes 0.799 more otter per year, but because the whale population decreases, the net change is very small: total predation by killer whales on otter increases from 10344 to 10348. In ecological terms, the reduced prey density (of sea lions) yields a numerical response by the predator (killer whales) given by the changes in N_8 , and a functional response by the predator given by the changes in predator demands, x_{85} and x_{87} .¹⁴

V. Impacts of Harvesting

V.A Harvests

Table 2 displays the natural steady and harvesting steady-state populations for a sample of constant harvest values from 0 to 2.2. These harvests are exogenous and not solutions to any economic maximization problem. Harvest values slightly greater than 2.2 led to a collapse of the pollock population in 6 or fewer periods. Because the natural steady-state pollock population is 6.227, a harvest of 2.2 represents about 32% of the natural stock. The data in Table 3 were used to estimate a relation between each species' steady-state populations and pollock harvests, and in all cases a linear function provided the best fit.¹⁵ The functions are given by:

$$N_i^{ss} = \hat{a}_i + \hat{b}_i h, \quad i = 1, \dots, 8 \quad (23)$$

where *ss* refers to steady state. For pollock and sea lions the estimated coefficients are $\hat{a}_4 = 6.140$, $\hat{b}_4 = -0.9597$, $\hat{a}_5 = 0.0908$ and $\hat{b}_5 = -0.0077$, and the estimates for the other species are available from the authors. All estimated coefficients were significantly different than zero, and each of the eight estimated equations had an adjusted $R^2 > .99$ except for Kelp which had $R^2 = .42$. Increases in pollock harvests positively impact zooplankton and sea otters but negatively impact the other six species.¹⁶

****Insert Table 2 Here****

V.B Recovery Plan and Harvests

Section II outlined a recovery plan within a social net benefit maximization problem given by (1) and (3)-(6). Conceptually, GEEM would provide the biological constraints, (3)–(6) in this problem. In the solution, if the shadow price of maintaining a minimum viable population of sea lions is positive in every period, thus constraining the harvests to lower values than in the absence of a recovery program, then constraint (5) is satisfied by equality in every period. In this

case, the constraints are sufficient to determine the sea lion growth in each period and given the one-to-one relationship between sea lion population, pollock population and harvesting, constraint (5) dictates the permitted harvesting over time until the target sea lion population is attained in period T .

Given the rapid decline in sea lion populations since 1980, any reasonable recovery plan would likely find constraint (5) to be binding and, therefore, to be determining harvests. In other words, the biology would determine harvests and economic optimization would be left to determine capital and labor factors and the timing of their use. Biologically determined harvests are consistent with the regulated open access fishery model introduced by Homans and Wilen (1997) that they describe as being a more realistic version of how harvests are determined in practice. In their model of a single species, the fishery manager sets harvests according to an equation $h^t = c + dN_4^t$ where c and d are constants. With GEEM the fishery manager can account for a more complete ecosystem by employing equation (5) when the sea lion population is a binding constraint on harvests.

To see how this might work, that is, to implement the recovery plan set out in II.B, note that the five SEIS alternatives do not specify \tilde{N}_5 , the target sea lion population in (5). However, if one were established then it could be used according to the rule: If the unconstrained net benefit maximization problem yields a steady-state harvest, h^{ss} , such that $N_5^{ss} \geq \tilde{N}_5$, then this harvest is acceptable. But if $N_5^{ss} < \tilde{N}_5$, then harvest must be lowered until $N_5^{ss} = \tilde{N}_5$. An acceptable harvest can be obtained from (23) as the solution to $N_5^{ss} = \hat{a}_5 + \hat{b}_5 h = \tilde{N}_5$.

