

## **TOWARD MERGING ECONOMICS AND ECOLOGY\***

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## **I. Introduction**

All economic activity ultimately depends on the environmental resource base and the ecosystems contained therein, but the extent to which the base is tapped has limits (Arrow, et al., 1995). By some accounts the limits have been reached and a depleted resource base is having negative impacts on living standards.<sup>1</sup> Monitoring depletion and predicting future resource limits requires a better understanding of the interplay between the ecology of natural systems and economic activity (Nordhaus and Kokkelenberg, 1999). The objective here is to develop a method to better capture the interplay. The method is useful for addressing the numerous conflicts that arise when economic development and environmental conservation appear at odds. Familiar examples include logging, harvesting wildlife, preservation of biodiversity (Weitzman, 1993) and endangered species (Shogren and Tschirhart, 2000), bioprospecting (Simpson, Sedjo and Reid, 1996), and, more generally, conserving the essential human services supplied by natural environments (Daily, 1997).

Brander and Taylor (1998) dramatically portray the pressure that economic activity places on ecosystems in a fascinating account of the rise and fall of civilization on Easter Island. The authors explain how human welfare ebbed and flowed with the ebb and flow of the island's renewable resource base. On a larger scale and in modern times, Sohngen and Mendelsohn (1998) examine economic impacts from large-scale ecosystem changes, paying particular attention to dynamic human adaptations to changing ecosystems. And Brander and Taylor (1997) use a general equilibrium model to show the conditions under which exploitation and trade of a renewable resource can be welfare reducing.

In these and in the many other economic papers that study renewable resources, logistic growth functions are employed to capture the resources' biology. Usually, a single growth function is employed to study one species, thereby omitting the other species in the ecosystem. Occasionally, two or three species are studied in a predator-prey relationship, or, as in Brander and Taylor (1998),

humans are the predator. The point is that in all this work entire ecosystems are reduced to one or two species, and a few parameters must summarize the numerous interactions that occur in real ecosystems. Moreover, the logistic growth functions depend on entire species' populations and as such they take a macro view in which species interactions, if present at all, are at an aggregated level. It is a black box approach.

We extend the renewable resource literature by opening the black box. The ecosystem is described by many interacting species in complex food webs and the analysis is at the micro level – individual organism behavior drives ecosystem behavior. Of course, modeling an ecosystem with many species is a challenge because everything depends on everything else (Amir, 1979; Crocker and Tschirhart, 1992). But economists face a similar challenge in modeling an economy in which everything depends on everything else. Economists rise to the challenge by developing general equilibrium models, and this is the tack taken here (Tschirhart, 2000). By exploiting the three themes fundamental to economics - rational behavior, efficiency and equilibrium - that have allowed economics to successfully invade other social science disciplines (Lazear, 2000), a general equilibrium model of an ecosystem is built, thereby allowing economics to invade ecology. The general equilibrium ecosystem model is then tied to a general equilibrium of an economy to examine the ecosystem/economy interplay.

The invasion of ecology by economics supports Becker's (1976) statement: "...economics and sociobiology would gain from combining the analytical techniques of economists with the techniques in the ... biological foundations of sociobiology" (p. 826). Becker demonstrated the power of assuming rational choice by nonhuman organisms to explain altruism within communities. In this paper, the rational choice paradigm is pushed further into ecology than has previously been attempted, resulting in a tight integration of economics and ecology. Combining the techniques Becker refers to permits simultaneous solutions for prices and outputs in the economy and energy

“prices” and populations in the ecosystem, thereby capturing the feedbacks between the systems. Organisms are assumed to maximize their flow of net energy taking energy “prices” as given, and maximization yields organism biomass demands for and biomass supplies to other organisms. In a general equilibrium, demands and supplies are equal at the species’ levels. The methodology is consistent with optimum foraging theory, which, according to Krebs and Houston (1989), began in 1966 (Emlen, 1966; MacArthur and Pianka, 1966). Tullock (1971) was the first economist to contribute to the theory and Rapport (1971) provided a diagrammatic representation employing standard indifference curve analysis. The foraging theory employed herein is most similar to Hannon (1973, 1976), who adopted net energy maximization as the foragers’ objective but did not consider a general equilibrium framework with multiple species.<sup>2</sup>

Competition is central to the model. To achieve a long-run general equilibrium, an economy depends on competition through the entry and exit of firms responding to profits. Analogously, “since Darwin (1859) ecologists have considered interspecific competition ...as the cornerstone of community structure.” (Smith, 1996, p.620) This notion is formalized by aggregating organisms’ net energies to the species level, and then adjusting species populations upward (downward) when the net energies are positive (negative).

Integrating an economic and ecosystem model requires identifying the points of contact between the systems. There are many: humans make consumptive and nonconsumptive use of nonhumans, growing human populations create habitat loss, industries generate toxic wastes, insects pollinate crops and spread disease, and so on. In the extant literature, perhaps nowhere have ecology and economics been integrated more closely than in fishery models. Following the work of Gordon (1954) and Scott (1955), economists have used the biology inherent in logistic growth functions to describe optimal harvesting of fish and other species under a variety of economic conditions including alternative market structures and property right assignments.<sup>3</sup> Because harvesting

represents a familiar and well-examined interaction between an economy and an ecosystem, it provides a good opportunity to illustrate the advantages of an integrated model. The integration shows that traditional harvesting models can lead to suboptimal outcomes, even fishery collapse under bioeconomic constraints, if ecosystem complexities are omitted.

In the next section, a static applied general equilibrium (AGE) model of an economy with a fisheries sector is presented. The ecosystem comprises only the harvested species so that the model is similar to Brander and Taylor (1997) except that it is in an AGE framework and it provides a benchmark for the fully integrated model. Section III presents the dynamic general equilibrium ecosystem model sans humans. Section IV presents dynamic integrated models both under incomplete information harvesting that does not account for changing carrying capacities, and full information harvesting that accounts for the endogeneity of carrying capacities. Welfare comparisons are made in Section V, and Section VI is a conclusion. Simulations are employed throughout Sections II-V.

## **II A Static AGE Model of a Fishery**

Two sectors produce a composite good and fish using capital and labor as two homogeneous primary factors of production. Both factors are perfectly mobile between industries and owned in different proportions by consumer types who are differentiated by their resource endowment. Government is omitted from the model as are savings, investment and discounting.

In simulations, commodity prices, final demands, factor employments, factor rewards, consumer incomes, fish populations and harvests are endogenously determined. Changes in these variables and welfare measures are observed as either the institutional arrangement of the fishery is changed from open access to socially optimal harvesting, or, in later sections, as the entire ecosystem responds to harvesting.

### **II.A General Framework**

The methods employed in the AGE model follow the bioeconomics in Clark (1990) and Hartwick and Olewiler (1998) and the general equilibrium techniques in Shoven and Walley (1984, 1992), de Melo and Tar (1992) and Ginsberg and Keyzer (1997). In this single species model, the dynamics of the fish population follow the discrete version of the well-known Verhulst-Pearl logistic equation of nonstochastic growth. Thus,

$$N_2^{t+1} = N_2^t + r_{s2}N_2^t\left(1 - \frac{N_2^t}{K_2}\right) \quad (1)$$

where  $N_2^t$  is fish population in period  $t$ ,  $K_2$  is carrying capacity and  $r_{s2}$  is the intrinsic growth rate of fish. The subscript 2 referring to fish is needed because other species are added below. (For convenience, all economic and ecosystem variables are defined in Table 1.)

### *The Structure of Production*

Production occurs in both sectors. Profit-maximizing, price-taking firms in both sectors use capital and labor (and harvests of the fish population in the fishery sector) to produce their output in a continuous, nonreversible, and bounded process, subject to a constant returns to scale production function (assuming a zero discount rate).

Fish harvests are given by the Cobb-Douglas function

$$H = dL_f^a K_f^b (N_2^t)^c, \quad (2)$$

where  $K_f$  and  $L_f$  are capital and labor and  $a$ ,  $b$ ,  $c$ , and  $d$  are parameters. The equilibrium harvests ( $H$ ) are dependent on the structure of the fishery. Under an open access equilibrium (OAE), all rents accruing to the unpaid resource (fish) are driven to zero in the long-run through entry and exit of firms. Each firm minimizes costs and applying Shepard's Lemma to cost function yields factor demands. Bioeconomic equilibrium levels of open-access harvests, factor employment ( $K_f$  and  $L_f$ ) and fish population are found when all firms in the industry earn zero profit

$$\mathbf{p}_f = p_f H - r_k K_f - r_l L_f = 0 \quad (3)$$

at output price  $p_f$ , and input prices  $r_k$  and  $r_l$ , and all firms hire capital and labor efficiently (equations (A.1a) and (A.1b) in the Appendix) subject to the bioeconomic constraint

$$r_{s2} N_2^t \left(1 - \frac{N_2^t}{K_2}\right) = H \quad (4)$$

equating total industry harvests to the growth of the fish population.

Under a social optimum equilibrium (SOE), the fishery is portioned such that every firm has well defined and identical property rights over harvesting in a particular region. Firms maximize long-run profits and internalize all stock externalities to find bioeconomic equilibrium levels of harvest, factor employment and fish population. As all firms are identical, the social optimum choices of a sole owner can be used to represent the fishery as a whole. The owner chooses capital, labor *and* the fish population to maximize profit subject to the bioeconomic constraint and harvest functions:

$$\begin{aligned} \max \quad & p_f H - r_k K_f - r_l L_f \\ \text{s.t.} \quad & r_{s2} N_2^t \left(1 - \frac{N_2^t}{K_2}\right) - H \quad \text{and} \quad H = d L_f^a K_f^b (N_2^t)^c \end{aligned} \quad (5)$$

The resulting efficient levels of capital and labor are given by equations (A.1c) and (A.1d) which equate the real costs of labor and capital (left side) to the marginal products of capital and labor, including external effects on the stock. Assuming an interior solution, these equations and the bioeconomic constraint can be solved for social optimum values of capital, labor and population and harvest. In the SOE, the rents accruing to the firms are distributed to the owners of fishery capital through use of markup functions as demonstrated by Ginsberg and Keyzer (1997).

Under the assumptions of constant returns to scale and perfect competition, each firm in the composite goods industry minimizes costs of production subject to a constant-elasticity of substitution (CES) production function

$$Q_c = \mathbf{f}^c \left[ \mathbf{d}_c L_c^{\frac{1}{s_c}} + (1 - \mathbf{d}_c) K_c^{\frac{1}{s_c}} \right]^{\frac{s_c}{s_c-1}} \quad (6)$$

where  $\mathbf{f}^c$  is an efficiency parameter,  $\mathbf{d}_c$  is the distribution parameter for labor inputs, and  $s_c$  is the composite goods production partial elasticity of factor substitution. Cost minimization yields the cost function for the composite good and applying Shepard's Lemma yields factor demands ( $L_c^*$  in equation (A.2a) and  $K_c^*$  in equation (A.2b)).

### *The Structure of Consumption*

Rich and poor consumers are assumed to have identical (within group) homothetic utility functions over composite goods and fish. Rich consumers are endowed with labor ( $\mathbf{w}_L^r$ ) and capital ( $\mathbf{w}_K^r$ ), while poor consumers are endowed only with labor ( $\mathbf{w}_L^p$ ). Each consumer maximizes a CES utility function over consumption of composite goods ( $x_c^r$  for rich consumers and  $x_c^p$  for poor consumers) and fish ( $x_f^r$  for rich consumers and  $x_f^p$  for poor consumers). Maximization is subject to budget constraints where expenditures must be less than or equal to income. Consumer income ( $I^r$  for rich and  $I^p$  for poor) is the sum of the sale of labor, and, for the rich who own capital, fishery rents ( $NR$ ). Consumers of type  $j$ ,  $j = r, p$ , solve the problem:

$$\max U^j = \left[ \mathbf{a}_c^{j(1/s_j)} x_c^j \frac{s_j-1}{s_j} + \mathbf{a}_f^{j(1/s_j)} x_f^j \frac{s_j-1}{s_j} \right]^{\frac{s_j}{s_j-1}} \quad s.t. \quad p_c x_c^j + p_f x_f^j \leq I^j, \quad (7)$$

where the  $\mathbf{a}_c^j$  and  $\mathbf{a}_f^j$  are consumer type  $j$ 's share parameters for composite and fishery goods, and the  $s^j$  are consumer type-specific partial elasticities of substitution between goods. From the maximization, the consumers' demands for the composite good and fish are obtained ((A.3a) and (A.3b)).

