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Efficient ecosystem services and naturalness in an ecological/economic model

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Abstract In an integrated economic/ecological model, the economy benefits from ecosystem services that include: (1) the consumptive use of a harvested species, (2) the non-consumptive use of popular species, and (3) naturalness, i.e., the divergence of the ecosystem's biodiversity from its natural steady state. The biological component of the model, which is applied to a nine-species Alaskan marine ecosystem, relies on individual optimizing behaviour by plants and animals to establish population dynamics. The biological component is used to define naturalness. By varying harvesting we arrive at different steady-state populations and humans choose from among these steady states. Welfare maximizing levels of the ecosystem services are derived, then it is shown that in the *laissez-faire* economy overharvesting occurs when the harvesting industry ignores ecosystem services (2) and (3). Lastly, we introduce efficiency restoring taxes and standards that internalize the ecosystem externalities.

Keywords Ecosystem services · Biodiversity · Naturalness · Harvesting

JEL classifications Q22 · Q28 · Q57 · Q58

1 Introduction

Biological resources provide inputs into both production processes and consumers' well being. These inputs are referred to as ecosystem services, and ultimately all economic activity depends on them. Unfortunately, economic activity is stressing the biological resources and jeopardizing the ecosystem services to the point where

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production processes and consumers' well being are being negatively impacted (Arrow et al. 1995; Norgaard 1994). To reverse this trend will require research that takes account of the interactions between the economic and biological systems (Daly 1968; Crocker and Tschirhart 1992; Barbier et al. 1994).

We develop an economic/biological model that captures some of the tradeoffs between maintaining natural ecosystems and consuming ecosystem services. For the biological component of the model, we employ a recently developed general equilibrium ecosystem model (GEEM) that is applied to a nine species ecosystem from which flow specific ecosystem services. GEEM is unique among ecological models in that it uses individual optimizing behavior of plants and animals to establish population dynamics of many species. The ecological component is integrated with a simple general equilibrium economic model in which the ecosystem services are choice variables. The services depend on the species' populations, and GEEM is used to obtain steady-state species populations for varying levels of economic activity. The humans select their activity by choosing from among the steady states.

The ecosystem services that flow from the species to the economy include: (1) direct consumptive use of a harvested species; (2) direct non-consumptive use of popular observable species; and (3) indirect use that stems from the existence of collections of species in their natural state. Service (3) requires that we be able to measure how the ecosystem diverges from its natural state, a state in which there is no anthropogenic intervention. Because biodiversity is a determinant of ecosystem processes from which ecosystem services flow, we assume that the divergence from natural biodiversity is a good proxy for the third service. Accordingly, we introduce a new measure of how the ecosystem's biodiversity diverges from its natural state, and importantly, the measure is dependent on the economic activity to which biodiversity contributes. By applying GEEM to an Alaskan marine ecosystem containing a harvested fish species, popular marine mammals, and five other lower profile species, we obtain values for the biodiversity divergence measure using real ecosystem data.[1]

The integrated model is used to analytically solve for an efficient (welfare-maximizing) allocation of a composite good and the ecosystem services. The efficient allocation is then compared to the allocation that is attained in a competitive economy. Because firms in the competitive economy do not take into account the impact that their activity has on the non-consumptive use of species or on the naturalness of the ecosystem, corrective taxes or standards are needed to internalize the ecosystem externalities.[2] A numerical example is used to calculate an efficient tax that reduces harvesting while restoring some of the ecosystem's naturalness.

There is a growing economics literature on valuing biodiversity. Weitzman (1992, 1998), Solow et al. (1993) and Polasky and Solow (1995) have measured biodiversity by genetic distances across species in order to determine which species are most important to preserve. Brock and Xepapadeas (2003) consider two agricultural species that may be damaged by two pest species. They find that welfare increases with greater biodiversity (two agricultural species instead of one),

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[1] See Jin et al. (2003) for an economy linked to a marine ecosystem with fish species, zooplankton and phytoplankton. The authors investigate the linkages between the systems, using an input–output model.

[2] An ecosystem externality occurs when economic activity causes an ecosystem to shift to an alternative state with different biodiversity, and the shifted ecosystem feeds back to impact economic activity (Crocker and Tschirhart 1992).

because a more diverse system is less susceptible to the pests. Li et al. (2001) consider optimal harvesting when either the numbers of species does or does not affect welfare. When welfare is increasing in numbers of species, optimal harvesting is smaller because harvesting lowers the number of species. Settle and Shogren (2002) constructed an integrated bioeconomic model to examine how invasive Lake trout affect native cutthroat trout in Yellowstone Lake, USA. Their optimal control/STELLA model simulated the integrated ecological–economic model of Yellowstone Lake to show how the integration of the biological and economic (fishermen and tourists) systems lead to different population results than treating the two systems as separate.