Suppose for demonstration that a target were set requiring 50% reduced sea lion mortality owing to pollock harvesting. Biologists believe that pollock harvesting and the other factors

discussed in section II.A moved the sea lion population from 180,000 in 1960 to 125,000 in 1980. These other factors (e.g.s, sea surface temperatures and subsistence hunting) are not included in the model. From Table 2, GEEM implies that after 1980 if harvesting were removed and in the absence of these other factors, the population would have stabilized at 118,610 (or 0.0912382 population units).¹⁷ Alternatively, if the other factors were absent but harvesting continued at 1980 levels ($h = 0.769$), the population would have stabilized at 110,079, and if harvesting were increased to mid 1990s levels ($h = 1.0$) the population would have stabilized at 107,687. However, the observed population in the mid 1990s was 52,000, and we assume this low number is attributable to the other factors and the mid 1990s harvesting. The implication is that mid 1990s pollock harvests account for 16.4% $((118,610 - 107,687)/(118,610 - 52,000))$ of the decline in the Steller sea lion population.¹⁸

Pollock can support a sea lion population of 118,610 in the absence of harvesting, while pollock can support a sea lion population of 107,687 if harvesting is at the mid 1990 levels ($h=1$). Therefore, relative to the natural steady state, mid 1990s harvesting implies 118,610 – 107,687 fewer sea lions, and cutting this by 50%, in line with our demonstration, implies a population of 113,149 (0.08704 in population units). Using (23), harvesting would have to be reduced from 1.0 to an estimated 0.488, or by 51.2%. (Again, these population figures are accounting only for pollock harvesting as a factor in sea lion mortality.)

Most bioeconomic fishery models use effort as a proxy for fishery factors of production, and this hypothetical lower harvest can be used to determine how much effort in the fishery would have to be reduced to achieve the 50% reduction in sea lion mortality. Finnoff and Tschirhart (2001) estimate a Schaffer harvest function,

$$h^t = qE^t N_4^t \tag{24}$$

with the estimate for the catchability coefficient $q = 5.35 \times 10^{-6}$. Substituting into (24) the mid 1990s harvest ($h = 1.0$) and population ($N_4 = 5.1803$) yield $E = 36,082$, while substituting into (24) the harvest ($h = 0.487$) and population ($N_4 = 5.6526$) post recovery policy yields $E = 16,047$, or a 56% reduction in fishing effort.

After pollock and Steller sea lions, the next species most impacted by pollock harvesting is the killer whale. Using (23) with $\hat{a}_g = 0.0075$ and $\hat{b}_g = -0.00064$, and comparing the natural steady-state whale population with the steady-state population at mid 1990s harvesting levels indicates a 10.3% decrease from 995 to 910. Fewer killer whales may mean greater populations of other species that whales prey on, although in the model the sea otter population increases by only a very small amount. The smaller killer whale population also means less preying on sea lions as discussed above. There will be an economic impact associated with the drop in the killer whale population to the extent that killer whales support ecotourism or provide other economic benefits to households, at least some of which can be measured (Loomis and White 1996).

VI. CONCLUSION

Like economies, ecosystems are complex, interconnected systems. When a human activity impacts one part of the system it sets up a sequence of impacts throughout. In some cases the sequential impacts are small so that examining the impacts in a partial equilibrium framework may be appropriate. But in other cases the sequential impacts are significant and a general equilibrium framework is desirable. A sequence of impacts that leads to unintended disturbances of other human activities is an ecosystem externality. GEEM is an attempt to capture the sequential impacts in order to account for ecosystem externalities.

In this paper the economic decision is about harvesting an endangered species' prey, and the results from GEEM bear on endangered species policy. Subject to the missing "other factors"

alluded to above, the results show that between 1980 and the mid 1990s harvesting pollock accounts for 16.4% of the decline in Steller sea lions, or 10,923 individuals. To cut this mortality in half would require reducing pollock harvests by about 51.2%; hence, there is a clear tradeoff between the social net benefits from pollock harvesting and sea lions populations. A policy that halves pollock harvests to increase sea lion populations by about 5500 no doubt would be controversial. Alternative 2 in SEIS calls for a harvest reduction between 31% and 55%, although Alternative 4, the stated preferred alternative, calls for a reduction between 5% and 9%. The alternatives do not translate these reductions into increased numbers of sea lions as is done here using GEEM.¹⁹

Part of the reason for the large harvest reduction is that the burden of recovering sea lions is being fostered on only one human activity. But there are numerous human activities that affect sea lions in Alaska, and changing the level of any one of these activities is a potential instrument for sea lion recovery. To spread the burden over more activities, GEEM could be expanded to more species and then integrated with a general equilibrium economic model that includes the human activities that impact sea lions. This is a tall order, but the close connections between ecological and economic systems suggest that it may be worth carrying out.