## *Market Equilibrium*

In equilibrium there exists a set of prices at which both commodity and factor markets clear as shown in equations (A.4a), (A.4b), (A.5a), and (A.5b). Firms enter and exit their respective markets until profits (net of rents in the fishery sector in the SOE) are zero. Zero profit forces the output prices to equal average costs (and marginal costs due to constant returns to scale) captured by conditions (A.6a) and (A.6b). Consumers' expenditures must equal incomes in equilibrium as given by equations (A.7a) and (A.7b). Finally, prices in the model are normalized as only relative prices are of consequence in an AGE model. Holding the total value of endowments constant at their benchmark value normalizes prices. The relevant equation is (A.8).

### **II.B Simulations**

The simulations were performed using GAMS software in a three-step process: 1) the economy is assumed to be in long-run equilibrium with the fishery in OAE, and, given a fish carrying capacity and consumer resource endowments, a benchmark data set is constructed with bioeconomic optimal levels of the fish population and of fish labor and capital; 2) the benchmark data set is used to calibrate parameters, after which the model necessarily replicates the benchmark data set; 3) using the parameters from (2), a long-run SOE is determined.<sup>4</sup> Parameters are presented in Table 2, except for the intrinsic rate of fish growth in Table 4. Prices, quantities, incomes, rents, fish populations and carrying capacities for the benchmark OAE and long-run SOE are in Table 3.

Comparing the benchmark OAE with SOE, OAE harvests are 20% greater and bioeconomic fish populations 9% lower. The reduced SOE harvests lead to a higher price for fish and consumers substitute into more of the composite good which increases factor employment there. These effects in the composite good sector of moving from OAE to SOE are reinforced by increased rich consumers' incomes due to the flow of rents from the fishery, and by increased poor and rich consumers' incomes due to the higher wage.

Moving from OAE to SOE has an ambiguous impact on welfare. Substituting equilibrium demands for the composite good and fish into the utility functions in (7) reveals that rich consumers' utility increases by 3.5% but poor consumers' utility decreases by 3.4%. The reason is that all rents enjoyed in SOE flow only to the rich as the sole owners of capital. This flow increases rich income by 10% allowing greater composite good consumption that more than offsets fewer fish in SOE. The poor income increases by only 4% and they are better off with the larger harvests in OAE. However, if compensation were possible by redistributing the composite good and fish, both consumer types can be made better off by moving to SOE. The ambiguous welfare result is not generally true, different utility and production function parameters can lead to both rich and poor being better off under SOE. The interesting point is that when consumers are differentiated by capital ownership in a general equilibrium model, then with compensation SOE is Pareto superior to OAE, but without compensation Pareto superiority is not guaranteed.

### **III General Equilibrium of an Ecosystem<sup>5</sup>**

Assume an ecosystem comprises  $m$  species indexed  $1, \dots, m$ , and organisms in higher numbered species may prey on organisms in lower numbered species, but not vice versa. If organisms in species  $i$  prey on organisms in species  $j$ ,  $i > j$ , species  $i$  is said to demand biomass from species  $j$ , and species  $j$  supplies biomass to species  $i$ . All energy in the system originates with the sun which is indexed by 0, and all species can potentially “prey” on the sun. The transfer of biomass takes place in an ecosystem market, and if there are  $m$  species in total, the maximum number of markets is

$$\sum_{i=1}^m i \quad (8)$$

Each organism behaves as if it is a net energy maximizer where net energy is the difference between energy inflows and outflows. A general expression for the net energy of a representative

organism from species  $i$  is given by:

$$R_i = [e_0 - e_{i0}]x_{i0} + \sum_{j=1}^{i-1} [e_j u_{ij} - e_{ij}]x_{ij} - \sum_{k=i+1}^m e_i u_{ik} y_{ik} - f^i \left( \sum_{j=0}^{i-1} x_{ij} \right) - \beta_i \quad (9)$$

The first term on the right side of (9) is the incoming energy (calories) from the sun. The  $e_0$  is the solar energy fixed for each unit of biomass,  $x_{i0}$  (grams), that the organism in species  $i$  produces in photosynthesis, and the  $e_{i0}$  is the energy spent to fix  $e_0$ .

The second term on the right side of (9) is the inflow of energy from organisms of other species. The  $e_j$  is the energy embodied in a unit of biomass from a member of species  $j$ ,  $e_{ij}$  is the energy the member of species  $i$  must spend to locate and capture a unit of biomass of species  $j$ , and  $x_{ij}$  is the biomass transferred from the member of species  $j$  to the member of species  $i$ . Predators are often unsuccessful in locating and capturing prey, and the  $u_{ij} < 1$  reflects this reality by allowing less than the full amount of embodied energy to flow to the predator. More is said about  $u_{ij}$  in the simulations.

The third term is the outflow of energy to members of species that prey on  $i$ . The  $e_i$  is the embodied energy in a unit of biomass from a member of species  $i$ , and  $y_{ij}$  is the biomass supplied by  $i$  to  $k$ . Again, the  $u_{ik}$  term reflects lack of success in predation, although here from the prey's perspective. The fourth and fifth terms in (9) represent respiration which is energy lost by the ecosystem to the atmosphere. Respiration is divided into two parts,  $f^i(\bullet)$  which depends on energy intake and includes feces, reproduction, defending territory, etc. Assuming differentiability,

$$\frac{f^i(\cdot)}{x_{ij}} > 0, \text{ for } i, j = 1, \dots, m, j > i \quad (10)$$

The second part of respiration,  $\beta_i$ , is basal metabolism and it is independent of energy intake.<sup>6</sup>

The embodied energy terms,  $e_i$ , are constants, but the energies spent in predation,  $e_{ij}$ , are the energy prices. As in an AGE model, the prices play a central role in the maximization process,

because an organism's choice of prey will depend on the relative energy prices it pays.<sup>7</sup> Also, organisms are assumed to be price takers because each is only one among many organisms in a predator species capturing only one of many organisms in a prey species. However, within the ecosystem the prices are endogenous, being determined in the biomass markets by demand and supply interactions.

Each organism would prefer to supply zero biomass ( $y_{ij} = 0$ ) to other organisms since outflows reduce net energy. However, an organism can supply zero biomass only if it demands zero biomass in the sense that to capture prey biomass the organism risks being captured by other predator organisms, and the more biomass an organism captures the more it is exposed and the more biomass it supplies to predators.<sup>8</sup> Because organisms are subject to predation risk, the biomass they supply can be written as a function of their demand:

$$y_{ik} = y_{ik} \left( \sum_{j=0}^{i-1} x_{ij} \right), \text{ for } i = 1, \dots, m, \quad (11)$$

This representation is similar to, but in reverse from, a firm whose supply of output determines its demand for inputs. Assuming differentiability of (11):

$$\frac{\partial y_{ik}(\cdot)}{\partial x_{ij}} > 0, \text{ for } i, j, k = 1, \dots, m, j < i < k \quad (12)$$

The representative organism in species  $i$ ,  $i = 1, \dots, m$ , behaves as if it maximizes expression (9) over its demands,  $x_{ij}$ .<sup>9</sup> Basically, an organism sets marginal energy received from predation equal to the marginal energy lost through predation, where the loss is a result of predation risk and respiration activities. For details of the necessary first and second-order conditions for a maximum and interpretations of prey switching based on marginal rates of substitution see Hannon (1976), Crocker and Tschirhart (1992) or Tschirhart (2000).

The first-order conditions can be solved for the  $x_j$  as functions of the energy prices to yield  $i$ 's demands:

$$x_{ij}(\mathbf{e}_i) \propto x_{ij}(e_{i0}, \dots, e_{i,i-1}), \text{ for } j = 0, \dots, i-1 \quad (13)$$

where the boldface  $\mathbf{e}_i = (e_{i0}, \dots, e_{i,i-1})$  is a vector of energy prices. Substituting these demands into the  $y_{ik}$  yields the representative member  $i$ 's supplies:

$$y_{ik}(\mathbf{x}_i(\mathbf{e}_i)) \propto y_{ik}(x_{i0}(e_{i0}, \dots, e_{i,i-1}), \dots, x_{i,i-1}(e_{i0}, \dots, e_{i,i-1})), \text{ for } k = i+1, \dots, m \quad (14)$$

where the boldface  $\mathbf{x}_i = (x_{i0}, \dots, x_{i,i-1})$  is a vector of demands. Comparative statics shows demands to be downward sloping and supplies to be upward sloping:

$$\frac{\partial x_{ij}}{\partial e_{ij}} < 0 \quad \text{and} \quad \frac{\partial y_{ji}}{\partial e_{ij}} > 0 \quad (15)$$

for all  $i = 1, \dots, m$  and  $j < i$ .

### III.A Short-Run and Long-run Equilibrium

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

To find a set of short-run prices that equates each demand with its associated supply, equilibrium equations are needed, one for each price to be determined. The equilibrium condition in a (non solar) market is constructed by equating the sum of all the predator organisms' demands with the sum of all the prey organisms' supplies. All organisms in a species are identical; therefore, to obtain the demand and supply sums multiply the representative organism's demands and supplies by the species' population. If  $N_i$  is the population of species  $i$ , then the equilibrium conditions are:

$$N_i x_{ij}(e_i) = N_j y_{ji}(x_j(e_j)) \quad (16)$$

for  $i = 2, \dots, m$  as  $j = 1, \dots, i-1$ . There is one condition for each market, and the number of markets is given in (1). The left side of (16) is the total demand of species  $i$  for species  $j$ , and the right side is the total supply of species  $j$  to species  $i$ .

The solar markets wherein primary producers (plants) prey on the sun are treated differently, because the sun as prey does not supply energy in response to prices. The sun's supply is assumed to be limitless which is consistent with instances when primary producers only fix a small fraction of the solar energy striking the earth's surface. Moreover, primary producers usually are stationary and the price they pay for solar energy may depend on their species population in its vicinity owing to competition for sunlight. Given these considerations, the solar market prices are determined in accordance with the population of the primary producer; that is,

$$e_{i0} = e_{i0}(N_i). \quad (17)$$

Finding a set of energy prices that yields a short-run equilibrium is a matter of simultaneously solving the first-order conditions from (9) and the equilibrium conditions from (16) for the demands and the energy prices. A system in short-run equilibrium moves toward long-run equilibrium through adjustments in the populations. Population changes will set into motion forces that will move the species toward zero net energy. For instance, suppose a species has positive net energy so that its population increases. This increase lowers the energy price predators must pay to capture species' members, because the species is more plentiful. Predators' demands for the species will increase by (15), the species' supply to predators will increase, and net energy will decrease. In addition, the price the species must pay for its prey will increase as there is more intra-species competition when the species' population grows. This price movement will also reduce the species' net energy as the species demands less prey, a result that follows by applying the envelope theorem

to (9). 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.

To adjust species' populations, consider species  $i$  with maximum net energy given by  $R_i(x_{ij}(e_i); N^t) = R_i(\cdot)$  and obtained by substituting the optimum demands as functions of energy prices into (9).  $N^t$  is a vector of species' populations and it appears in  $R_i(\cdot)$  to indicate that net energies in time period  $t$  depend on all populations in time period  $t$ . There are numerous functional forms that can be used to make the population adjustments; a simple form consistent with the model is  $N^{t+1} = N^t(1 + rR(\cdot))$  implying that population increases (decreases) for positive (negative)  $R(\cdot)$ . However, population adjustments are made using the Verhulst-Pearl logistic equation in (1) in order to make comparisons with extant literature. A major difference from the literature is that here the carrying capacity for species  $i$  is endogenous.

According to (1), the population will increase (decrease) if  $N_i < (>) K_i$ ; thus:

$$R_i(\cdot) > 0 \Rightarrow N_i^t < K_i^t \quad \text{and} \quad R_i(\cdot) < 0 \Rightarrow N_i^t > K_i^t \quad (18)$$

Expression (18) implies that carrying capacity depends on biotic factors including net energies, biomass demands, energy prices and populations. The procedure is to adjust the carrying capacity in period  $t$  to be greater than or less than the period  $t$  population according to (18). Thus,

$$K_i^t = N_i^t \pm z_i(R_i(\cdot))N_i^t \quad (19)$$

where  $z$  is the carrying capacity adjustment as an increasing function of the net energy. In practice,  $z$  will be species dependent and bounded from above. Finally, the new population in period  $t+1$  is obtained using (1) and (19):

$$N_i^{t+1} = N_i^t + r_{si}N_i^t[1 - N_i^t / K_i^t] \quad (20)$$

### III.B Simulating an Ecosystem Containing Fish

A food web illustrated in Figure 1 from a marine ecosystem in Alaska's Aleutian Islands

(See Estes et al., 1998) is used to simulate the model. The primary producers include various species of algae which are aggregated into a single species called kelp. Similarly, all fish species which utilize the kelp forest are aggregated into a single species called fish. Stellar sea lions and harbor seals prey on the fish and are combined into one species called pinnepeds. Sea urchins also prey on the kelp and in turn are preyed upon by sea otters. Killer whales are the top predators and prey on both pinnepeds and otters.

