Harvesting Prey while Protecting an Endangered Predator in a General Equilibrium Ecosystem Model

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Abstract

Endangered species are in predator/prey, mutualistic, competitive, or other types of relationships with many other species that share their habitat. Understanding these ecological relationships is an important part of designing endangered species policies. We employ a general equilibrium model of an ecological community containing a human harvested species that is preyed on by an endangered species subject to a recovery plan. The model is applied to an Alaskan marine ecosystem in which pollock are harvested and Steller sea lions are endangered, and both interact with six other species. Results indicate the impact harvesting has on the endangered sea lions.

I. Introduction

There is growing evidence cited in popular and scientific publications about the decline of biodiversity in ecological systems resulting from increasing per capita resource consumption of increasing numbers of people.[1] At the same time there are indications that biodiversity is essential for human existence (Gowdy, 1997). 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. Endangered species are in predator/prey, mutualistic, competitive, or other types of relationships with many other species that share their habitat. These other species may be directly impacted by human activity so that the activity indirectly impacts endangered species. Understanding these ecological relationships is an important part of designing endangered species policies. (Hayward, et al. 2001)

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

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

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 combines general equilibrium calculations, similar to those used in computable general equilibrium (CGE) economic models, with dynamic population updating used in ecology. 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, while 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).

The next section 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 the ecological theory underpinning GEEM. 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. Describing the Problem

Starting with 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, let $U(H^t)$ be the benefit derived from harvesting in period t, H^t, and let $C(H^t, N^t)$ be the cost of harvesting in period t that depends on the harvest and on the stock or population, N^t. Given an initial stock, N^0, the problem is to choose a vector of harvests, $H = (H^0, H^1, \ldots, \mathrm{H}^t, \ldots)$, and populations, $N = (N^1, N^2, \ldots., \mathrm{N}^t, \ldots)$, to

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

$$\text{subject to} \quad N^{t+1} = N^t + Y(\mathrm{N}^t) - H^t \quad t = 0, \ldots, \tag{2}$$

where r is the rate of return on investment in the economy, and $Y(N^t)$ is the growth of the population in period t. Solving (2) for the H^t and substituting into the objective function, and using the first order condition for any period t, yields the condition:

$$\frac{[U_{H^{t+1}} - C_{H^{t+1}}] - [U_{H^t} - C_{H^t}]}{U_{H^t} - C_{H^t}} + \frac{U_{H^{t+1}} - C_{H^{t+1}}}{U_{H^t} - C_{H^t}} Y_{N^t} - \frac{C_{N^{t+1}}}{U_{H^t} - C_{H^t}} = r \tag{3}$$

Subscripts on U and C in (3) denote partial derivatives, and equations (2) and (3) determine the time paths for the harvests and populations that maximize net benefits. In a steady state, $N^{t+1} = N^t$, $H^{t+1} = H^t$, and (3) reduces to the familiar optimality condition for harvesting a renewable resource:

$$Y_{N^t} - \frac{C_{N^{t+1}}}{U_{H^t} - C_{H^t}} = r \tag{4}$$

See HO for interpretations of (3) and (4).

HO extend this model by adding a second species that preys on the harvested species so that the species' growths are interdependent[2]. Let N_1^t and N_2^t be the prey and predator species' populations in period t and let $Y(N_1^t, N_2^t)$ and $D(N_1^t, N_2^t)$ be the prey and predator growth functions, respectively. The population update equation for the predator is:

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[2] Similar models in continuous time include those in Ragozin and Brown (1985), Wilen and Brown (1986), Tu and Wilman (1992), and Kaplan and Smith (2000).

$$N_2^{t+1} = N_2^t + D(N_{1,}^t N_2^t) \tag{5}$$

In HO, the predators are sharks that feed on tuna, and an welfare optimum policy is derived where sharks also are harvested so that more tuna are available to humans. In this paper, the predator population is assumed to be a threatened or endangered species for which the government has established a recovery plan to increase the population to $\overline{N}_2$ over T periods, where $\overline{N}_2$ is considered the safe minimum population. Given initial stocks, N_1^0 and N_2^0, the welfare problem is restated as:

$$\text{maximize} \quad \sum_{t=0}^{\infty} \frac{1}{(1+r)^t} [\, U(H^t) - C(H^t, N_1^t)] \tag{6}$$

$$\text{subject to} \quad N_1^{t+1} = N_1^t + Y(N_1^t,\, N_2^t) - H^t \qquad t = 0, \ldots, \tag{7}$$

$$N_2^{t+1} = N_2^t + D(N_{1,}^t N_2^t) \qquad t = 0, \ldots, \tag{8}$$

$$D(N_1^t,\, N_2^t) \geq \frac{1}{T-t} [\overline{N}_2 - N_2^t] \qquad t = 0, \ldots, T\text{-}1 \tag{9}$$

$$D(N_1^t,\, N_2^t) \geq 0 \qquad t = T, \ldots, \tag{10}$$

The objective function does not change from that used in the single species problem. Benefit still depends on harvests alone implying 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]

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.