APPENDIX

The net energy objective functions for representative individuals of the eight species are:

$$R_1 = [e_{01} - e_{10}]x_{10} - e_1[1 + t_1 e_{31}]d_{13}x_{10}^5 - r_1 x_{10}^2 - \beta_1 \quad (\text{phytoplankton}) \quad (\text{A.1})$$

$$R_2 = [e_{02} - e_{20}]x_{20} - e_2[1 + t_2 e_{62}]d_{26}x_{20}^5 - r_2 x_{20}^2 - \beta_2 \quad (\text{kelp}) \quad (\text{A.2})$$

$$R_3 = [e_1 - e_{31}]x_{31} - e_3[1 + t_3 e_{43}]d_{34}x_{31}^5 - r_3 x_{31}^2 - \beta_3 \quad (\text{zooplankton}) \quad (\text{A.3})$$

$$R_4 = [e_3 - e_{43}]x_{43} - e_4[1 + t_4 e_{54}]d_{45}x_{43}^5 - r_4 x_{43}^2 - \beta_4 \quad (\text{pollock}) \quad (\text{A.4})$$

$$R_5 = [e_4 - e_{54}]x_{54} - e_5[1 + t_5 e_{85}]d_{58}x_{54}^5 - r_5 x_{54}^2 - \beta_5 \quad (\text{sea lion}) \quad (\text{A.5})$$

$$R_6 = [e_2 - e_{62}]x_{62} - e_6[1 + t_6 e_{76}]d_{67}x_{62}^5 - r_6 x_{62}^2 - \beta_6 \quad (\text{sea urchin}) \quad (\text{A.6})$$

$$R_7 = [e_6 - e_{76}]x_{76} - e_7[1 + t_7 e_{87}]d_{78}x_{76}^5 - r_7 x_{76}^2 - \beta_7 \quad (\text{sea otter}) \quad (\text{A.7})$$

$$R_8 = [e_5 - e_{85}]x_{85} + [e_7 - e_{87}]x_{87} - r_8 x_{85}^2 - r_8 x_{87}^2 - \beta_8 \quad (\text{killer whale}) \quad (\text{A.8})$$

The first-order conditions with respect to the individual demands are the derivatives of (A.1)-(A.8) with respect to the x_{ij} . There are nine first-order conditions, two for the whales and one for each of the other species. The demand/supply conditions for biomass transfers are:

$$N_1 x_{10} = \tau_1 1300000 \quad (\text{phytoplankton equated with area of EBS, } \tau_1 \text{ is from Table 1}) \quad (\text{A.9})$$

$$N_2 x_{20} = \tau_2 26000 \quad (\text{kelp equated with area of AI, } \tau_2 \text{ is from Table 1}) \quad (\text{A.10})$$

$$N_3 x_{31} = N_1 d_{13} x_{10}^5 \quad (\text{zooplankton demand equals phytoplankton supply}) \quad (\text{A.11})$$

$$N_4 x_{43} = N_3 d_{34} x_{31}^5 \quad (\text{pollock demand equals zooplankton supply}) \quad (\text{A.12})$$

$$N_5 x_{54} = N_4 d_{45} x_{43}^5 \quad (\text{sea lion demand equals pollock supply}) \quad (\text{A.13})$$

$$N_6 x_{62} = N_2 d_{26} x_{20}^5 \quad (\text{sea urchin demand equals kelp supply}) \quad (\text{A.14})$$

$$N_7 x_{76} = N_6 d_{67} x_{62}^5 \quad (\text{sea otter demand equals sea urchin supply}) \quad (\text{A.15})$$

$$N_8 x_{85} = N_5 d_{58} x_{54}^5 \quad (\text{killer whale demand equals sea lion supply}) \quad (\text{A.16})$$

$$N_8 x_{87} = N_7 d_{78} x_{76}^5 \quad (\text{killer whale demand equals sea otter supply}) \quad (\text{A.17})$$

After calibrating as explained in Table 1 (calibration equations are available in the code at the authors' websites), the first-order conditions and (A.9)-(A.15) are used in each short-run equilibrium calculations to solve for the x_{ij} and e_{ij} . The x_{ij} and e_{ij} are then substituted into (A.1)-(A.8) to obtain the optimum net energies that are used to update the populations using (19) and (20). The short-run calculations and the updating are repeated until steady states are attained.