In another paper by Brock and Xepapadeas (2002), the authors address management of a joint economic/ecological system. It is perhaps the closest to our work, because it employs a specific ecological framework, in particular, Tilman's (1982) ecological resource-competition models that use parametric representations of species to show which species will survive given limited nutrient resources. Brock and Xepapadeas include two ecosystem services, a harvested species, our service (1), and a catchall service that is similar to our service (2). They investigate, which species will survive in a natural ecosystem versus two managed ecosystems, one under private management and the other under social management. They also investigate incentives that move a privately managed system closer to a natural one.

Our focus is not on which species will survive under different management practices, nor on which species are most desirable to preserve.[3] The desirability of preserving biodiversity here is that preservation means maintaining a natural state, and this enhances the flow of ecosystem services. Like Brock and Xepapadeas we employ a specific ecological framework, although our focus is more applied, at least on the ecological side. We employ optimizing plant and animal individuals in multiple species from which we can examine how human decisions lead to macro-ecological outcomes (i.e., species population changes) by influencing micro-ecological behavior (i.e., individual optimization). By using real ecosystem data, we hope to sustain the process of integrating ecology and economics for improvements in renewable-resource policy.

GEEM shares similarities and differences with other models in the ecological literature. It combines two dissimilar ecological modeling approaches: optimum foraging models and dynamic population models. The former approach has been likened to consumer theory (Stephens and Krebs 1986) and describes how individual predators search for, attack and handle prey to maximize net energy intake per unit time. Optimum foraging models do not account for multiple species in complex food webs and do not track species population changes. Dynamic population models track population changes by using a difference or differential equation for each species. The familiar logistic-growth model used extensively in the economics literature is the simplest example, although extensions include resource competition models (e.g., Gurney and Nisbet 1998) and the Lotka-Volterra predator/prey model and its variations. However, the parameters in the dynamic equations represent species-level aggregate behavior: optimization by individual plants or animals or by the species is absent, Alternatively, GEEM employs optimization at the individual level as in foraging models, and uses the results of the optimization to develop difference

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[3] Although our harvested fish species can become extinct if over harvested, this does not jeopardize the fish's predator species because the predator will switch to a different fish species in the food web.

equations that track population changes. There is a suite of interesting models (ECOPATH and its derivatives, Polovina 1984; Ulanowicz 1986; Christensen and Pauly 1992) that account for whole ecosystems and include many species and the flows of energy and biomass between them. A rough analogy is that ECOPATH is to GEEM as an economic input–output model is to a computable general equilibrium model.

In the next section the economic problem is laid out and the ecosystem services, including the measure of naturalness, are introduced. Section 3 contains the description of the GEEM and the Alaskan marine ecosystem. An efficient allocation is derived in Sect. 4 and the competitive economy with its market failures are in Sect. 5. Section 6 is a conclusion and an appendix follows.

2 The economic problem

The representative consumer's preferences are given by the twice-differentiable, quasi-concave utility function:

$$u = U\left(\underset{+}{h}, \underset{+}{x}, \underset{+}{n_i}, \underset{+}{n_j}, \underset{+,-}{s}\right), \tag{1}$$

where h is harvesting, x is the consumption of an aggregate composite good, n_i and n_j are the population densities of the ith and jth species in the ecosystem, and s measures the state of the ecosystem defined below, Signs below each argument indicate the signs of the partials of U. The aggregate consumption good x is produced with labor l_x according to the twice differentiable, quasi-concave production function

$$x = X\left(\underset{+}{l_x}\right). \tag{2}$$

The economy is linked to an ecosystem from which consumers derive utility in the form of three ecosystem services. The first ecosystem service is the consumer's direct consumptive use of a harvested species that is used as food. Harvesting is carried out according to the twice-differentiable, quasi-concave harvesting function

$$h = H\left(\underset{+}{l_h}, \underset{+}{n_k}\right), \tag{3}$$

where l_h is labor and n_k is the population density of the kth species in the ecosystem. The signs indicate positive marginal products for labor and density.