Constraints (9) and (10) represent the recovery plan. Constraint (9) stipulates that the predator population must move toward the safe minimum population, $\overline{N}_2$, 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 again chooses vectors of harvests and harvested species populations to maximize net benefits. Constraints (7) and (8) can be substituted into the objective function,[5] to form the Lagrange expression:

$$\begin{aligned} L(N_1) = {} & \sum_{t=0}^{\infty} \frac{1}{(1+r)^t} [U(N_1^t - N_1^{t+1} + Y(N_1^t, N_2^{t+1} - D(N_1^t, N_2^t))) - \\ & C(N_1^t - N_1^{t+1} + Y(N_1^t, N_2^{t+1} - D(N_1^t, N_2^t)), N_1^t)] \\ & + \sum_{t=1}^{T-1} \frac{l^t}{(1+r)^t} [T-t][D(N_1^t, N_2^t) - \overline{N}_2 + N_2^t] + \sum_{t=T-1}^{\infty} \frac{l^t}{(1+r)^t} D(N_1^t, N_2^t) \end{aligned} \tag{11}$$

The Lagrange multipliers, l^t, are discounted because they are period-by-period shadow prices on the minimum viable population. Thus, l^{t+1} is a shadow price of the minimum viable population in period t +

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[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.

[4] Kaplan and Smith present a general constraint over the predator population. Denoting the recovered predator population as Y_R and Y_t the population in any period t up to the specified endpoint t, the authors' constraint is $Y_t{}^{3}Y_R$ for t^{3} t.

[5] Since the initial stocks of both species are given in period zero, together they also determine from (8) the stock of species two in period one. Thus, (8) does not constrain the system for t = 0, nevertheless, t = 0 is included in (8) because it is used in the substitutions.

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, p. 11.)

For any period t, using the Kuhn-Tucker condition with respect to N_1^t, and assuming $N_1^t > 0$ at the optimum, yields the condition:

$$\frac{[U_{H^{t+1}} - C_{H^{t+1}}] - [U_{H^t} - C_{H^t}]}{U_{H^t} - C_{H^t}} + \frac{U_{H^{t+1}} - C_{H^{t+1}}}{U_{H^t} - C_{H^t}}[Y_{N_1^t} - Y_{N_2^t} D_{N_1^t}] - \frac{C_{N^{t+1}}}{U_{H^t} - C_{H^t}} + \frac{l^t t\, D_{N_1^t}}{U_{H^t} - C_{H^t}} = r \qquad (12)$$

where

= *T – t –1*, for *t = 0,…, T-2*

and = *1*, for *t > T-2*.

The first and third terms on the left side of (11) are the same as the first and third terms in (3). The second term is the marginal stock effect, and it is changed to account for the interaction between the predator and prey. The bracketed term indicates how changes in the harvested population affect directly the growth of the harvested species, and affect indirectly the growth of the harvested species through changes in the growth of the predator population.

The fourth term on the left side of (12) follows from the added constraints in the two-species problem. Applying the envelope theorem to (11) yields:

$$\frac{\partial W}{\partial \bar{N}_2} = -\sum_{t=1}^{T-1} l^t \qquad (13)$$

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, $\bar{N}_2$. Thus, the fourth term gives lost net benefits in period *t* of moving toward the safe minimum population by increasing the prey population via smaller harvests. For periods beyond *T - 1*, the fourth term is the marginal cost of maintaining the safe minimum population.[6] Finally, in a steady state where neither population is changing, which can only occur after the minimum viable population is attained, (12) reduces to:

$$[Y_{N_1^t} - Y_{N_2^t} D_{N_1^t}] \quad - \quad \frac{C_{N^{t+1}}}{U_{H^t} - C_{H^t}} \quad + \quad \frac{l^t D_{N_1^t}}{U_{H^t} - C_{H^t}} = r \qquad (14)$$