From (9), the net energies of a representative organism of kelp, fish, urchin, pinneped, otter and whale, indexed by 1-6, respectively, are given by (21)-(26), respectively:

$$R_1 = [e_0 - e_{10}]x_{10} - e_1[1 - te_{21}]d_{12}x_{10}^{a_{12}} - e_1[1 - te_{31}]d_{13}x_{10}^{a_{13}} - r_1x_{10}^{g_1} - b_1 \quad (21)$$

$$R_2 = [e_1[1 - te_{21}] - e_{21}]x_{21} - e_2[1 - te_{42}]d_{24}x_{21}^{a_{24}} - r_2x_{21}^{g_2} - b_2 \quad (22)$$

$$R_3 = [e_1[1 - te_{31}] - e_{32}]x_{31} - e_3[1 - te_{53}]d_{35}x_{31}^{a_{35}} - r_3x_{31}^{g_3} - b_3 \quad (23)$$

$$R_4 = [e_2[1 - te_{42}] - e_{42}]x_{42} - e_4[1 - te_{64}]d_{46}x_{42}^{a_{46}} - r_4x_{42}^{g_4} - b_4 \quad (24)$$

$$R_5 = [e_3[1 - te_{53}] - e_{53}]x_{53} - e_5[1 - te_{65}]d_{56}x_{53}^{a_{56}} - r_5x_{53}^{g_5} - b_5 \quad (25)$$

$$R_6 = [e_4[1 - te_{64}] - e_{64}]x_{64} + [e_5[1 - te_{65}] - e_{65}]x_{65} - r_{6p}x_{64}^{g_{6p}} - r_{6o}x_{65}^{g_{6o}} + [x_{64} + x_{65}]^{g_6} - b_6 \quad (26)$$

The terms in (21)- (26) containing  $\delta$  and  $\alpha$  parameters are the supply functions:  $y_{ik} = d_{ik} x_{ij}^{a_{ik}}$  in which the  $i$ th species is supplying biomass to the  $k$ th species, and demanding biomass from the  $j$ th species. The terms containing the  $r$  and  $g$  parameters are the variable portions of respiration in (9). For the whales, variable respiration is divided into three parts which allows for differences in the prices whales must pay in equilibrium for otters and pinnepeds. The terms containing  $t$  represent energy not transferred owing to unsuccessful hunting attempts.<sup>10</sup>

A short-run equilibrium is obtained by solving fourteen equations for the seven demands ( $x_{ij}$ ) and the seven prices ( $e_{ij}$ ). Seven equations are the derivatives of (21) – (26) with respect to the

demands set equal to zero, and seven equations are the equilibrium conditions:

$$N_2 x_{21} = N_1 \mathbf{d}_{12} x_{10}^{a_{12}} \quad (27) \quad N_3 x_{31} = N_1 \mathbf{d}_{13} x_{10}^{a_{13}} \quad (28)$$

$$N_4 x_{42} = N_2 \mathbf{d}_{24} x_{21}^{a_{24}} \quad (29) \quad N_5 x_{53} = N_3 \mathbf{d}_{35} x_{31}^{a_{35}} \quad (30)$$

$$N_6 x_{64} = N_4 \mathbf{d}_{46} x_{42}^{a_{46}} \quad (31) \quad N_6 x_{65} = N_5 \mathbf{d}_{56} x_{53}^{a_{56}} \quad (32)$$

$$e_{10} = pN_1^q \quad (33)$$

Conditions (27)-(32) are from (16) and condition (33) is from (17) with  $p$  and  $q$  as parameters.

To make the population adjustments, consider fish as an example. Let  $R_2(\cdot)$  be the maximum net energy for fish in short-run equilibrium and let

$$z_2 = v_1 - \text{Exp}[v_2[\mathbf{u}R_2(\cdot)\mathbf{u} + v_3]] \quad (34)$$

where parameters  $v_1$ ,  $v_2$  and  $v_3$  are chosen so that the fish carrying capacity adjuster  $z_2 \hat{\mathbf{I}} [0, v_1)$  and if  $R_i = 0$  then  $z_2 = 0$ . By (19), period  $t$  carrying capacity becomes:

$$K_2^t = N_2^t \pm z_2 N_2^t \quad (35)$$

where the plus (minus) obtains if  $R_2(\cdot) > (<) 0$ . Finally, following (20), the new population in period  $t+1$  is determined by:

$$N_2^{t+1} = N_2^t + r_{s,2} N_2^t [1 - N_2^t / K_2^t] \quad (36)$$

Parameter values used in the simulations of this ecosystem are in Table 4. There is insufficient data for the Aleutian ecosystem, or any other ecosystem, to claim the values are representative of real ecosystem functions, but the simulations illustrate the potential of the rational organism, general equilibrium approach.<sup>11</sup>

Table 5 reports populations, demands, prices and net energies for the first five short-run equilibriums. For example, in column four, row two, the initial sea urchin population is 384907, and given all parameter values and initial populations of the other five species, the representative urchin

demands 71.6 kelp biomass units for which it pays an energy price of 87.5 per unit. This yields the urchin 15.2 net energy after respiration. Moving down the column, because its net energy is positive the urchin population increases, and based on the adjustment equations the period two population is 406828. The other species populations adjust as well according to their net energies, and for the urchin the new demand and energy price in period two are 69.1 and 90.7, respectively. Because demand decreased and price increased the new net energy is less in period two at -228.4. The negative implies a decrease in population in period three to 354521.

Consider the predator/prey dynamics of the otter/urchin interaction illustrated in Table 5. Between periods two and three, urchins decrease and otters increase. The decrease in urchins makes preying on them more costly to the otter, and the increase in otters also makes preying on urchins more costly owing to competition among otters. The result is a slight increase in the price of capturing urchins (8.895 to 8.910) and a decrease in otter demand (575 to 516). Between periods three and four, the urchins and otters decrease. Here the affect of population changes work in opposite directions on price, and the net result is that the price of capturing urchins decreases (8.910 to 8.857) causing otter demand to increase (516 to 597). Between periods four and five the populations of urchins and otters both increase. Again these changes have opposite influences on price of capturing urchins, and the net result is the price decreases slightly (8.857 to 8.875) causing demand to increase slightly (597 to 587).

Figure 2 shows the populations for all six species over 122 periods. The populations have been rescaled to fit in the same graph, so only relative values matter. In period 1, the populations are shown starting at the long-run equilibriums.<sup>12</sup> These populations are long-run equilibriums because if they are substituted into the population adjustments expressions (34)-(36), zero net energies are returned and populations would appear as horizontal lines in Figure 2. However, the long-run equilibriums are unstable: in repeated attempts at disturbing only one population by small amounts,

all populations moved into roughly the same stable limit cycles.<sup>13</sup> Consequently, most of this paper concentrates on dynamic adjustments between short-run equilibriums.

For Figure 2, each population was disturbed downward by 25% in period 2 to demonstrate the moves to stable limit cycles, oscillating at levels below the long-run equilibriums. Kelp oscillate from a peak of 49,200,000, to a trough of 48,900,000. Fish (pinneped) peak at 441,000 (43,900) and fall to a trough of 386,000 (39,200). Urchins (otters) peak at 471,000 (43,000) to a trough of 412,000 (38,600), Finally, killer whales peak at 779, diving to a trough of 697. When the kelp population is high it means more energy available to the food web, although most of the increase is accounted for by kelp respiration. The fish and pinneped populations and the urchin and otter populations in Figure 2 conform to familiar predator-prey cycles with the peaks and valleys of the predator species lagging the peaks and valleys of the prey species. The peaks and valleys for the whales and its two prey species are less obvious in the Figure.

#### **IV Integrating the General Equilibrium Models with a Dynamic Ecosystem**

Three scenarios are considered: A) single species with incomplete information harvesting, B) six species with incomplete information harvesting, and C) six species with full information harvesting. Incomplete information is defined as humans knowing the fish population in each period and the fish carrying capacity in some period, but treating the carrying capacity as exogenous and constant over time. Full information is defined as knowing the fish population and endogenous fish carrying capacity in the current and the next period. Knowledge of the carrying capacity beyond the next period is assumed unavailable. Thus, full information does not imply humans maximizing the present value over all future periods, although this would be an interesting extension. (Costello, Polasky and Solow, 2000, show when optimal management requires only a one period forecast.)

Scenario A) is the traditional bioeconomic model with dynamics but in a general equilibrium framework, while B) and C) integrate the general equilibrium ecosystem model and the dynamic

adjustment equations with the economics. Consider first the following four step procedure for C) and full information harvesting.

Step 1: Given the fish population and carrying capacity, compute a general equilibrium for the economy, which includes the bioeconomic fisheries equations, and which yields prices, incomes, factor employment, composite good output and fish harvest.

Step 2: Given the six species populations, including the fish population used in Step 1 and the harvest obtained in Step 1, compute a short-run ecosystem equilibrium that yields biomass demands and supplies, energy prices, and net energies.

Step 3: Using the net energies from Step 2, calculate the six carrying capacity adjustments (the  $z$  in (19)).

Step 4: Using the harvest from Step 1 and the  $z$  adjusters from Step 3, adjust the six species' populations and carrying capacities. The fish population and carrying capacity are used in Step 1 of next period and all six populations are used in Step 2 of next period. Fish population adjustments account for human harvesting by changing (36) to

$$N_2^{t+1} = N_2^t + r_{s2}N_2^t\left(1 - \frac{N_2^t}{K_2^t}\right) - H. \quad (36a)$$

Scenarios A) and B) are presented to illustrate the problems associated with using extant fisheries models that do not use full information. Scenario A) shows the dynamics in a general equilibrium framework, but there is only the fish species so Steps 2 and 3 are omitted, the fish carrying capacity is an exogenous constant, and in Step 4 the only population adjusted is the fish using the harvest from Step 1. The purpose of Scenario B) is to show what can go wrong in Scenario A), especially by not recognizing the endogeneity of the fish carrying capacity. For

Scenario B), the carrying capacities and populations are adjusted in Step 4, but the fish carrying capacity used to calculate harvest in Step 1 is an exogenous constant.

Step 1 requires further explanation. As in Section II, long-run optimum fish harvests, factor inputs and fish populations can be calculated which are consistent with prices and fish carrying capacities. But in the dynamics, *actual* harvests and factor inputs must be based on the *current* period fish population, which is not likely to be the long-run optimum population. In addition, long-run equilibrium values change period to period along with prices. One might try applying the long-run optimum harvest to all periods, but then the harvests and factor inputs would not reflect current prices. Alternatively, one might try harvesting bioeconomically, that is, harvesting all the growth at the current population, but this would not represent an optimum response to current economic and ecosystem conditions. Instead, the approach used is to simultaneously determine in each period both long-run optimum fish harvest, population and factor inputs, *and* current optimum fish harvest and factor inputs based on the current period fish population, while constraining the two harvests to be equal. Actual harvests are not restricted by the bioeconomic constraint. With this method, both long-run equilibrium values, which are targets, and current optimum actual values, depend on current prices. Moreover, next period's fish population and optimum values will depend on the previous periods' economy and ecosystem.

#### **IV.A Simulations of Single Species under Incomplete Information**

The dynamics start with a fish population away from the single-species long-run equilibrium in Table 3. Specifically, the starting point for human harvesting is period 50 in the ecosystem sans humans shown in Figure 2. The endogenous carrying capacities change period to period in Figure 2 attaining peak, trough or intermediate values, and the initial period 50 carrying capacity used in the single species scenario is intermediate.

The general equilibrium framework does not alter the stability properties of the traditional

single-species harvesting model. In open access (OA) or social optimum (SO), all economic prices and quantities and the fish population converge within thirty periods to the OAE or SOE in Table 3. Convergence is ensured by the choice of intrinsic growth rate parameters (Conrad, 1999), and it is smooth for both cases as shown in Figure 3. However, the single species model omits the complexities of the ecosystem, and its use can lead to unexpected and even ruinous results.

#### **IV.B Simulations of Six Species under Incomplete Information**

This section addresses how single species incomplete information harvesting performs in a more complex ecosystem where fish carrying capacity depends on ecosystem dynamics.<sup>14</sup> Traditional harvesting models treat the fish carrying capacity as exogenous, and this is captured by having humans begin harvesting after observing the current period's fish carrying capacity and then assuming this carrying capacity does not change.<sup>15</sup> Because the AGE results are sensitive to the initial carrying capacity, six cases are considered based on either OA or SO and on observing either an intermediate carrying capacity (starting in period 50 of Figure 2), a trough carrying capacity (starting in period 52), or a peak carrying capacity (starting in period 51).