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Notes

¹ E.g.s, Perrings et al. 1995; Arrow et al. 1995; Grime 1997; Daily 1997; Gowdy, 1997; Barrett and Odum 2000; Heal 2000.

² Aggregating species in food webs is common practice in ecological modeling (Solow and Beet 1998).

³ Another possibility is to make the predator population a choice variable along with the prey population. But the two populations are not independent, biological and environmental factors imply a functional relationship between the populations that yield a feasible set. Subsequent sections below provide a method for obtaining this set. The predator population is also omitted from the harvesting cost function, because the predator population is assumed not to aid nor hinder harvesting operations. Of course, the predator population affects the prey population that does appear in the cost function, but these affects are captured through the growth functions.

⁴ Kaplan and Smith present a general constraint over the predator population. Denoting the recovered predator population as N_R and N_t the population in any period t up to the specified endpoint t , the authors' constraint is $N_t \geq N_R$ for $t \leq t$.

⁵ Since the initial stocks of all species are given in period zero, together they also determine from (3) the stock of species in period one. Thus, (3) does not constrain the system for $t = 0$, nevertheless, $t = 0$ is included in (3) because it is used in the substitutions.

⁶ If in any period t constraints (9) or (10) are satisfied by an inequality, then $\tau_t = 0$ and there is no net benefit loss in that period from implementing the recovery plan. There is the possibility that if the constraints are satisfied by inequalities then the safe minimum population can be exceeded. Assuming that the government would harvest more in every period in the absence of a recovery plan, then there is a positive cost of the plan, $\tau_t > 0$ in each period, and the safe minimum population will not be exceeded.

⁷ More detail of the model can be found in Tschirhart (2000, 2002), Pethig and Tschirhart (2002), and Finnoff and Tschirhart (2002). The Mathematica GEEM code in used in this paper is available at either authors' website.

⁸ Energy is singled out as a maximand for several reasons. As long ago as Cowles (1899), for plants light energy has been referred to as one of the main limiting resources (along with nitrogen), and the importance of energy efficiency has its roots in Lotka's "maximum power principle" (1922). Huston and Smith (1987, p. 174) state that: "...light competition provides the clearest and most important example of the complexity of competitive ability for a single resource." According to Herendeen (1991) energy has been the most frequently chosen maximand in ecological maximization models, and energy maximization as adopted here is closely aligned with Hannon (1973, 1976) and expanded to multiple species in Tschirhart and Crocker (1987), Crocker and Tschirhart (1992) and to the individual level in Tschirhart (2000). Energy per time is also the individual's objective in the extensive optimum foraging literature (e.g., Stephens and Krebs 1986).

⁹ This tradeoff between foraging gains and losses is called predation risk (See, e.g., Lima and Dik 1990).

¹⁰ 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.

¹¹ 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.

¹² 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.

¹³ The populations were disturbed from their steady-state values and they returned to their steady states for various combination of disturbances of 50% or less. The simulations suggest some measure of stability, although general stability properties are left for further research.

¹⁴ Estes et al. (1998) hypothesize that the reduced sea lion populations may have led killer whales to switch to sea otter and cause decreases in the otter population. Our results suggest killer whale switching (functional response) may be offset by killer whale population changes (numerical response) caused by pollock harvesting. Extant ecological models do not typically track both numerical and functional responses.

¹⁵ Although GEEM is nonlinear, population changes with respect to harvests are close to linear, because the functional responses (see footnote 14) are small relative to the numerical responses. In (15) for all predator and prey, the x 's do not change much, and because the harvest is directly subtracted from N_4 , the populations do more of the adjusting.

¹⁶ The magnitude of impacts on kelp, urchins and otters are all very close to zero even though they are significantly different than zero.

¹⁷ Recall that in the calibrations, the net energy of the sea lions in 1980 was set to a negative value that would yield the actual decline in the population in 1981. Thus, whatever factors were causing the population decline, their impact was taken into account in constructing parameter values.

¹⁸ In 2001 there were 1,715 sea lion losses above natural attrition of which between 943-1286 were not attributable to known factors (Loughlin and York 2001). The model predicts that 254 of the losses are attributable to pollock harvesting.

¹⁹ Montgomery, Brown and Adams (1994) estimate the cost of increasing the *probability* of survival of the Northern Spotted Owl. GEEM is an extension of this approach because it yields *numbers* of endangered species.