A major difficulty with implementing a recovery plan is the lack of information about the growth functions *Y(·)* and *D(·)* and how harvesting impacts steady-state populations. Moreover, any two species in a predator/prey relationship also are in predator/prey or mutualistic relationships or in resource competition with other species. Therefore, in an *n* species ecosystem the growth functions for the harvested species and its predator become $Y(N_1^t, \ldots, N_n^t)$ and $D(N_1^t, \ldots, N_n^t)$, respectively, and for each of the other *n* – 2 species a growth function and update equation must be appended to the optimization problem. Writing these new growth functions as:

$$G_j(N_1^t, \ldots, N_n^t), \quad j = 3, \ldots, n$$

and then substituting from each new species' update equation into (6) and (7) yields the steady-state condition:

$$[Y_{N_1^t} - Y_{N_2^t} D_{N_1^t} - Y_{N_3^t} G_{3N_1^t} - \ldots\ldots - Y_{N_n^t} G_{nN_1^t}] \quad - \quad \frac{C_{N^{t+1}}}{U_{H^t} - C_{H^t}} \quad + \quad \frac{l^t D_{N_1^t}}{U_{H^t} - C_{H^t}} = r \qquad (14')$$

The marginal stock effect in brackets now accounts for the interactions between the harvested species in addition to all other species.

Because these additional *n* – 2 species also may provide direct benefits to humans, or indirect benefits through their impacts on species providing direct benefits, their inclusion in the model may be

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[6] If in any period t constraints (9) or (10) are satisfied by an inequality, then $_t$ = 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, $_t$ > 0 in each period, and the safe minimum population will not be exceeded.

critical for formulating optimum harvesting policies. In the remaining sections an ecosystem model is used that tracks relationships between harvesting and steady-state populations, and that accounts for other species besides one harvested and one endangered species.

III. The Ecological Model [7]

The general equilibrium ecological model is fundamentally different from the familiar Lotka-Volterra predator/prey models and their variations, from familiar resource competition models (e.g., Gurney and Nisbet, chpt. 6), and from large simulation models (e.g., Christensen and Pauly, 1992). First, its basic unit is an individual organism and not a species, and decisions are made by the individual. Second, it recognizes that natural selection requires plants and animals to maximize their net energy flows; thus an optimization approach is used to capture efficient energy use by all individuals. 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.

A marine ecosystem that links Alaska's Aleutian Islands (AI) with the Eastern Bering Sea (EBS) is used to illustrate the model. 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.[8] 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 and 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 a groundfish in the EBS that feed on zooplankton and support an important fishery. Steller sea lions, an endangered pinneped 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

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[7] More detail of the model can be found in Tschirhart (2000, 2002) , Pethig and Tschirhart (2002), and Finnoff and Tschirhart (2001).

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

recovery program.

The sun, phytoplankton, kelp, zooplankton, pollock, Steller sea lion, urchin, otter and killer whale are indexed 0-8, respectively, and the net energies of a representative individual pollock and Steller sea lion are given by (15)-(16), respectively:

$$R_4 = [e_3 - e_{43}]x_{43} - r_4 x_{43}^2 - b_4 - e_4[1 + t_4 e_{54}]d_{45} x_{43}^{.5} \tag{15}$$

$$R_5 = [e_4 - e_{54}]x_{54} - r_5 x_{54}^2 - b_5 - e_5[1 + t_5 e_{85}]d_{58} x_{54}^{.5} \tag{16}$$

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

The first term on the right side of (15) is the inflow of energy to the pollock from consuming zooplankton. The e_3 is the energy (heat content) embodied in a unit of biomass of zooplankton, e_{43} is the “energy price” described below and it represents the energy lost to the atmosphere that the pollock must spend to locate and capture 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 (16) is similar to that in (15), except that the energy and biomass is flowing from pollock to the representative sea lion.

The second and third terms in (15) represent respiration which is energy lost by the individual to the atmosphere. Following Gurney and Nisbet (1998), respiration is divided into two parts: 1) the variable respiration that includes feces, reproduction, defending territory, etc., and that depends on energy intake according to the functional form $r_4 x_{43}^2$; and 2) the resting metabolic rate, b_4, which is independent of energy intake. Both $r_4 x_{43}^2$ and b_4 are measured in Watts, and r_4 is a constant coefficient determined by calibration. The second and third terms in (16) are the variable and fixed respirations for the representative sea lion.

The fourth term on the right side of (15) is the outflow of energy lost by the pollock owing to sea lion predation. The e_4 is the embodied energy in a unit of pollock biomass, and the term in brackets is the energy the pollock uses in attempts to escape capture. Pollock's escape energy is assumed to be a linear function of the energy sea lions use to capture pollock (e_{54}) : the more energy sea lions expend, the more energy pollock expend escaping. In a sense, t_4 is a tax on the pollock because it loses energy above what is loses owing to being captured. The biomass supplied by the pollock to sea lions is assumed to take the functional form $d_{45} x_{43}^{.5}$. In maximizing (15), 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.[9] (Note that this representation is similar to, but in reverse from, a firm whose supply of output determines its demand for inputs.) The last term in (16) is similar except that it is the loss of sea lion energy owing to predation by killer whales.