With the intermediate carrying capacity as the start of harvesting, Figures 4 and 5 display the populations for OA and SO, respectively. (Like Figure 2, the populations have been rescaled to fit on the same graph. Similarly, in any below graph that shows no units on the vertical axis, the plotted values have been rescaled for convenience.) OA harvests are too large and the fish population crashes in about 30 periods. (That is, in period 80, 30 periods beyond the initial harvesting period 50 in which carrying capacity was intermediate.) The pinneped population follows the fish into a local extinction; and a falling kelp population, which eventually levels off, means less total energy into the ecosystem so that the otter, urchin and whale populations also decline but eventually level off.<sup>16</sup> The fish collapse begins after a period where there is relatively large natural growth that exceeds the harvest. The price fish must pay for kelp increases while the

price pinnepeds pay for fish decreases. This leads to negative net fish energy and a lower true carrying capacity for fish in the next period. The resulting negative natural growth in the next period, coupled with a harvest based on an incorrectly large, exogenous carrying capacity, is too much for the fish to recover.

Alternatively, under SO the fishery does not collapse; but the populations follow stable limit cycles in Figure 5 that differ significantly from the cycles in the ecosystem sans humans shown in Figure 2. Moreover, after the periods in which the fish populations dip to local minimums, the recovery time for the population varies dramatically owing to harvesting.

In the economy, prices and quantities in the OA track the collapsing fish population: Figure 6 displays the prices and Figure 7 displays the quantities. Falling fish populations lead to declining harvests in spite of ever increasing labor and capital employment in the fishery. As a result, rents for the owners of fish capital also decline. The flow of labor and capital into the fishery is matched by an outflow from the composite good and production in this sector falls. Basically, as the fishery proceeds to collapse, the economy is strapped with increasingly inefficient use of its labor and capital as these factors chase fewer and fewer fish.

Economic prices and quantities in the SO also track the cycles in the ecosystem: Figure 8 displays the prices and Figure 9 displays the quantities. In the fishery, large swings in capital and labor employment are driven by the changing harvests which exacerbates problems with stabilizing the industry. Although the employment shifts in the fishery must be equal and opposite the swings in the composite good sector, the lower bases in the fishery makes the shifts proportionately greater.

The cycles in the fish populations, harvests, prices and fishery factor employment reveal the problem of incomplete information about the carrying capacities. For SO in Figure 9 when fish populations and harvests are small, capital and labor flow into the fishery. The flows occur when the true fish carrying capacity is less than the exogenous carrying capacity used by the fishery

manager, and the actual fish population is below the true carrying capacity. The manager believes the productivity, i.e., the natural growth of the fish population, is greater than it really is and too much capital and labor is misallocated to fishing.

Simultaneously, the misallocation means lower real incomes and a decrease in consumer demand for fish such that, in spite of the lower quantity of fish available, the price of fish goes down slightly in Figure 8. Consequently, both the fish price and fishery rents are not acting as signals of scarcity; they are positively correlated with fish populations and harvests.

The other four cases for OA and SO where the exogenous carrying capacity is taken from a trough period and a peak period are not discussed in detail. Generally, the peak (trough) yields wider (narrower) swings in the cycles of prices, quantities and fish measures compared to the intermediate case but the patterns are similar. Under OA the fishery collapses as it did in the intermediate carrying capacity case, although it does not collapse in the trough case. Under SO the fishery does not collapse for either peak or trough.

#### **IV.C Simulations of Six Species under Full Information**

The ecosystem model is now fully integrated with the economic model. The bioeconomic decisions are based on the endogenous carrying capacity which changes period to period owing to fish interactions with other species. Three full information simulation runs are performed in which humans begin harvesting either in period 50, 51 or 52 corresponding to the three incomplete information harvesting starting points from above. Details are presented for the period 50 start only.

Figure 10 shows the familiar stable limit cycles in species populations, and again, unlike in the ecosystem sans humans in Figure 2, harvesting creates very different patterns in the fish and pinned populations, with the fish experiencing varying recovery times after population nadirs. The interesting point is that even when the fishery manager is aware of the true carrying capacity and harvests accordingly, fish populations still experience periodic sharp drops. The reason follows

form “natural” ecosystem behavior. In Figure 10, when the fish population is on an upward climb the fish enjoy positive optimum net energy. Eventually, the fish population becomes too large for its own good. That is, the energy price fish pay for kelp is high and the energy price pinned pay for fish is low so fish net energy turns sharply negative and the population plummets.

Figure 11 displays the prices and Figure 12 displays the quantities for SO under full information harvesting starting in the intermediate carrying capacity period 50. Fishery factor employment undergoes swings as in incomplete information harvesting; however, the pattern is profoundly different. Under SO in Figure 12 when fish populations and harvests are small, capital and labor flow away from instead of into the fishery. The fishery manager is aware of the true carrying capacity and knows the fishery is relatively unproductive; therefore, capital and labor are not misallocated into the fishery in an inefficient attempt to chase too few fish. Additionally, capital and labor employment is much more uniform than under incomplete information harvesting, with large swings isolated only to the single periods when harvests are small. Unsurprisingly, full information about the carrying capacity helps the fishery manager plan for the downturns.

At the same time, Figure 11 shows prices and rents moving opposite to the directions they moved under incomplete information. When the fish population and harvests are low (high), prices and rents are high (low). More efficient use of capital and labor implies that real incomes and the demand for fish do not decrease as much when harvests are low as they did when the fish carrying capacity was exogenous; instead, the price of fish and rents are acting as signals of scarcity and causing decreases in the quantity of fish demanded.

## **V Welfare**

Welfare across scenarios is measured by rich and poor consumer relative utilities; however, the differences in the utility values cannot be interpreted as meaningful cardinal differences in

consumer well being. Moreover, the differences in utilities across scenarios are small compared to total utilities reflecting the unchanging endowments of labor and capital.

The utilities for the intermediate scenarios are plotted in Figure 13 and for all scenarios their means and standard deviations across periods are listed in Table 6. Consumer utilities go through cycles indicating the link between human welfare and the ecosystem that drives the cycles. The utilities crash in the two cases of the OA ecosystem collapse, and the utilities are not calculated for Table 6. Collapse may be extreme because in reality consumers and producers can be expected to substitute away from the fishery at some point; nevertheless, fisheries that have collapsed certainly have resulted in large welfare losses.<sup>17</sup>

In Figure 13, the rich and poor utilities shift together, although the magnitudes of the shifts are more pronounced for the poor. Consider first the rich and refer to Table 6. All three full information utilities exceed all four incomplete information utilities. Moreover, regardless of which period humans start harvesting, the rich are always better off under full information harvesting. In addition, with one exception, the period-by-period variance in utilities is less under full information. The one surprising result is that when incomplete information harvesting begins in the trough carrying capacity, OA utility exceeds SO utility for the rich. The reason is that the trough carrying capacity usually is less than the true carrying capacity; therefore, the fishery is more productive than the fisheries manager believes and underharvesting is the result. Because SO generally yields less harvesting than OA, the underharvesting is more pronounced under SO.

The poor utilities tell a different story. The greatest utility is enjoyed when incomplete information harvesting begins in a period of peak carrying capacity. The next three largest utilities all occur under full information. Thus, the poor are better off using full information when harvests start in the intermediate or trough period, but worse off starting in the peak period. Under incomplete information in the peak case, the manager believes the carrying capacity is usually

larger than it truly is and harvests are relatively large. In periods when the population of fish and harvests plunge, employment in the fishery and wages increase while rents decrease. The poor enjoy the wage increase but are not directly affected by the low rents since they own no capital. They do worse under full information because the demand for labor and wages in the fishery go down when harvests are small, plus the price of fish spikes upward making fish less affordable. Thus, although total welfare for both rich and poor consumers is always greatest under full information, without compensation in the peak case, the poor are worse off because inefficient factor employment is especially burdensome on workers. Finally, as with the rich, when incomplete information harvesting begins in the trough carrying capacity, OA poor utility exceeds SO poor utility.

## **VI Conclusion**

Although ecosystems provide myriad services to economies, only one service is considered in most renewable resource models. The more complete ecosystem introduced here makes clear that ecosystem interactions influence that one service and in doing so impact human welfare. In fact, the consumer utilities understate the ecosystem contributions to welfare even in the limited ecosystem studied here, because the whale, otter and pinniped species typically provide benefits to consumers in the form of wildlife viewing and existence value. An extension of this work could include these species as public goods in consumer utilities, thereby making cycles in consumer utilities even more dependent on ecosystem cycles.

This last observation is tied to five key points made in this paper:

- 1) Consistent with renewable resource models, in the single-species incomplete information AGE model with an exogenous carrying capacity, long-run equilibriums are stable. But stability is not representative of real ecosystems; populations tend toward stable limit cycles. Adding multiple species and accounting for their interactions in a micro

framework offers a promising approach to track these limit cycles.

2) Measures of economic performance, including human welfare, are linked to ecosystem performance; where species populations experience cycles, economic measures reflect those cycles.

3) Under relatively natural settings, ecosystem management is complicated by the stable limit cycles, and periods of low populations may simply be nature's "plan." However, human intervention in the ecosystems can alter the cycles by changing their amplitudes and recovery times, thereby exacerbating ecosystem management problems.

4) Renewable resource managers need to be aware of the bioeconomics so factor resources are not misallocated. However, the bioeconomics depend on how the resource is impacted by other species, and understanding the impacts requires more data than is typically available. Whether sufficient data to monitor important ecosystems can be obtained at reasonable cost is problematic.

5) Under the assumptions in this model, harvesting under full information always benefits the rich and usually benefits the poor, although both groups benefit if compensation is possible. SO harvesting can make poor consumers worse off than under OA if they do not own capital and collect fishery rents. And relatively small harvests obtained when an incorrectly small carrying capacity is used can yield a SO that generates less welfare than an OA.<sup>18</sup>

The objective of this work is to integrate economic and ecological models so that policies directed to either system, but which inevitably affect the other system, are better informed. Many extensions and improvements can be made to both the economic and ecological aspects of this integrated approach, and many problems in data gathering remain unresolved. Nevertheless, this paper is a step toward integration of disciplines with common structures and goals.

## Mathematical Appendix

### Fishery Sector

$$K_f = \frac{b}{(a+b)r_k} \left[ r_k \left[ \frac{(br_l/ar_k)^a}{d(HN_2^t)^c} \right]^{a+b} + r_l \left[ \frac{(ar_k/br_l)^b}{d(HN_2^t)^c} \right]^{a+b} \right] \quad (\text{A.1a})$$

$$L_f = \frac{a}{(a+b)r_l} \left[ r_k \left[ \frac{(br_l/ar_k)^a}{d(HN_2^t)^c} \right]^{a+b} + r_l \left[ \frac{(ar_k/br_l)^b}{d(HN_2^t)^c} \right]^{a+b} \right] \quad (\text{A.1b})$$

$$\frac{r_l}{p_f} = \left[ \frac{acd^2(L_f)^{2a-1}(K_f)^{2b}(N_2^t)^{2c-1}}{r_{s2} - 2N_2^t/K_2^t - cd(L_f)^a(K_f)^b(N_2^t)^{c-1}} \right] + ad(L_f)^{a-1}(K_f)^b(N_2^t)^c \quad (\text{A.1c})$$

$$\frac{r_k}{p_f} = \left[ \frac{bcd^2(L_f)^{2a}(K_f)^{2b-1}(N_2^t)^{2c-1}}{r_{s2} - 2N_2^t/K_2^t - cd(L_f)^a(K_f)^b(N_2^t)^{c-1}} \right] + bd(L_f)^a(K_f)^{b-1}(N_2^t)^c \quad (\text{A.1d})$$

### Composite Goods Sector

$$L_c^* = \left[ \frac{Q_c}{f^c} \right]^{(1-s_c)} \left[ \frac{Q_c}{f^c} \left[ d_c^{s_c} r_l^{(1-s_c)} + (1-d_c)^{s_c} r_k^{(1-s_c)} \right]^{\frac{s_c}{1-s_c}} \left( \frac{d_c}{r_l} \right)^{s_c} \right] \quad (\text{A.2a})$$

$$K_c^* = \left[ \frac{Q_c}{f^c} \right]^{(1-s_c)} \left[ \frac{Q_c}{f^c} \left[ d_c^{s_c} r_l^{(1-s_c)} + (1-d_c)^{s_c} r_k^{(1-s_c)} \right]^{\frac{s_c}{1-s_c}} \left( \frac{1-d_c}{r_k} \right)^{s_c} \right] \quad (\text{A.2b})$$