Table 1. Initial Variables and Parameters for the Marine Ecosystem

	Phytoplank.	Zooplank.	Pollock	Steller sea lion	Killer whale	Sea otter	Urchin	Kelp
Variables								
Populations N_i^a (units km^{-2})	87.6923 ^b 1 unit = 1×10^{12} ind.	162.308 ^c 1 unit = 1×10^9 ind.	6.16215 ^d 1 unit = 1000 ind.	0.096154 ^e 1 unit = 1 ind	0.007723 ^f 1 unit = 0.1 ind.	0.050631 ^g 1 unit = 100 ind.	10.7692 ^h 1 unit = 1×10^7 ind.	1076.92 ⁱ 1 unit = 1×10^4 ind
Biomass or Biomass Flow x_{ij}	435.6 ^j kg unit^{-1}	1782.7 ^k $\text{kg unit}^{-1} \text{y}^{-1}$	7440 ^l $\text{kg unit}^{-1} \text{y}^{-1}$	2663 ^m kg y^{-1}	486.6 ⁿ kg $\text{unit}^{-1} \text{y}^{-1}$ (Steller) 28.3 kg unit ⁻¹ y^{-1} (otter)	255,500 ^o $\text{kg unit}^{-1} \text{y}^{-1}$	330,000 ^p $\text{kg unit}^{-1} \text{y}^{-1}$	21024 ^q kg unit^{-1}
Parameters								
Embodied Energy e_i	400 ^r kcal kg^{-1}	559 ^s kcal kg^{-1}	1128 ^t kcal kg^{-1}	2000 ^u kcal kg^{-1}	NA ^v	1810 ^w kcal kg^{-1}	717 ^x kcal kg^{-1}	821 ^y kcal kg^{-1}
Light Absorption e_{0i}	15150 ^z $\text{kcal kg}^{-1} \text{yr}^{-1}$	NA ^{aa}	NA ^{aa}	NA ^{aa}	NA ^{aa}	NA ^{aa}	NA ^{aa}	650 ^{ab} $\text{kcal kg}^{-1} \text{yr}^{-1}$
Resting Metabolic Rate b_i	395948 ^{ac} $\text{kcal unit}^{-1} \text{yr}^{-1}$	178270 ^{ad} $\text{kcal unit}^{-1} \text{yr}^{-1}$	1247688 ^{ae} $\text{kcal unit}^{-1} \text{yr}^{-1}$	731326 ^{af} kcal yr^{-1}	130356 ^{ag} $\text{kcal unit}^{-1} \text{yr}^{-1}$	32193000 ^{ah} $\text{kcal unit}^{-1} \text{yr}^{-1}$	67732500 ^{ai} $\text{kcal unit}^{-1} \text{yr}^{-1}$	819936 ^{aj} $\text{kcal unit}^{-1} \text{yr}^{-1}$
Weight w_i	435.6 ^{ak} kg unit^{-1}	3.757 ^{al} kg unit^{-1}	1000 ^{am} kg unit^{-1}	250 ^{an} kg	399.6 ^{ao} kg unit^{-1}	2800 ^{ap} kg unit^{-1}	87600 ^{aq} kg unit^{-1}	21024 ^{ar} kg unit^{-1}
Predation d_{ij}^{as}	158.09306	6.6900	0.48175	0.75731	NA	0.008539	2.08162	22.9660
Plant Congestion τ_i^{at}	0.0293837	NA	NA	NA	NA	NA	NA	870.814
Var. Resp. r_i^{au} (kcal yr^{-1})	5.57396	0.083377	0.023100	0.133994	0.548683	0.000494	0.000624	0.005010

Table 1. Notes

NA – not applicable or not needed.

^a 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. Killer whales are divided by both areas.

^b 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.

^c 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.

^d Pollock biomass estimates for the years 1980-84 are 8.01×10^9 kgs (Witherell 2000). Assuming pollock are 1 kg on average, this is 8.01×10^9 individuals which converts to 8.01×10^6 population units. On a km^2 basis: $8.01 \times 10^6 \text{ units} / 1,300,000 \text{ km}^2 = 6.16215$ Recall, 1,300,000 is the ecosystem size in km^2 .