In addition to (15) and (16), 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, for all species are constants and assumed to be invariant.

The energies spent in predation, the e_{ij}, are the energy prices. There is one price for each biomass market and there are 9 markets in total, one market for each predator/prey relationship (including the two plant species "preying" on the sun), and two markets for the killer whales that prey on both otter and sea lion. As in economic GE 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,

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[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

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 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.

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 demand equals supply in every biomass market. 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 perfectly competitive economic model is that the number of firms in an industry changes according to whether profits are positive or negative.)

To find a set of prices that equate demands and supplies, an equilibrium equation is needed for each price. For example, the market 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, then letting N_i be the population of species i, the equilibrium condition between sea lion and pollock is:

$$N_5 x_{54} = N_4 \, d_{45} x_{43}^{.5} \qquad (17)$$

The left side of (17) is the total sea lion demand for pollock, and the right side is the total supply of pollock to sea lion. For the markets where plants prey on the sun, the condition is similar except the supply depends on the size of the space occupied by the plants.

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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 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 market clearing conditions similar to (17).

III.A 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 and their population increases. This increase 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 increases, and sea lion net energy will decrease. In addition, 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. 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 are derived as follows. Consider population changes for the killer whales whose objective function in (18) 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:

$$R_8 = [e_5 - e_{85}]x_{85} + [e_7 - e_{87}]x_{87} - r_8 x_{85}^2 - r_8 x_{87}^2 - b_8 \qquad (18)$$

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:

$$1/s_8 \qquad (19)$$

Next consider the killer whale's maximum net energy function given by $R_8(x_{8j}; \boldsymbol{N}^t) = R_8(\cdot)$ which is obtained by substituting the whale optimum demands as functions of energy prices into (18). ($\boldsymbol{N^t}$ is a vector of all species' populations and it appears in $R_8(\cdot)$ to indicate that net energies in time period t depend on populations in time period t.) In the steady state, $R_8(\cdot)=0$. 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. Let $\hat{V}_8$ be the steady-state variable respiration, and let $r\hat{V}_8$ be the proportion of this variable respiration devoted to reproduction. Thus, in steady state the energy given by $r\hat{V}_8$ yields a per capita birth rate of $1/s_8$. Next, suppose the whales are not in steady state and that $R_8(\cdot) \quad 0$ and variable respiration is V_8. Assuming that the proportion of $R_8(\cdot)$ that is available for reproduction is the same as the proportion of variable respiration available for reproduction, the energy now available for reproduction is $[\, R_8(\cdot) + V_8 \,]$. Finally, assuming that reproduction is linear in available energy, then it follows that if $r\hat{V}_8$ yields a per capita birth rate $1/s_8$, then $[\, R_8(\cdot) + V_{i8}]$ yields a per capita birth rate of:

$$(1/s_8)\,[\, R_8(\cdot) + V_{i8}]/\,\hat{V}_8\,. \tag{20}$$

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 (20), the population adjustment equation is

$$\begin{aligned} N_8^{t+1} &= N_8^t + N_8^t\,[\,\frac{R_8(\cdot)+V_8}{s_8\hat{V}_8} - \frac{1}{s_8}\,] \\ &= N_8^t + N_8^t\,\frac{1}{s_8}\,[\,\frac{R_8(\cdot)+V_8}{\hat{V}_8} - 1\,] \end{aligned} \tag{21}$$

Expression (21) reduces to the steady state if $R_8(\cdot)=0$ (in which case $V_8 = \hat{V}_8$), because the bracketed term is zero. Alternatively, $R_8(\cdot) >(<) 0$ implies that $V_8 >(<) \hat{V}_i$, in which case population increases (decreases).[11]

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, 2002a).

$$N_i^{t+1} = N_i^t + N_i^t [p + \frac{(1-p)^s}{s}][\frac{\mathrm{R}_i(\cdot) + V_i}{\hat{V}_i} - 1] \qquad (22)$$

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.

Some of the issues involved in assembling the data can be seen by considering 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

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[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.

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 market equilibrium condition for 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 (21) and (22) 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 (22) 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 (21) and (22) contain the constant steady-state variable respiration terms, $\hat{V}_i$, that are constructed from the r_i parameters. But steady-states depend on harvests, so from what harvest are these steady-state respiration terms obtained? 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

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[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.