### Consumption

$$x_c^{j*} = \frac{I^j a_c^j}{p_c^{s_j} (a_c^j p_c^{(1-s_c)} + a_f^j p_f^{(1-s_j)})} \quad (\text{A.3a})$$

$$x_f^{j*} = \frac{I^j a_f^j}{p_f^{s_j} (a_c^j p_c^{(1-s_c)} + a_f^j p_f^{(1-s_j)})} \quad (\text{A.3b})$$

### Commodity Markets

$$H = x_f^r + x_f^p \quad (\text{A.4a})$$

$$Q_c = x_c^r + x_c^p \quad (\text{A.4b})$$

### Factor Markets

$$\mathbf{w}_L^r + \mathbf{w}_L^p = L_f + L_c \quad (\text{A.5a})$$

$$\mathbf{w}_K^r = K_f + K_c \quad (\text{A.5b})$$

### Unit Costs

$$p_f = \left[ \frac{r_k K_f + r_l L_f + NR}{H} \right] \quad (\text{A.6a})$$

$$p_c = \left[ \frac{r_k K_c + r_l L_c}{Q_c} \right] \quad (\text{A.6b})$$

### Incomes

$$I^r = r_l \mathbf{w}_L^r + r_k \mathbf{w}_K^r + NR \quad (\text{A.7a})$$

$$I^p = r_l \mathbf{w}_L^p \quad (\text{A.7b})$$

### Price Normalization

$$r_l (\mathbf{w}_L^r + \mathbf{w}_L^p) + r_k \mathbf{w}_K^r = r_l^o (\mathbf{w}_L^r + \mathbf{w}_L^p) + r_k^o \mathbf{w}_K^r \quad (\text{A.8})$$

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**Table 1. Definition of Endogenous Variables**

<b>Variable</b>	<b>Definition</b>	<b>Variable</b>	<b>Definition</b>
$\mathbf{p}_c$	Price of composite commodity	$\mathbf{x}_{10}$	Kelp demand for solar energy
$\mathbf{p}_f$	Price of fishery commodity	$\mathbf{x}_{21}$	Fish demand for kelp
$\mathbf{r}_l$	Wage rate	$\mathbf{x}_{31}$	Urchin demand for kelp
$\mathbf{r}_k$	Rental rate of capital	$\mathbf{x}_{42}$	Pinneped demand for fish
$\mathbf{L}_c$	Labor in composite goods production	$\mathbf{x}_{53}$	Otter demand for urchins
$\mathbf{K}_c$	Capital in composite goods production	$\mathbf{x}_{64}$	Whale demand for pinnepeds
$\mathbf{L}_f$	Labor employed in fishery	$\mathbf{x}_{65}$	Whale demand for otters
$\mathbf{K}_f$	Capital employed in fishery	$\mathbf{e}_{10}$	Kelp energy price for solar energy
$\mathbf{Q}_c$	Composite production	$\mathbf{e}_{21}$	Fish energy price for kelp
$\mathbf{H}$	Harvests (whether OAE or SOE)	$\mathbf{e}_{31}$	Urchin energy price for kelp
$\mathbf{x}_f^r$	Rich demand for fishery commodity	$\mathbf{e}_{42}$	Pinneped energy price for fish
$\mathbf{x}_c^r$	Rich demand for composite commodity	$\mathbf{e}_{53}$	Otter energy price for urchins
$\mathbf{x}_f^p$	Poor demand for fishery commodity	$\mathbf{e}_{64}$	Whale energy price for pinnepeds
$\mathbf{x}_c^p$	Poor demand for composite commodity	$\mathbf{e}_{65}$	Whale energy price for otters
$\mathbf{I}^r$	Rich income	$\mathbf{R}_1$	Fish net energy
$\mathbf{I}^p$	Poor income	$\mathbf{R}_2$	Kelp net energy
$\mathbf{NR}$	Rents attributable to fish population	$\mathbf{R}_3$	Urchin net energy
$\mathbf{N}_1^t$	Period t kelp population	$\mathbf{R}_4$	Pinneped net energy
$\mathbf{N}_2^t$	Period t fish population	$\mathbf{R}_5$	Otter net energy
$\mathbf{N}_3^t$	Period t urchin population	$\mathbf{R}_6$	Whale net energy
$\mathbf{N}_4^t$	Period t pinneped population	$\mathbf{K}_1^t$	Period t kelp carrying capacity
$\mathbf{N}_5^t$	Period t otter population	$\mathbf{K}_2^t$	Period t fish carrying capacity
$\mathbf{N}_6^t$	Period t whale population	$\mathbf{K}_3^t$	Period t urchin carrying capacity
		$\mathbf{K}_4^t$	Period t pinneped carrying capacity
		$\mathbf{K}_5^t$	Period t otter carrying capacity
		$\mathbf{K}_6^t$	Period t whale carrying capacity

**Table 2. Economy Parameters**

<b>Parameter</b>	
$S_c$	.9
$S_r$	.9
$S_p$	.9
<b>a</b>	.2
<b>b</b>	.4
<b>c</b>	.4
<b>d</b>	.54
$w_L^r$	59455.69
$w_K^r$	65020.94
$w_L^p$	25554.78
$p_f^o$	1
$p_c^o$	1
$r_l^o$	1
$r_k^o$	1
$a_c^r$	0.803
$a_f^r$	0.197
$a_c^p$	0.783
$a_f^p$	0.217
$d_c$	.638
$f_c$	1.931

**Table 3. Benchmark And Equilibriums**

<b>Variable</b>	<b>OAE Benchmark</b>	<b>SOE</b>
$p_c$	1	1.004
$p_f$	1	1.337
$r_l$	1	1.036
$r_k$	1	.953
$Q_c$	120000	129104
$H$	30031	24950
$L_c$	75000	78449
$K_c$	45000	50751
$L_f$	10010	6562
$K_f$	20021	14269
$x^r_f$	24477	20547
$x^r_c$	100000	108598
$x^p_f$	5555	4403
$x^p_c$	20000	20507
$I$	124477	136510
$P$	25555	26476
$NR$	0	12955
$N_2$	364119	396973
$K_2$	502179	502179

**Table 4. Ecosystem Parameters**

<b>Parameter</b>		<b>Parameter</b>	
<b>e<sub>0</sub></b>	500	<b>g<sub>1</sub></b>	2
<b>e<sub>1</sub></b>	200	<b>g<sub>2</sub></b>	2
<b>e<sub>2</sub></b>	10	<b>g<sub>3</sub></b>	2
<b>e<sub>3</sub></b>	10	<b>g<sub>4</sub></b>	2
<b>e<sub>4</sub></b>	1	<b>g<sub>5</sub></b>	2
<b>e<sub>5</sub></b>	0.8	<b>g<sub>6p</sub></b>	2
<b>p<sub>e</sub></b>	0.25	<b>g<sub>6o</sub></b>	2
<b>q</b>	0.25	<b>g<sub>6</sub></b>	0.5
<b>t</b>	0.0005	<b>b<sub>1</sub></b>	130
<b>d<sub>12</sub></b>	0.5	<b>b<sub>2</sub></b>	2100
<b>d<sub>13</sub></b>	0.6	<b>b<sub>3</sub></b>	3319
<b>d<sub>24</sub></b>	8	<b>b<sub>4</sub></b>	355
<b>d<sub>35</sub></b>	6	<b>b<sub>5</sub></b>	264
<b>d<sub>46</sub></b>	4	<b>b<sub>6</sub></b>	765
<b>d<sub>56</sub></b>	1.5	<b>b<sub>1</sub></b>	0.3
<b>a<sub>12</sub></b>	0.5	<b>b<sub>2</sub></b>	0.3
<b>a<sub>13</sub></b>	0.5	<b>b<sub>3</sub></b>	0.3
<b>a<sub>24</sub></b>	0.5	<b>b<sub>4</sub></b>	0.3
<b>a<sub>35</sub></b>	0.5	<b>b<sub>5</sub></b>	0.3
<b>a<sub>46</sub></b>	0.5	<b>b<sub>6</sub></b>	0.3
<b>a<sub>56</sub></b>	0.5	<b>r<sub>s1</sub></b>	0.4
<b>r<sub>1</sub></b>	150	<b>r<sub>s2</sub></b>	0.3
<b>r<sub>2</sub></b>	0.6	<b>r<sub>s3</sub></b>	0.3
<b>r<sub>3</sub></b>	0.7	<b>r<sub>s4</sub></b>	0.25
<b>r<sub>4</sub></b>	0.001	<b>r<sub>s5</sub></b>	0.25
<b>r<sub>5</sub></b>	0.0009	<b>r<sub>s6</sub></b>	0.25
<b>r<sub>6p</sub></b>	0.00002	<b>v<sub>1</sub></b>	0.3
<b>r<sub>6o</sub></b>	0.00002	<b>v<sub>2</sub></b>	- 0.1
		<b>v<sub>3</sub></b>	12.03973

**Table 5. Ecosystem Results**

<b>period 1</b>	<b>kelp</b>	<b>fish</b>	<b>urchins</b>	<b>pinnepeds</b>	<b>otters</b>	<b>whales</b>	
						<b>pinnepeds</b>	<b>otters</b>
<b>Populations</b>	40377750	360952	384907	36130	35110	642	
<b>Demands (xij)</b>	1.293	63.611	71.6	637	557	5688.179	1936.806
<b>Prices (eij)</b>	19.928	107.884	87.5	8.603	8.928	.778	.728
<b>Net Energies</b>	1.896	10.183	15.189	.851	.598	.792	

<b>period 2</b>	<b>kelp</b>	<b>fish</b>	<b>urchins</b>	<b>pinnepeds</b>	<b>otters</b>	<b>whales</b>	
						<b>pinnepeds</b>	<b>otters</b>
<b>Populations</b>	41173554	378367	406828	36346	35260	645	
<b>Demands (xij)</b>	1.294	61.882	69.1	655	575	5768.802	1966.668
<b>Prices (eij)</b>	20.026	109.708	90.7	8.569	8.895	.774	.727
<b>Net Energies</b>	2.089	-115.694	-228.387	23.028	19.498	21.913	

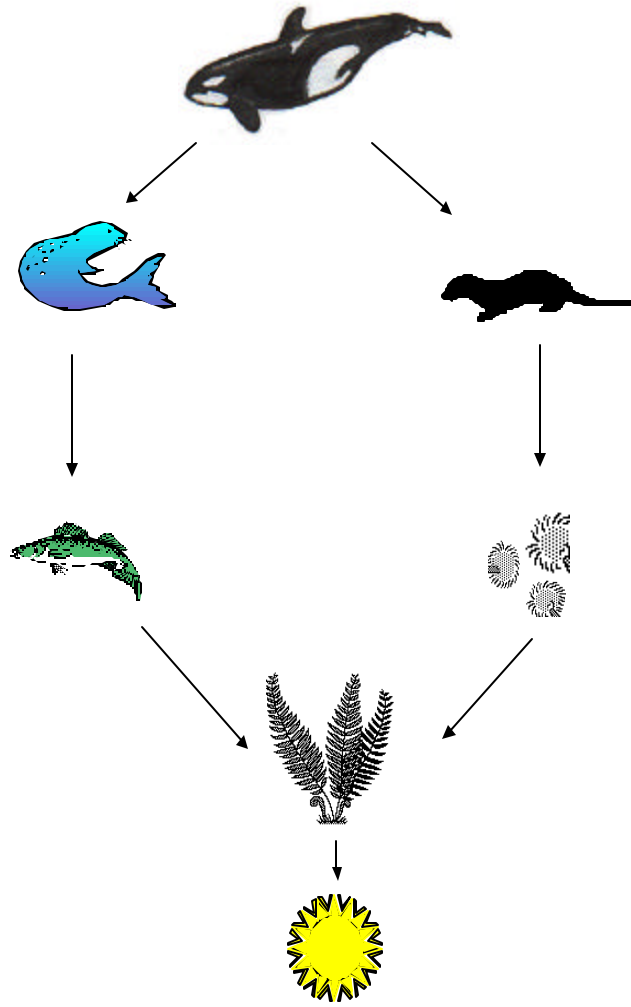
<b>period 3</b>	<b>kelp</b>	<b>fish</b>	<b>urchins</b>	<b>pinnepeds</b>	<b>otters</b>	<b>whales</b>	
						<b>pinnepeds</b>	<b>otters</b>
<b>Populations</b>	42055157	329720	354521	38278	37064	679	
<b>Demands (xij)</b>	1.291	72.453	80.9	587	516	5461.448	1860.128
<b>Prices (eij)</b>	20.132	98.524	75.9	8.701	8.910	.787	.731
<b>Net Energies</b>	.309	710.712	989.509	-59.355	-37.925	-56.467	