The second ecosystem service is the consumer's direct non-consumptive use of high profile species. Examples of such non-consumptive use include viewing wolves in Yellowstone Park, whale watching from boats or ashore, and birding. Numerous contingent valuation studies have demonstrated that consumers are willing to pay to preserve a wide range of species including Gray wolves, Sea otter, Whooping cranes and other equally or less high profile species (See Loomis and White 1996 or Coursey 2001 for summaries.) The population densities of the ith and jth species in

(1) are assumed to be good proxies for non-consumptive use, because the greater are the population densities the greater is the consumer's chance of encountering individuals of species i or j.

The third ecosystem service measures the state of the ecosystem that is defined here as how natural, or how free of anthropogenic intervention, is the ecosystem.[4] That naturalness enters the utility function is based on the notion that consumers place value on two ecosystem attributes: (1) the community of species that stands apart from how consumers value species individually; and (2) the extant to which the ecosystem is not altered by humans. Valuing communities "is the appreciation for the variation or richness we observe in the ecosystems; it is based on the contemplation of the ecosystem as an ensemble of life forms..." (Goulder and Kennedy 1997, p. 34). Valuing naturalness is inherent in society's willingness to set aside wilderness areas. "Preserving wilderness areas has an existence value to many individuals who may never use the area for recreation but who prefer that significant land areas are left as wilderness." (Forsyth 2000, p. 414) This preference for naturalness is exemplified by the Council Directive 92/43EEC on the conservation of natural habitats and of wild fauna and flora (Habitat Directive) of the European Union, and by the 1964 Wilderness Act of the United States that defines wilderness as "...an area of undeveloped Federal land retaining its primeval character and influence, without permanent improvements or human habitation, which is protected and managed so as to preserve its natural conditions..."

The problem is how to measure naturalness in a concise and practical manner. Beyond their inherent appeal to consumers, natural ecosystems also contribute essential services to human production processes that include pest and flood control, water filtration, soil fertilization, pollination and decomposition of organic matter (Daily 1997). Biodiversity is a determinant of ecosystem processes from which flow this panoply of services (Tilman 1999), and it is a measure of the ensemble of life forms on which consumers place value; therefore, biodiversity is a candidate for use as the measure of the third ecosystem service.[5] But there are many measures of biodiversity in the ecological literature to choose from.[6] Most of the ecological measures are based on species populations, and they range from species richness that is simply the number of species present, to the popular Shannon index that is based on species abundance and their populations. Communities that have a small variance in the numbers of individuals in each species have higher Shannon index values than communities that have a large variance because the Shannon index heavily weights species evenness.

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[4] The sign of the partial derivative of the utility function (1) with respect to the state of the ecosystem may be positive or negative because there may be natural states that are undesirable such as wetlands with disease vectors, or unnatural states that are desirable, such as non-native wildflower meadows. But for simplicity, in this paper we assume that naturalness is associated with the richest set of ecosystem services and leave other possibilities to future research.

[5] Ecologists are not in agreement on the relationship between biodiversity and ecosystem function from which ecosystem services flow (Mooney et al. 1995; Armsworth et al. 2004). The consensus is that ecosystem function is a strictly concave increasing function over low levels of biodiversity and may or may not level off at higher levels. Moreover, there may be a critical level of biodiversity below which ecosystem function is severely impaired (Grime 1997; Cervigni 2001).

[6] See Magurran (2004) for a synopsis of measures, most of which use numbers of species and their populations.

For our purposes, a drawback of the biodiversity measures is that they do not address naturalness, or its converse, the degree of anthropogenic intervention. In reality, natural populations have large variances in the numbers of individuals across species; species lower down the food web tend to have greater numbers of individuals, calling into question the importance of evenness. Moreover, if natural biodiversity is associated with resiliency of ecosystems and relatively stable populations, then the natural state potentially may provide the greatest flow of ecosystem services: for examples, rapid water filtration or stable populations of edible species. But the very act of establishing an economy and drawing upon these services necessarily diminishes naturalness. A useful measure of naturalness, therefore, should account for the tradeoffs between using ecosystem services provided by natural ecosystems and the degree to which naturalness is lost in the process. Using familiar measures such as the Shannon index can be misleading if anthropogenic intervention results in diminished naturalness and ecosystem services, without a concomitant change in biodiversity. For example, suppose in North America that anthropogenic intervention causes Eurasian house mice to displace native voles, or invasive European starlings to displace Eastern meadowlarks. Naturalness is clearly diminished, yet based on numbers of species and their populations, the index may show little change in biodiversity.