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 (23) and (24) are added to the fifteen:

$$N_4^t\,[\,p+\frac{(1-p)^{s_i}}{s}\,]\,[\frac{R_4(\hat{x}_{43};N_4^t)+V_4}{\hat{V}_4}-1] = h \qquad (23)$$

$$R_4(\hat{x}_{43};N_4^t)=0 \qquad (24)$$

where $p = \dfrac{d_{45}x_{43}^{.5}}{w_4}$ is described in (22). The purpose of adding (23) and (24) is to solve for the pollock variable respiration parameter and the pollock biomass demand in a natural steady state. Equation (23) sets the fish population growth on the left side (from (22)) with the 1980 harvest, *h*. The x_{43} in (23) 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 (23) was solved for in the calibration. This latter biomass demand was used in (24) which is the pollock net energy in steady state *as if there was no harvesting*, and (24) 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 to recognize that the population was decreasing, where the –200,000 yielded a decrease in 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 (23) to obtain the final variable respiration parameters used in all the results presented below.

IV.C Simulations and Harvests Figure 2 displays the populations of the eight species over a non-specific twenty-three years. Because the population magnitudes vary so widely, they are rescaled to fit in the Figure. The ecosystem is in a natural steady state up to year 4 when constant pollock harvesting at 1980 levels ($h = 0.76$) commences.[13] Setting the populations to their natural steady-state values, subtracting the harvest from the pollock population, and then calculating a short-run equilibrium simulate harvesting. The short-run results are used in the update equations to obtain next period's populations in the usual manner, 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 harvest is reached.

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 market 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

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[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.

and otter energy intake, calculated as the ratio of derivatives of the respiration functions in (18) 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 3 displays the natural steady and harvesting steady-state populations for a sample of constant harvest values from 0 to 2.2. 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. The functions are given by:

$$N_i^{ss} = \hat{a}_i + \hat{b}_i h\,, \quad i = 1,\ldots,8 \qquad (25)$$

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[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 reponses.

where *ss* refers to steady state. The estimated slopes and intercepts are:

Coefficient	Phyto	p-value	Zoo	p-value	Pollock	p-value	Sea Lion	p-value
$\hat{a}_i$	87.693 (.00003)	0.0000	162.252 (.00964)	0.0000	6.14 (0.02912)	0.0000	.0908 (.00014)	.0000
$\hat{b}_i$	-0.002 (.00003)	0.0000	0.5249 (.00742)	0.0000	-.9597 (0.02242)	0.0000	-.0077 (.00011)	.0000
Adjusted R^2	0.998		.998		0.994		.998	
F-Test: $F_{(1,10)}$	5329.86	0.0000	5003.11	0.0000	1831.58	0.0000	4845.51	.0000
Coefficient	Kelp	p-value	Urchin	p-value	Otter	p-value	Whale	p-value
$\hat{a}_i$	1076.92 ($0.98\text{x}10^{-7}$)	0.0000	10.769 ($0.66\text{x}10^{-10}$)	0.0000	0.0506 ($0.12\text{x}10^{-9}$)	0.0000	0.0075 ($0.12\text{x}10^{-4}$)	0.0000
$\hat{b}_i$	$-0.22\text{x}10^{-6}$ ($0.76\text{x}10^{-7}$)	0.0139	$-.319\text{x}10^{-7}$ ($0.51\text{x}10^{-10}$)	0.0000	$0.252\text{x}10^{-7}$ ($0.92\text{x}10^{-10}$)	0.0000	-0.00064 ($0.92\text{x}10^{-5}$)	0.0000
Adjusted R^2	0.416		0.999		.999		0.998	
F-Test: $F_{(1,10)}$	8.85	0.0139	398944.7	0.0000	74362.88	0.0000	4418.97	0.0000

All estimated coefficients are clearly significantly different than zero, and each estimated equation displays a high level of goodness of fit (apart from Kelp). Changes in pollock harvests negatively impact all species in the ecosystem apart from zooplankton and sea otters[15]. Combining (25) for pollock and sea lion yields a relation between their steady-state values:

$$N_4^{ss} = \frac{\hat{b}_4[N_5^{ss} - \hat{a}_5]}{\hat{b}_5} + \hat{a}_4 \tag{26}$$

V.B Recovery Plan and Harvests 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 which 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.

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[15] Noting that the magnitude of impacts on kelp, urchins and otters are all very close to zero even though they are significantly different than zero.

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 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. Consider that harvesting and the other factors discussed above moved the sea lion population from 180,000 in 1960 to 125,000 in 1980. Using (25), the model predicts that if harvesting and these other factors were removed in 1980, then the population would have stabilized at 118,040.[16] Alternatively, if the other factors were removed but harvesting continued at 1980 levels (h = 0.769), the population would have stabilized at 110,602, and if harvesting were increased to mid 1990s levels (h = 1.0) the population would have stabilized at 108,290. Adding back the other factors and keeping the mid 1990s harvesting yields the observed decline in the population to 52,000 in the mid 1990s. The implication is that mid 1990s pollock harvests account for 14.8% ((118,040 –

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[16] 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.