<b>period 4</b>	<b>kelp</b>	<b>fish</b>	<b>urchins</b>	<b>pinnepeds</b>	<b>otters</b>	<b>whales</b>	
						<b>pinnepeds</b>	<b>otters</b>
<b>Populations</b>	42207180	352547	379065	34192	33220	607	
<b>Demands (xij)</b>	1.292	68.032	75.9	680	597	5881.012	2006.403
<b>Prices (eij)</b>	20.150	103.211	82.1	8.520	8.857	.770	.725
<b>Net Energies</b>	.973	348.492	456.221	55.744	41.670	51.645	

<b>period 5</b>	<b>kelp</b>	<b>fish</b>	<b>urchins</b>	<b>pinnepeds</b>	<b>otters</b>	<b>whales</b>	
						<b>pinnepeds</b>	<b>otters</b>
<b>Populations</b>	42664124	376955	405308	36159	35113	641	
<b>Demands (xij)</b>	1.292	64.332	71.8	669	587	5831.844	1989.137
<b>Prices (eij)</b>	20.205	107.124	87.2	8.542	8.875	.772	.726
<b>Net Energies</b>	1.478	63.685	36.357	40.752	31.416	38.559	

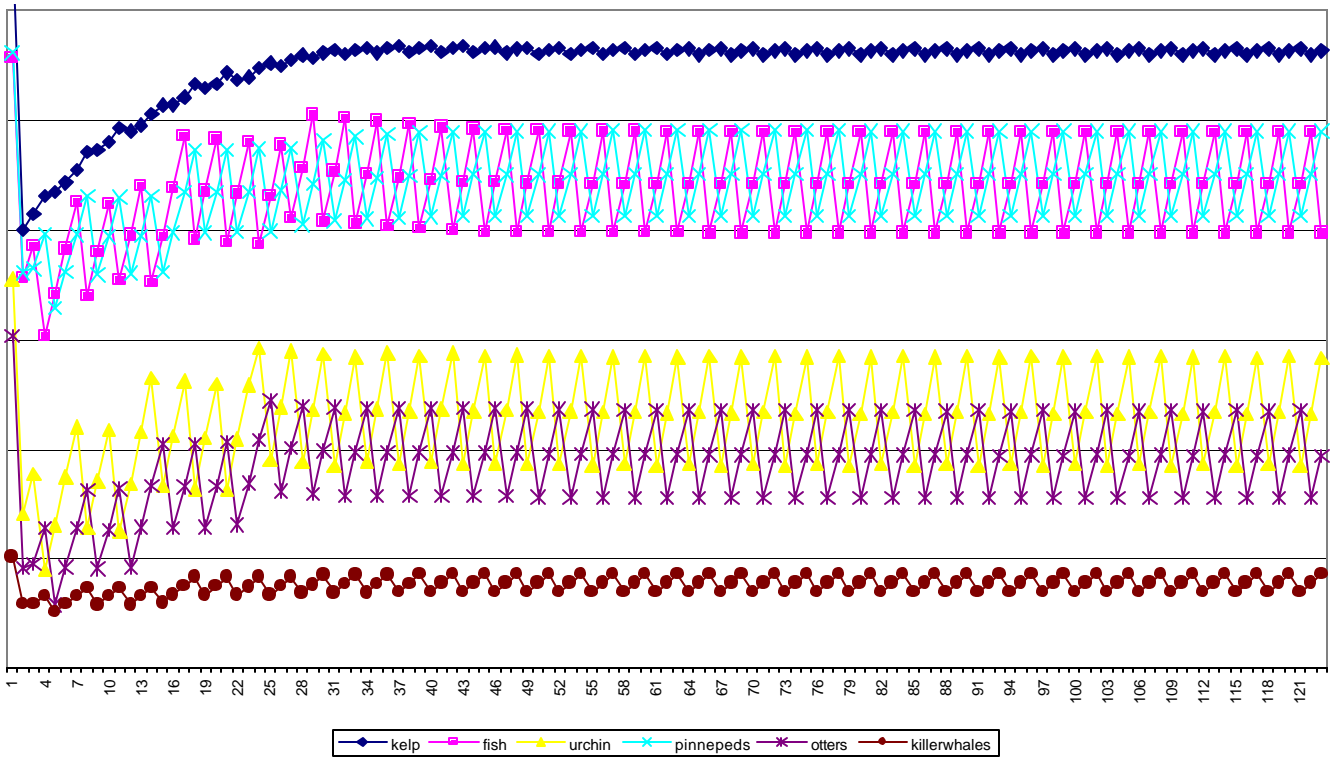
**Table 6. Mean Consumer Utilities**

<b>Initial Harvest Period</b>	<b>Harvesting Method</b>	<b>Access</b>	<b>Variable</b>	<b>U<sup>r</sup></b>	<b>U<sup>p</sup></b>	<b>Total Utility</b>
<i>Intermediate K<sub>2</sub></i>	<i>Full information</i>	<i>SO</i>	Mean	128867	24788	153655
			Std. Dev.	547	217	659
	<i>Incomplete information</i>	<i>SO</i>	Mean	128622	24692	153314
			Std. Dev.	648	45	693
<i>Trough K<sub>2</sub></i>	<i>Full information</i>	<i>SO</i>	Mean	128846	24781	153627
			Std. Dev.	572	220	688
	<i>Incomplete information</i>	<i>OA</i>	Mean	128758	24466	153244
			Std. Dev.	614	26	640
<i>Peak K<sub>2</sub></i>	<i>Full information</i>	<i>SO</i>	Mean	128769	24764	153534
			Std. Dev.	540	224	659
	<i>Incomplete information</i>	<i>SO</i>	Mean	128675	24827	153502
			Std. Dev.	684	48	731



**Figure 1. Food Web**

Figure 2. Populations sans Humans



**Figure 3. Single Species Incomplete Information**

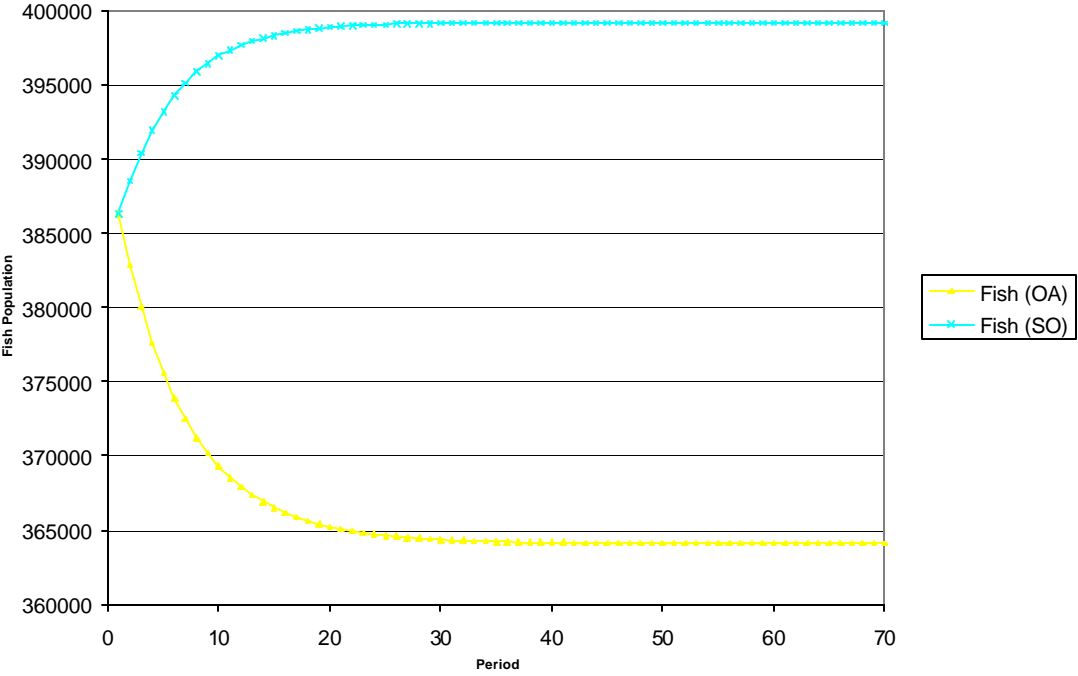
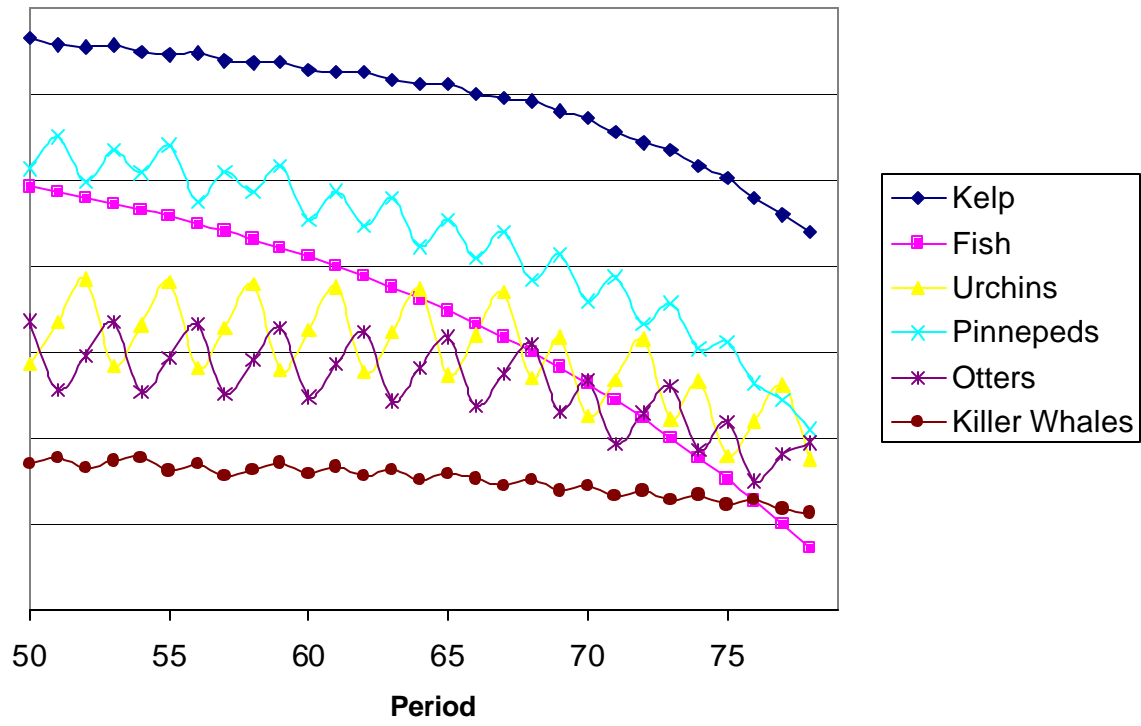