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

^f Based on 1024 individuals (SAFE 2000, 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.

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

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

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

^j 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.

^k 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 $1782.7 \text{ kg unit}^{-1} \text{ yr}^{-1}$.

^l Trites et al. (1997) p. 186. Pollock eat mostly zooplankton (Witherell 2000) although adults may eat smaller fish including juvenile pollock. Here their diet is assumed to be 80% zooplankton.

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

ⁿ 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 walruses 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.

^o 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.

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

^q Average biomass of an urchin is 0.00876 kg (Estes and Duggins 1995) and multiplied by the urchin population (vii) yields 943382 kg for the population. Assuming prey biomass is 1.2 times predator biomass (Kerr 1974), and assuming 5% of predation on kelp is by sea urchin, yields a biomass for kelp of $943382 (1.2)/.05$. Per population unit this is 21024 kg.

^r Weighted average of caloricity measures of three phytoplankton species groupings (Petipa et al. 1970, Table 7).

^s Weighted average of caloricity measures of three zooplankton species groupings (Petipa et al. 1970, Table 7).

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

^u Estimated based on blubber content in a sea lion versus otter which have no blubber. (Costa 1978) (See ^w).

^v Not needed because killer whales are at the top of the food web and are not prey.

^w Estes et al. (1998).

^x Costa (1978).

^y Lembi and Waalan (1988).

^z 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 ^b, x_{10} from ^j, N_2 from ^c, x_{21} from ^k and e_1 is from ^r.)

^{aa} Not applicable because only plants photosynthesize.

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

^{an} 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 $395,948 \text{ kcal yr}^{-1}$.

^{ad} An average of respiration as a % of body weight over multiple zooplankton species yields 25%. (Petipa et al. 1970, Table 2). Calculations are similar to ^{ac}.

^{ae} Pollock are assumed to have an average respiration of 30%. Their incoming energy from zooplankton is $7440 \text{ kg unit}^{-1} \text{ y}^{-1} 559 \text{ kcal kg}^{-1}$ which is then multiplied by 30%.

^{af} For mammals, resting metabolic rate in kcal d^{-1} (M) is related to body weight (W) by the formula $M = 67.61W^{0.756} 5\%$ (Kleiber 1975). Using 250 kg as sea lion weight and extrapolating to one year yields $1603786 \text{ kcal yr}^{-1}$. The RMB used in the simulations is lowered by $(76\%)(60\%)$ to reflect that sea lions are preying on more than just Pollock (See ^m.)

^{ag} Use the formula from ^{af} 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 ⁿ).

^{ah} Use the formula from ^{af} and an average weight of 28 kg and a +5% because otter have high metabolic rates (Costa 1978).

^{ai} Similar to the estimate in ^{ad} except urchin are assumed to respire at about 25%.

^{aj} Calculated as in ^{ac} except algae respiration (kelp) is assumed to be 15% of the value of photosynthesis (Petipa et al. 1970, Table 2).

^{ak} Phytoplankton are plants; therefore, weight is given in (ix).

^{al} Average of multiple zooplankton herbivore species (Petipa et al. 1970, Table 1).

^{am} Average of adult and juvenile, both are taken by fisheries and Steller sea lions. (See ^d.)

^{an} Based on weights of immature sea lions in Rosen and Trites (2000) and adult weights in Audubon Field Guide to North American Mammals (1980).

^{ao} Average of male and female adults is 3996 kg (Estes et al. 1998).

^{ap} Average of male and female adults is 28 kg (Costa 1978).

^{aq} Urchins at six locations in the Aleutians averaged 8.76 gm each with a wide variance (Estes and Duggins 1995, Table 2).

^{ar} Kelp are plants; therefore, weight is given in ^q.

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

^{at} 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.