108,290)/(118,040 – 52,000)) of the decline in the Steller sea lion population.[17]

With respect to a recovery plan, the SEIS alternatives do not establish a specific target as shown in (9) for future sea lion populations. However, suppose for demonstration that a target were set requiring 50% reduced sea lion mortality owing to pollock harvesting. Pollock can support a sea lion population of 118,040 in the absence of harvesting, while pollock can support a sea lion population of 108,290 if harvesting is at the mid 1990 levels (h=1). Therefore, relative to the natural steady state, mid 1990s harvesting implies 118,040 – 108,290 fewer sea lions, and cutting this by 50% implies a population of 113,165 (0.08705 in adjusted terms). Using (25) and (26), harvesting would have to be reduced from 1.0 to 0.487 or by 51.3%. (Again, these population figures are accounting only for pollock harvesting as a factor in sea lion mortality; the actual sea lion populations are currently below 50,000.)

This hypothetical lower harvest can also be used to determine how much effort in the fishery would have to be reduced. Finnoff and Tschirhart (2001) estimate a Schafer harvest function,

$$h^t = qE^t N_4^t \tag{27}$$

with the estimate for the catchability coefficient q = 5.35 x 10^{-6}. Substituting into (27) the mid 1990s harvest (h = 1.0) and population (N_4 = 5.1803) yield E = 36,082, while substituting into (27) 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 (25), 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

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[17] 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.

in the killer whale population to the extent that killer whales support a tourist industry 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 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 necessary. GEEM is an attempt to capture the sequential impacts so they can be included in economic decisions.

The model presented here can be extended in many directions on the ecological side, especially by including in it the other factors that are believed to be causing Steller sea lion declines. On the economic side we did not introduce any specific harvesting policies or institutional structures nor did we introduce other industries, such as tourism, that depend on species other than the pollock. However, the approach allows for such introductions within a framework that can trace complex economic/ecological interactions.

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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 †	(i) 87.6923 units km^{-2} 1 unit =1x10^{12} ind.	(ii) 162.308 units km^{-2} 1 unit =1x10^{9} ind.	(iii) 6.16215 units km^{-2} 1 unit =1000 ind.	(iv) 0.096154 km^{-2} 1 unit = 1 ind	(v) 0.007723 units km^{-2} 1 unit = 0.1 ind.	(vi) 0.050631 units km^{-2} 1 unit = 100 ind.	(vii) 10.7692 units km^{-2} 1 unit = 1 x 10^{7} ind.	(viii) 1076.92 units km^{-2} 1 unit = 1x10^{4} ind
Biomass or biomass flow x_{ij}	(ix) 435.6 kg unit^{-1}	(x) 1782.7 kg unit^{-1} y^{-1}	(xi) 7440. kg unit^{-1} y^{-1}	(xii) 2663. kg y^{-1}	(xiii) 486.6 kg unit^{-1} y^{-1} (Steller) 28.3 kg unit^{-1} y^{-1} (otter)	(xiv) 255,500 kg unit^{-1} y^{-1}	(xv) 330,000. kg unit^{-1} y^{-1}	(xvi) 21024. kg unit^{-1}
Parameters								
Embodied energy e_i	(xvii) 400. kcal kg^{-1}	(xviii) 559. kcal kg^{-1}	(xix) 1128. 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 e0i	(xxv) 15150. kcal kg^{-1} yr^{-1}	(xxvi) NA	(xxvii) NA	(xxviii) NA	(xxix) NA	(xxx) NA	(xxxi) NA	(xxxii) 650 kcal kg^{-1} yr^{-1}
Resting metabolic rate b_i	(xxxiii) 395948 kcal unit^{-1} yr^{-1}	(xxxiv) 178270 kcal unit^{-1} yr^{-1}	(xxxv) 1247688. kcal unit^{-1} yr^{-1}	(xxxvi) 731326. kcal yr^{-1}	(xxxvii) 130356. kcal unit^{-1} yr^{-1}	(xxxviii) 32193000 kcal unit^{-1} yr^{-1}	(xxxix) 67732500. kcal unit^{-1} yr^{-1}	(xl) 819936 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) 250 kg	(xlv) 399.6 kg unit^{-1}	(xlvi) 2800 kg. unit^{-1}	(xlvii) 87600. kg unit^{-1}	(xlviii) 21024. 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 $1.3\text{x}10^6$ km^2, the approximate area of the EBS, and nearshore populations are divided by 26,000 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 biomass estimates for the years 1980-84 are $8.01\text{x}10^9$ kgs (Witherell, 2000). Assuming pollock are 1 kg on average, this is $8.01\text{x}10^9$ individuals which converts to $8.01\text{x}10^6$ population units. On a km^2 basis: $8.01\text{x}10^6$ units/1,300,000 km^2 = 6.16215 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 km^2 = 0.096154.