To remedy this drawback in extant biodiversity indices as measures of naturalness, a new measure is introduced and labeled the divergence from natural biodiversity (DNB). Consumers' preferences for biodiversity and naturalness are assumed to depend on DNB defined as:

$$s = S\left(\underline{h}\right) = -\sum_{i=1}^{N} \left(\frac{n_i(h) - \bar{n}_i}{\bar{n}_i} \right)^2 \tag{4}$$

In (4), h denotes the degree of anthropogenic intervention, N is the total number of species, $n_i(h)$ is the population of species i as a function of anthropogenic intervention, and $\bar{n}_i$ is a reference population level. In the following, we focus on the special case $\bar{n}_i = n_i(0)$ where $n_i(0)$ is the natural, steady-state population of species i.[7] If there is no anthropogenic intervention, then $h = 0$ and $s = 0$.[8] As anthropogenic intervention increases, populations can be expected to diverge further from their natural levels and s decreases owing to the negative sign in (4). As s approaches 0 from below, consumers are assumed to be better off, other things equal, as shown by the positive partial on s in (1). Of course, knowing what configuration of populations

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[7] In its present form (4) is only applicable to ecosystems with unique steady states. However, (4) can be generalized to multiple steady states and to stable limit cycles. In case of multiple steady states denote by n_i^k the stationary population of species i in steady state k, define $s^k = -\sum_{i=1}^{N} \left(\frac{n_i(h) - n_i^k}{n_i^k} \right)^2$ where s^k measures the deviation to the steady state k and $s = \min\,[s^l, \ldots, s^k]$ enters the utility function (1). In case of stable limit cycles divide the cycle into k points. Then, n_i^k is the population level of the limit cycle point, s_i^k is the deviation to that point and $s = \min[s^l, \ldots, s^k]$ again is the consumers' preference for naturalness.

[8] Anthropogenic intervention, h, is a scalar here and in the empirics it represents harvesting a species. However, h could be treated as a vector and additional anthropogenic interventions could include impacts on the ecosystem through pollution, habitat loss, introduction of invasive species, global climate change, and so on. These interventions could be included in the ecosystem model of Sect. 3.

is feasible and how populations diverge with changes in h are central for using DNB, and this is taken up in the next section.

DNB has several useful properties not shared by most biodiversity measures. First, the preferred value of DNB for any ecosystem is zero and this is independent of the natural richness or evenness of species in the ecosystem. Second, it accounts for anthropogenic intervention in the ecosystem, and because the four leading threats to biodiversity all stem from such intervention, accounting for it is important.[9] Third, two species that diverge from their natural populations by the same percentages contribute the same to DNB. Thus, evenness, which has been shown to be negatively related to richness (Stirling and Wiley 2001), is not per say a positive property in DNB as it is with the Shannon index.[10] Fourth, with divergences of species from their natural populations DNB decreases ($\partial S/\partial n_i < 0$) at a decreasing rate ($\partial^2 S/\partial {n_i}^2 < 0$). Species whose populations are declining become increasingly difficult to recover (Beissinger and Perine 2001); therefore, DNB values reflect the difficulty of returning a community to its natural state.

Listing the labor constraint completes the description of the simple economic model

$$l_h + l_x = \bar{l}, \tag{5}$$

where the labor supply $\bar{l} > 0$ is exogenously given. Equation (5) represents a conventional scarcity constraint accounting for the demand and supply of labor.

3 The ecosystem

GEEM. To measure DNB, the ecosystem model must yield natural steady-state populations and divergences from these populations following anthropogenic intervention in the ecosystem. Because ecosystems are complex with each species connected in a web of life with many other species, and the populations of the species are determined by the behavior of individuals in the species, the approach taken here is to use the general equilibrium approach along the lines of those recently developed by Tschirhart (2000, 2002, 2004), Pethig and Tschirhart (2001) and Eichner and Pethig (2005).

GEEM has parallels with computable general equilibrium economic (CGE) models. Species populations are like industries and individuals within species are like firms. In all species, each individual maximizes its net energy intake which is the difference between energy from photosynthesis for plants or energy obtained from predation for animals, and energy lost to respiration and energy lost to predation for

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[9] According to Wilcove et al. (1998), in the U.S. the leading threats to biodiversity starting with the greatest threat are; habitat loss to development, introduction of non-native species, pollution and overharvesting. Worldwide the major threats are the same although overharvesting and pollution switch places (IUCN Red List).