Figure 4. OA Populations under Incomplete Information



**Figure 5. SO Populations under Incomplete Information**

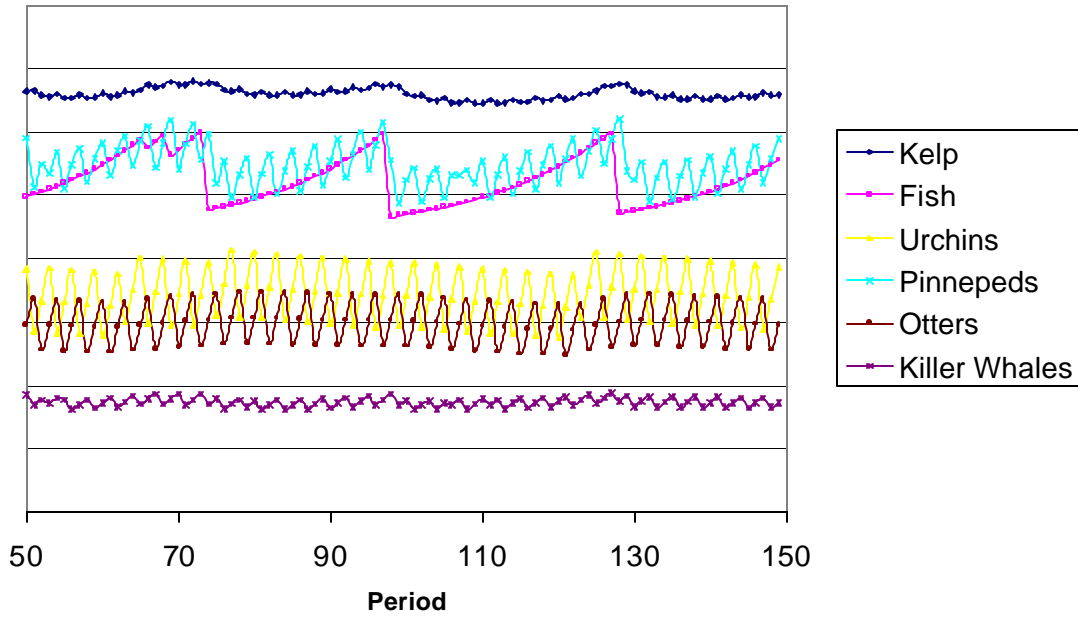


Figure 6. OA Prices under Incomplete Information

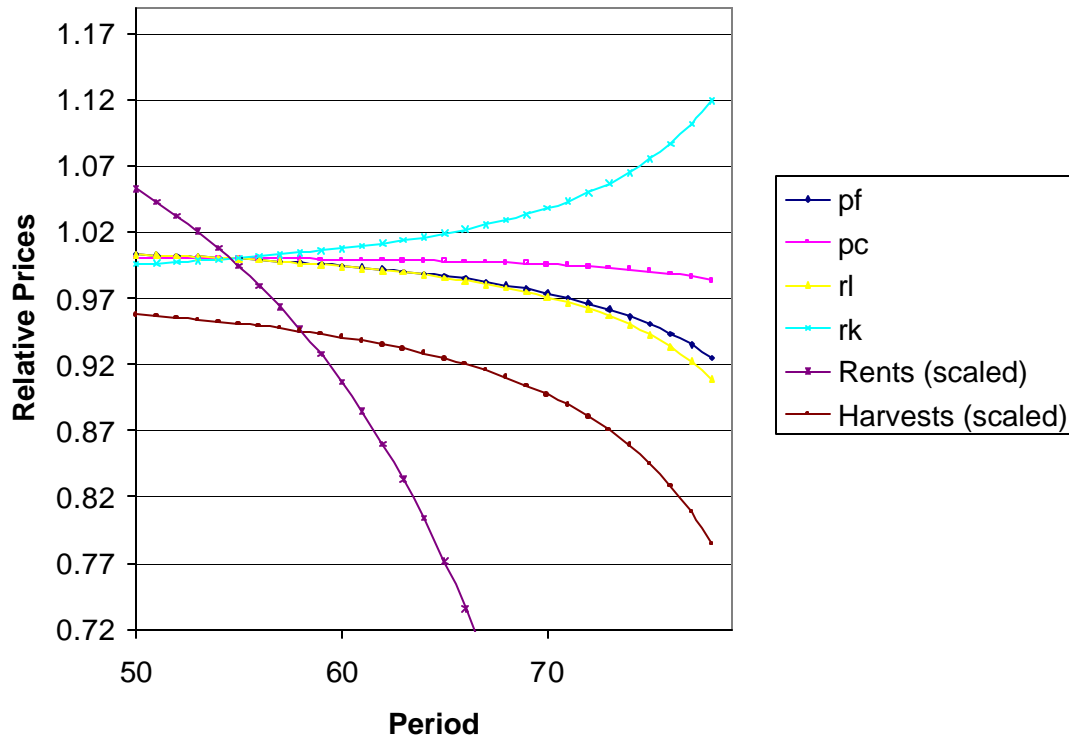


Figure 7. OA Factors and Outputs under Incomplete Information

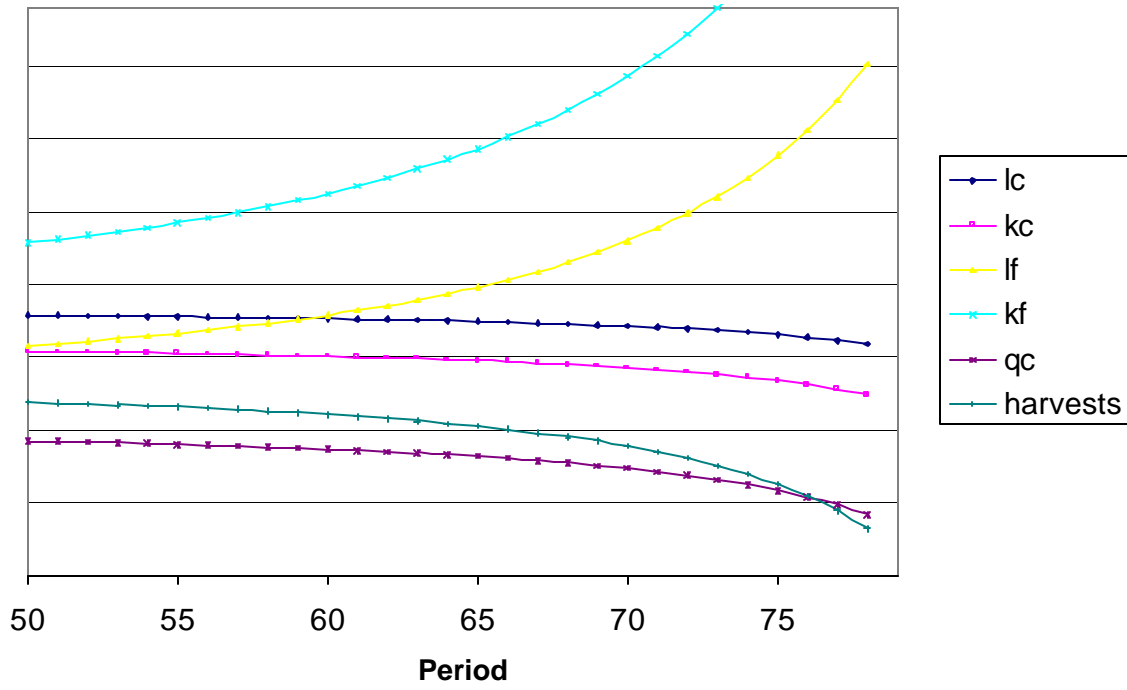
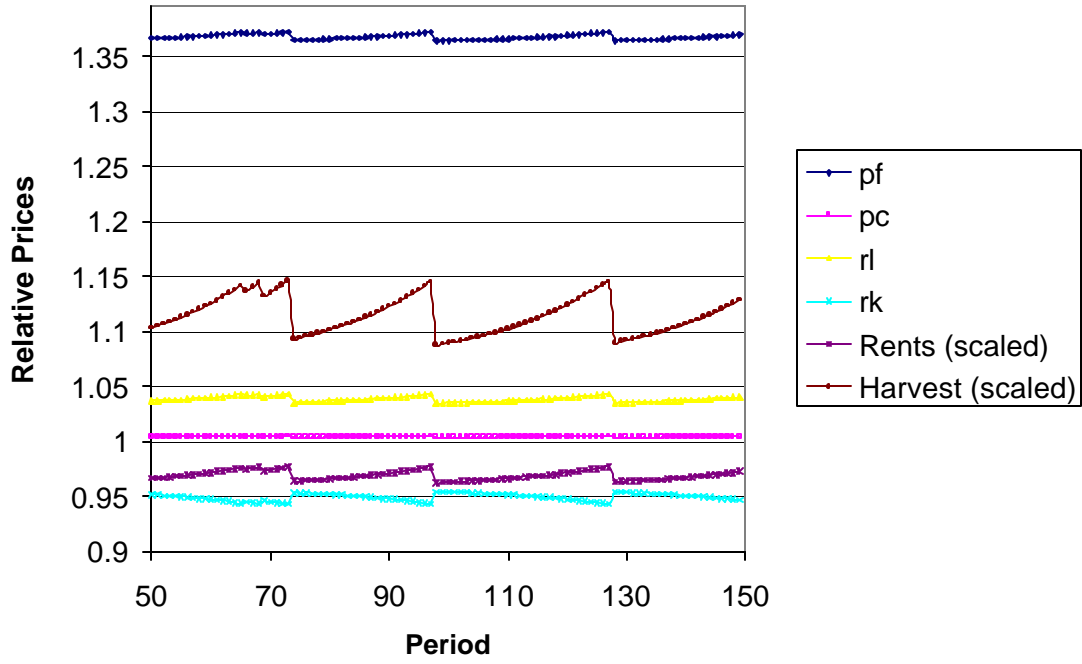


Figure 8. SO Prices under Incomplete Information



**Figure 9. SO Factors, Outputs, and Fish under Incomplete Information**

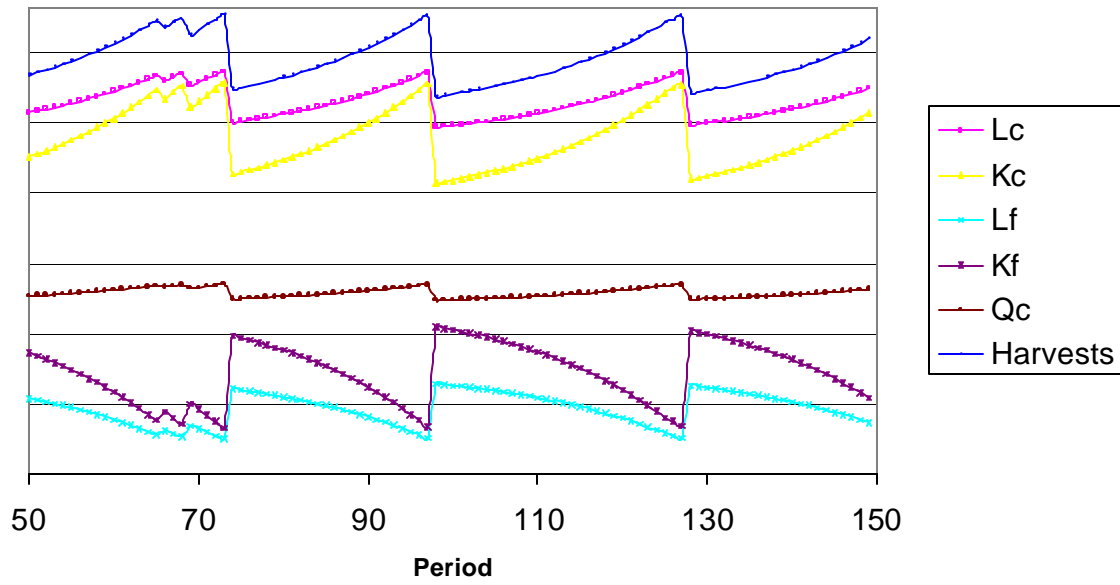


Figure 10. Populations under Full Information Harvests

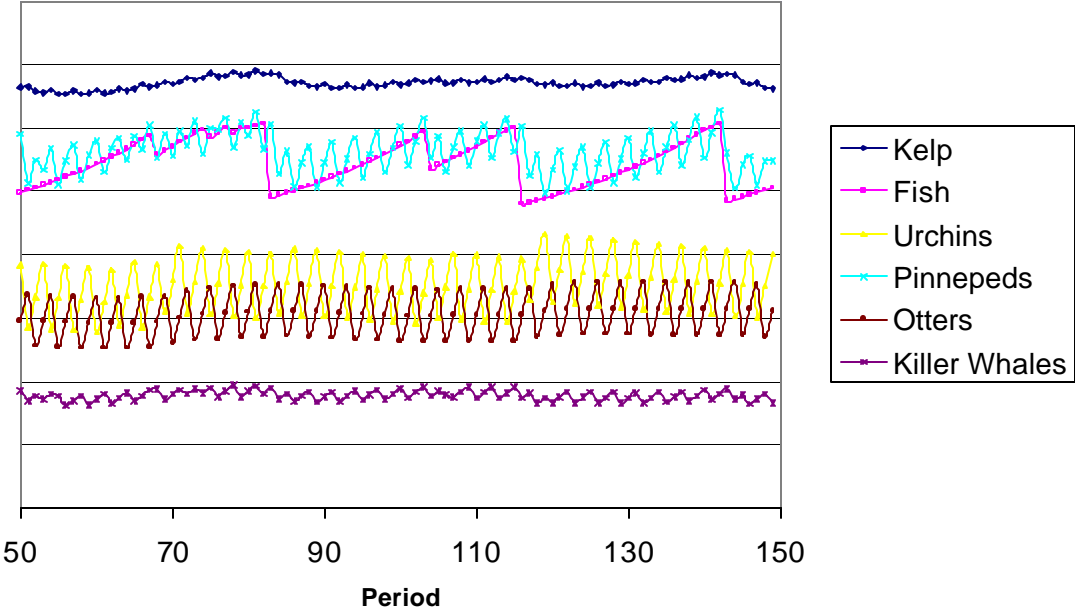
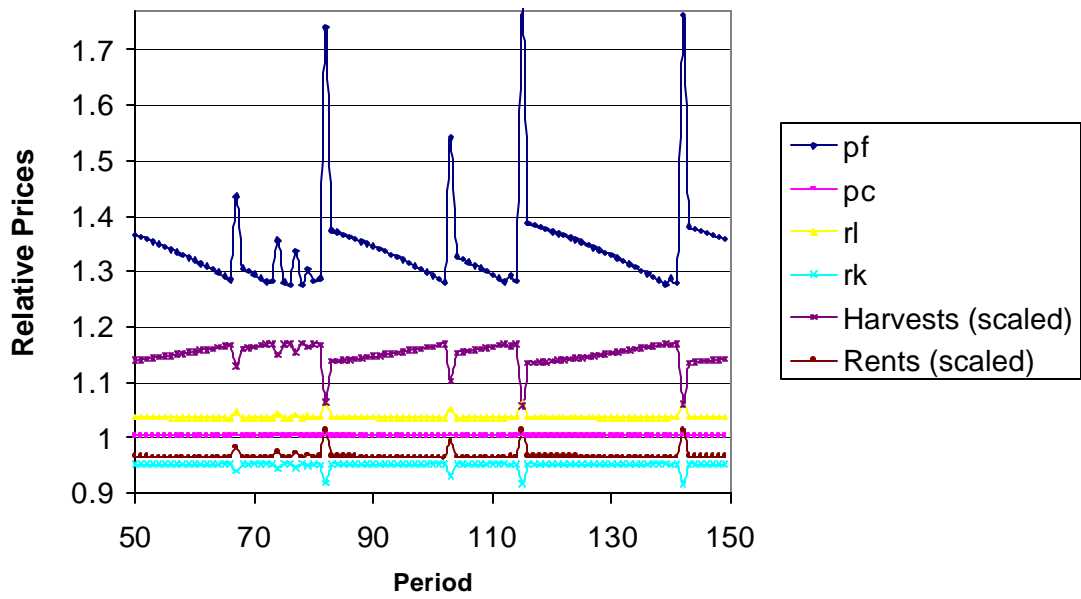