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

Table 2 – Steady-state Populations and Harvests

	N_1^{ss}	N_2^{ss}	N_3^{ss}	N_4^{ss}	N_5^{ss}	N_6^{ss}	N_7^{ss}	N_8^{ss}
Harvest	Phyto.	Kelp	Zoo.	Pollock	Sea lion	Urchin	Otter	K. whale
0	87.6924	1076.92	162.28	6.227	0.0912	10.7692	0.05063	0.00754
0.2	87.6920	1076.92	162.37	5.987	0.0895	10.7692	0.05063	0.00740
0.4	87.6917	1076.92	162.46	5.756	0.0877	10.7692	0.05063	0.00726
0.6	87.6913	1076.92	162.56	5.536	0.0860	10.7692	0.05063	0.00712
0.8	87.6909	1076.92	162.66	5.326	0.0844	10.7692	0.05063	0.00698
1.0	87.6906	1076.92	162.76	5.126	0.0828	10.7692	0.05063	0.00685
1.2	87.6902	1076.92	162.86	4.395	0.0813	10.7692	0.05063	0.00672
1.4	87.6897	1076.92	162.97	4.753	0.0798	10.7692	0.05063	0.00660
1.6	87.6893	1076.92	163.08	4.580	0.0783	10.7692	0.05063	0.00648
1.8	87.6889	1076.92	163.20	4.416	0.0769	10.7692	0.05063	0.00636
2.0	87.6884	1076.92	163.31	4.259	0.0756	10.7692	0.05063	0.00625
2.2	87.6880	1076.92	163.43	4.111	0.0743	10.7692	0.05063	0.00615