[10] Species that have stronger interactions with their neighbors than other species are often labeled “keystone” species (Mills et al. 1993). Keystone species play a larger role in determining community structure. The third property of DNB does not imply that all species have equal impacts on the ecosystem and on $S(h)$. Population changes of keystone species relative to non-keystone species will cause greater numbers of other species to deviate from their natural steady-state populations. Therefore, keystone species have a greater impact on $S(h)$.

plants and animals. Individuals must pay an energy price to obtain energy. For example, a predator optimally forages by choosing among various prey, and the energy it must expend to locate, capture and handle prey is the price. Energy prices act as signals of scarcity because they are determined by the relative abundances of the predator and prey species. Any individual predator or prey has no influence over energy prices because it is only one of many individuals; however, the energy prices are determined endogenously through the demand and supply conditions that require the total amount of biomass lost by each prey species to equal the total amount of biomass acquired by the predators of that prey species. This transfer of biomass has similarities to economic markets; but a crucial difference is that in the ecosystem transfer there is no exchange. Both biomass and energy flow in one direction from predator to prey and this requires modifications to CGE models (Tschirhart 2003).

GEEM is dynamic in that each period the populations are updated with difference equations, one for each species. Unlike other dynamic population models, in GEEM the parameters in the difference equations are not exogenous and not set at the species level. Instead, the parameters are derived from the net energies attained by each individual in each period and then aggregated over the species. Thus, in each period the current biomass transfers and energy prices obtained from the maximization problems and for given populations are used to update the populations for the next period. If the populations are stable over time then a steady state is said to be attained. Anthropogenic interventions into a steady-state system may move the populations to a new steady state, possibly after oscillations. The individual plant and animal net energy functions, the biomass demand/supply balance equations, and the population update equations are in Appendix B that is available from the authors upon request.

GEEM and DNB. To obtain values for DNB, GEEM is applied to a specific marine ecosystem that connects Alaska's Aleutian Islands with the Eastern Bering Sea. The ecosystem, illustrated in Fig. 1, is a food web comprised of nine species including mammals, fish and plankton. Indexing is as follows: sun (0), phytoplankton (1), zooplankton (2), herring (3), pollock (4), Stellar sea lion (5), kelp (6), sea urchin (7), sea otter (8), killer whale (9). Anthropogenic intervention is introduced through harvests in the walleye pollock (*Theragra chalcogramma*) fishery, one of the world's largest. Steller sea lions (*Eumetopias jubatus*), an endangered species, are one of the mammals that prey on pollock and are prey for killer whales (*Orcinus orca*). Killer whales exhibit switching behavior in predation as they substitute between sea lions and sea otter (*Enhydra lutris*) depending on the relative energy prices the whales pay. Data for the model were taken from existing literature and include species population estimates, plant and animal biomasses, animal biomass demands, energy embodied in plant and animal biomass and resting metabolic rates.[11] (See Finnoff and Tschirhart 2003a, b for details.)

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[11] Data on biomass demands and populations, along with several physiological parameters, are used to calibrate GEEM. But the data are taken from an ecosystem that has been harvested for many decades and not from a natural system. Therefore, the calibration contains two complete sets of net energy, first-order and balance equations, one set representing the harvested system and the other the natural system, and both sets are solved simultaneously. In this way we obtain a set of parameters that apply to both the harvested and, natural systems, and the parameters can be used to find the populations that would have been present prior to harvesting. More detail on the method is available from the authors upon request.