Figure 11. Prices under Full Information Harvests



**Figure 12. Factors and Outputs under Full Information Harvests**

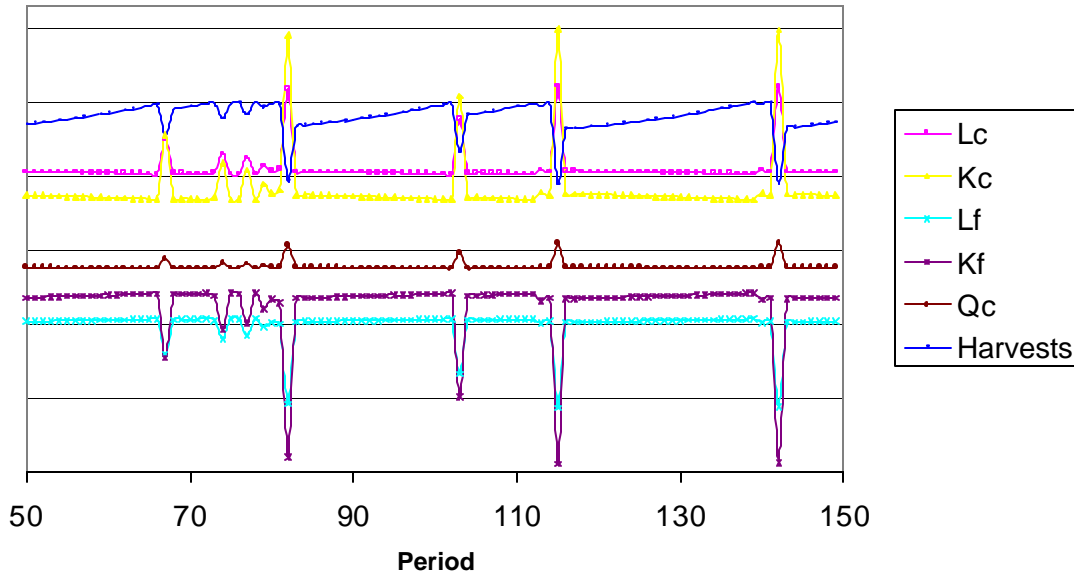
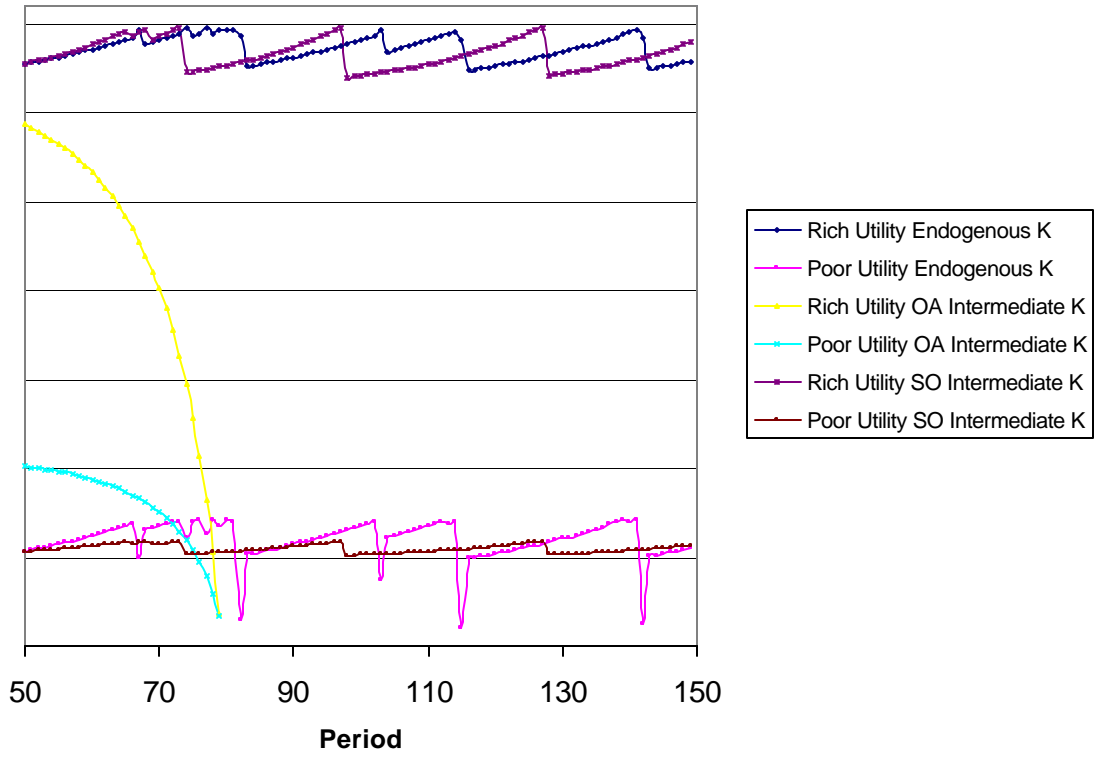


Figure 13. Consumer Utilities



## Endnotes

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<sup>1</sup> See Norgaard (1994) or the Worldwatch Institute annual report *State of the World* published from 1984-2000)

<sup>2</sup> Although optimum foraging theory began in 1966, observing the parallels between economics and biology dates back centuries. Alfred Marshall borrowed from Darwin who borrowed from Malthus to develop their arguments, and Huxley and Wells "...defined ecology as biological economics or an extension of economics to the whole world of life." (Rapport and Turner, 1977)

<sup>3</sup> See Munro and Scott (1985) and Conrad (1995) for synopses.

<sup>4</sup> Model calibration is the process through which several parameters in the model are determined so that the model replicates the benchmark data set. The calibration routine sets benchmark input and output prices ( $r^o_l, r^o_k, p^o_f, p^o_c$ ) equal to unity (by constant returns to scale and the units of the initial data being in value terms). Using all first-order conditions from profit maximization, cost minimization, and utility maximization, and the benchmark data and prices, values of  $\phi^c, \delta_c, \alpha^r_f, \alpha^r_c, \alpha^p_f, \alpha^p_c$ , and found as presented in Table 2. Values for the substitution elasticities were chosen indiscriminately, and the Cobb-Douglas harvest function parameters a, b, and c were chosen to represent the obvious importance of fish population and capital to the level of harvest. The value d was chosen to provide reasonable harvest levels as in Homans and Wilen (1997).

<sup>5</sup> More detail on the model presented here can be found in Tschirhart (2000).

<sup>6</sup> Not all organisms' maximization problems will contain all the terms in (9). For examples, plants typically will prey only on the sun so the second term on the right side of (9) would vanish, and top predators typically do not prey on the sun, and the first term in (9) would vanish.

<sup>7</sup> 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 AGE model through the equilibrium conditions involving many species, and not in the organisms' individual maximization problems.

<sup>8</sup> This tradeoff between foraging gains and losses is called predation risk (See Lima and Dik, 1990).

<sup>9</sup> A problem of interpretation arises in the maximization problem, because once a member of species i is successfully preyed upon, it is gone. No further maximization takes place for this member. To avoid this discrete, zero/one problem, the maximization problem is assumed to represent the 'average' member of species i. Thus, when the organism is captured it does not lose its entire biomass, but rather it loses biomass equal to the mean loss over all members of its species.

<sup>10</sup> Suppose predator j makes n attempts at locating and capturing prey k, and s attempts are successful and u are not,  $s+u = n$ . The energy to the predator is  $[se_k - ne_{jk}] = [ne_k - ue_k - ne_{jk}]$  and from the prey is  $[se_k + ne_{esc}] = [ne_k - ue_k + ne_{esc}]$  where  $e_{esc}$  is energy spent escaping capture which is ignored

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in this paper so that  $e_{esc}=0$ . Success in locating and capturing prey is assumed to be a function of how much energy is spent on these activities; for example, a lynx that spends little energy locating and/or capturing a hare is enjoying successful hunts. The function is assumed to take the simple form  $u(e_{jk}) = nte_{jk}$  where  $t$  is chosen to ensure  $u < n$ . Substituting  $nte_{jk}$  for  $u$  above, the energy to the predator becomes  $[ne_k - nte_{jk}e_k - ne_{jk}]$  and from the prey becomes  $[ne_k - nte_{jk}e_k]$ . Dividing both terms by  $n$  to put the energy on a per unit of biomass basis yields the net price terms in (21)-(26).

<sup>11</sup> Bounds on parameters can be set: 1) from observations about the relationships between population densities and predation, 2) based on necessary and sufficient conditions for a maximum to the net energy problem, and 3) using estimates of ecological efficiencies. (See Tschirhart, 2000.)

<sup>12</sup> A long-run equilibrium is calculated by solving the fourteen equations used in the short run in addition to setting the six net energy expressions, (21) – (26), equal to zero and solving for the populations. Results are  $N_1= 53,837,000$ ,  $N_2= 481,270$ ,  $N_3= 513,210$ ,  $N_4= 48,173$ ,  $N_5= 46,813$  and  $N_6= 855$ .

<sup>13</sup> May (1973) discusses stable limit cycles that are common in ecological systems.

<sup>14</sup> Computing simultaneous long-run equilibriums for both the ecosystem and economy is possible for the six species cases; however, because they are unstable and very likely never achieved, they are not discussed or presented.

<sup>15</sup> Some authors note that carrying capacities are not fixed and make them stochastic to reflect “epidemic disease, oil spills, water temperature, and the presence of predators.” (Hartwick and Olewiler, 1998) In our model the species interactions account for some of this stochasticity.

<sup>16</sup> Kelp follows the decline of the fish population in spite of the fact that there are fewer fish to prey on kelp. As the fish are over harvested, each fish faces less intraspecies competition for kelp so the energy price the fish pays decreases while its biomass demand increases. Both changes lead to more energy reaching each fish. At the same time, each kelp’s demand for solar energy remains relatively constant, while the energy it loses to the fewer, but more voracious, fish increases. Thus, because each kelp is losing more energy to fish, it’s net energy is decreasing and stays negative; negative net energy means less reproductive success and a smaller carrying capacity so that the kelp population falls. Removing a predator from a food web as fish are removed here can affect the ecosystem in unexpected and complex ways. In a survey of field studies regarding the affects of predator removal, Sih, et al. (1985) detected certain trends one of which is that removal of a predator usually increases the predator’s primary prey, although other prey may decrease. This is at odds with the decreased kelp population herein, although if the kelp were disaggregated to include a variety of marine plants, some populations would increase while others decrease in the model.

<sup>17</sup> The collapse of the North Atlantic cod fishery left 30,000 Canadians unemployed according to *Time* magazine (Spring 2000, Special Edition, “How to Save the Earth.”)

<sup>18</sup> Although this last point is a modeling possibility, it may not be germane in practice given the degraded state of fisheries around the world.