(v) Based on 1024 individuals (Appendix D, 2000). Because killer whale habitat includes both ocean and nearshore systems, the population was divided by 1,300,000 + 26,000 to put on a square kilometer basis.

(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 ($4.35615\text{x}10^{-10}$ kg., Petipa et al., 1970, Table 1), in units of $1 \text{ x } 10^{12}$ phytoplankton.

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

(xi) 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 are assumed to be 80% zooplankton.

(xii) 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) = 2663kg/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 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.

(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) 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.

(xvi) 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.

(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, 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 kJ g^{-1})(1Mcal/4.184MJ)(1 MJ/1000kJ)(1000kcal $Mcal^{-1}$)(1000g kg^{-1}) = 1128 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. kcal kg^{-1} 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)-(xxxi) 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%) $N_2 x_{20} e_{02} = N_6 x_{62} e_2$ and solve to obtain e_{02} = 650 kcal kg^{-1} yr^{-1}.

(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 kcal yr^{-1}.

(xxxiv) 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 (xxxiii).

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

(xxxvi) For mammals, resting metabolic rate in kcal d^{-1} (M) is related to body weight (W) by the formula $M = 67.61W^{0.756}$ 5% (Kleiber, 1975). Using 250 kg as sea lion weight and extrapolating to one year yields 1603786 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 (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) Similar to the estimate in (xxxiv) except urchin are assumed to respirate at about 25%.

(xl) Calculated as in (xxxiii) except algae respiration (kelp) is assumed to be 15% of the value of photosynthesis (Petipa et al., 1970, Table 2).

(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) and adult weights in Audubon Field Guide to North American Mammals (1980).

(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).
(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 – Steady-state Populations and Harvests

harvest	N_1^{ss} **phyto.**	N_2^{ss} **kelp**	N_3^{ss} **zoo.**	N_4^{ss} **pollock**	N_5^{ss} **sea lion**	N_6^{ss} **urchin**	N_7^{ss} **otter**	N_8^{ss} **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