FIGURE 1 FOOD WEB

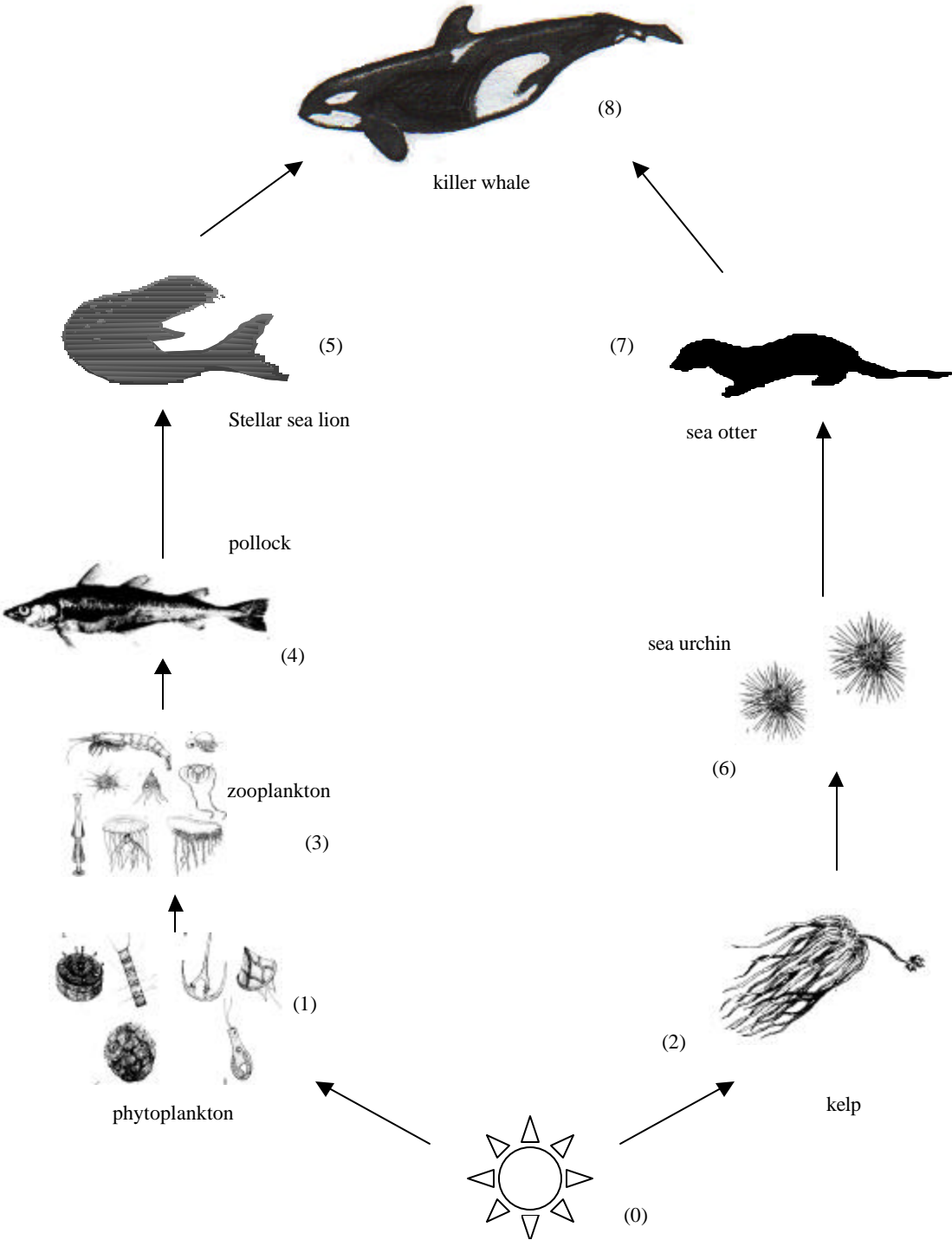
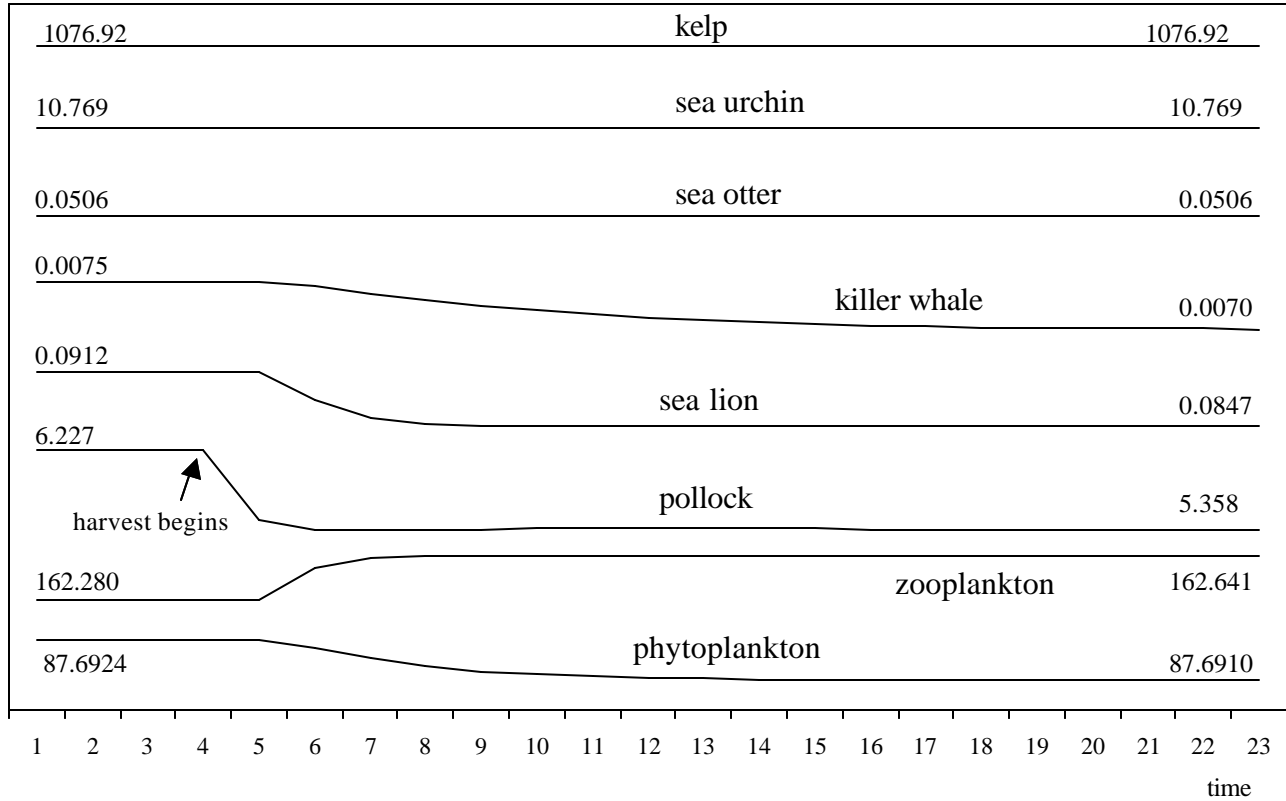


FIGURE 2 POPULATIONS PRE AND POST HARVEST



The ecosystem is in a natural steady state when harvesting begins in period 4. There is an immediate impact on the pollock population and a lagged impact on other species. The numbers are in population units.