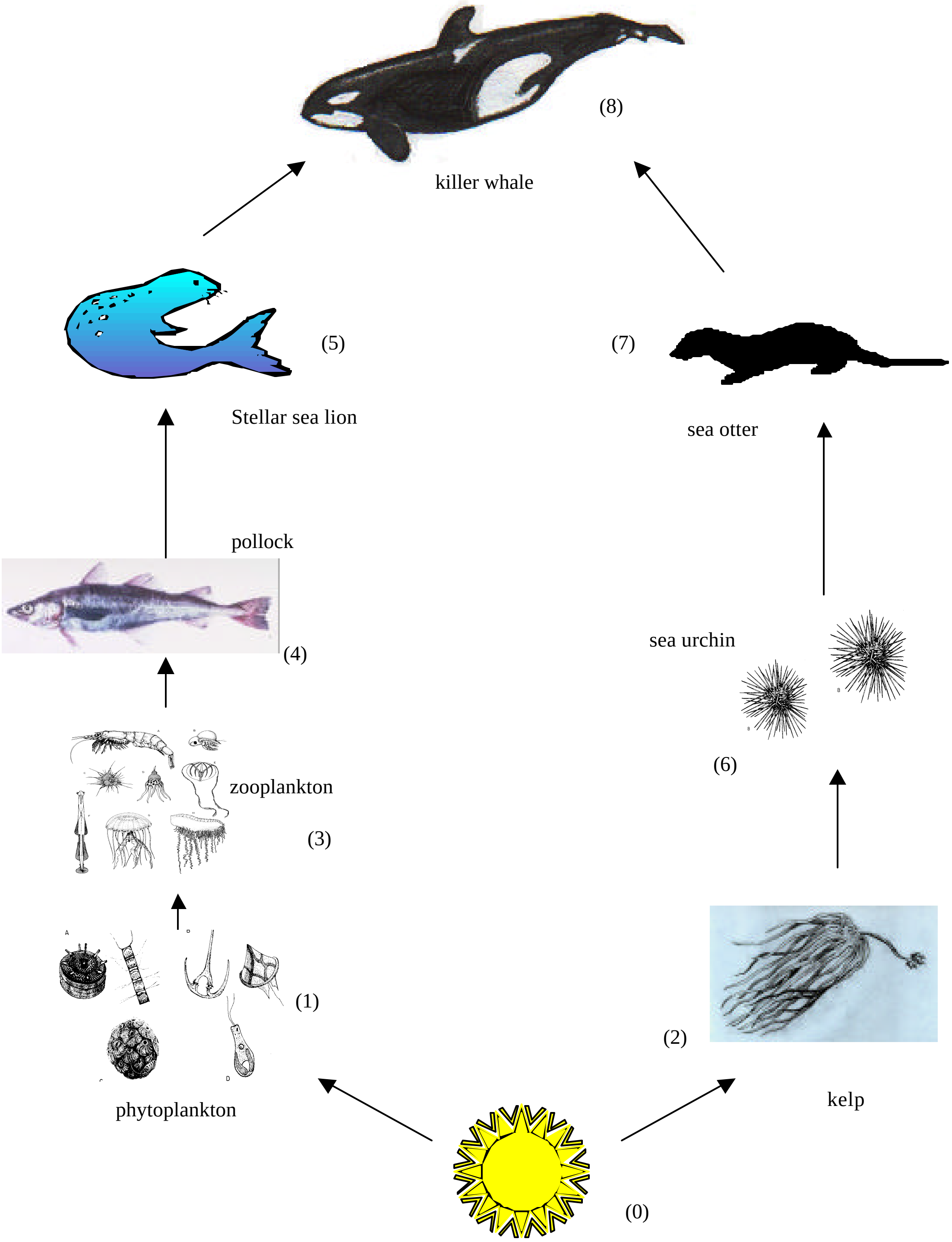
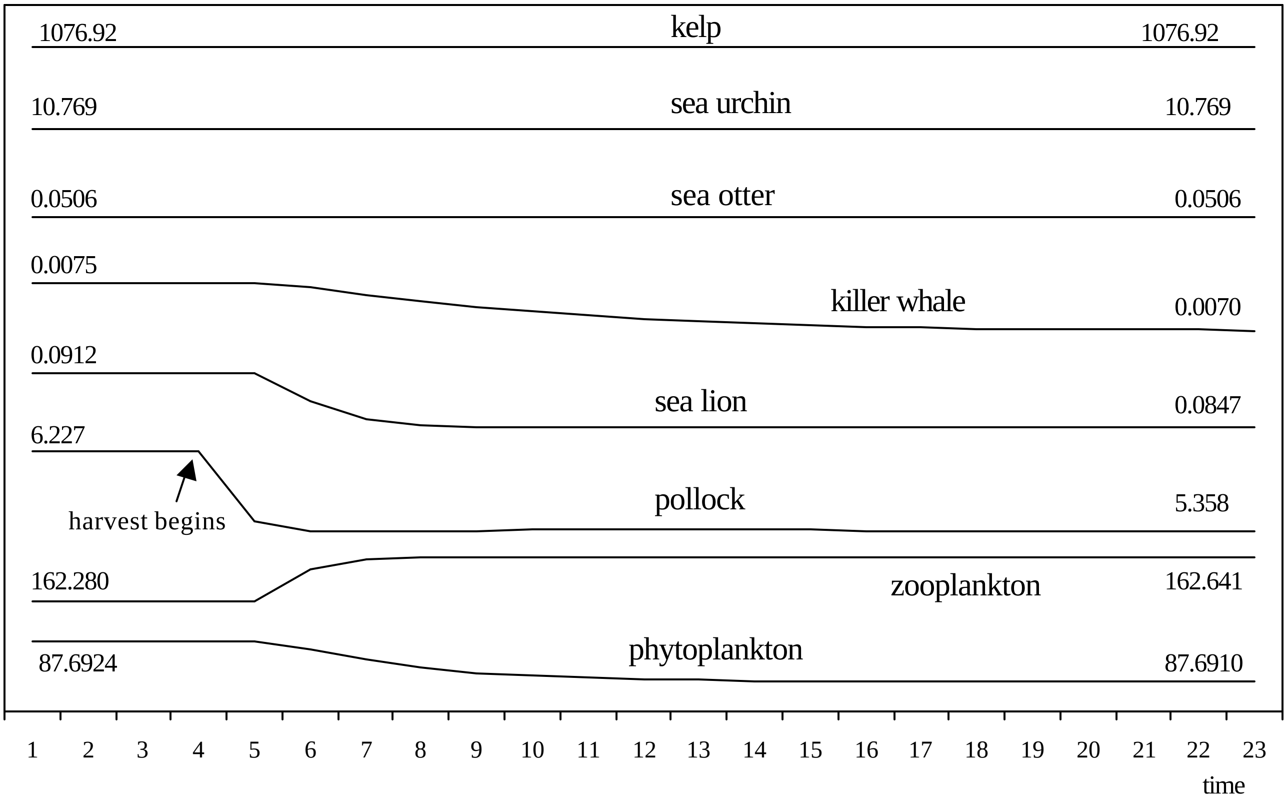


Figure 1 - Food Web
(index #)

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.