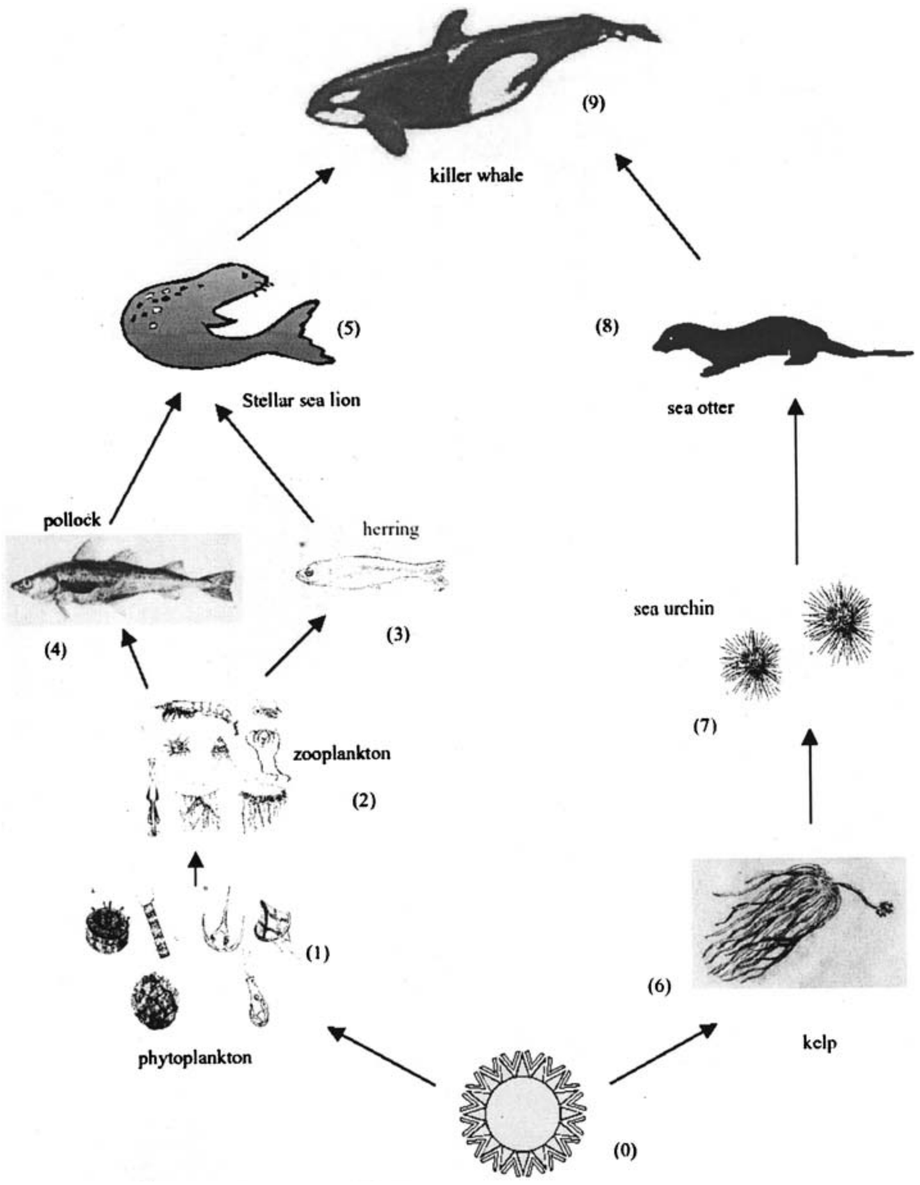

Fig. 1 Food web

The Alaskan ecosystem, or any ecosystem, contains many more than nine species, in addition to complex interactions and a bewildering array of strategies practiced by the individual plants and animals. While some ecological models capture more of these complications than does GEEM, they do not account for interacting individuals exhibiting optimizing behavior. In this way, GEEM is like CGE models which do account for efficient behavior at the individual consumer and firm level, but that ignore most complex human interactions and traits that are part of a social system.

Such detail may be of secondary importance for trying to understand the broad movements of a few key variables.

Running GEEM consists of two repeated steps: (1) calculating a general equilibrium given a set of populations, and (2) updating the populations with the general equilibrium net energies and carrying the new populations to the next step (1): the empirical data of the marine ecosystem provide unique equilibria for step (1). The two steps comprise one period and they are repeated until a steady state is reached. For the Alaskan ecosystem a period is 1 year. Simulations were run without harvesting, and then for ten different constant harvest levels, and each time a new steady state was attained within 10 years. Table 1 displays the natural steady state and harvesting steady-state population units for a sample of exogenous harvest values from $h = 0$ to $h = 2.2$.[12] Actual populations were converted to population units for ease of computations. For examples, one pollock unit is 1.3 billion individuals, one sea lion unit is 1.3 million individuals, and one killer whale unit is 0.13 million individuals. Thus, using Table 1, in moving from $h = 0$ to $h = 0.25$ pollock harvests, an increase of 325 million harvested pollock, the steady-state pollock population decreased by about 463 million pollock while the steady-state killer whale population decreased by 17 individuals; from 1098 to 1081.

The population movements in Table 1 are what would be expected from food web dynamics. As the population of pollock declines with increased harvesting, the population of herring which is a competitor species of pollock rises, the population of zooplankton which is prey for pollock rises, and the population of phytoplankton, the prey of zooplankton, falls. On the other side of the food web from pollock, the population of sea lions that prey on pollock falls, and the population of killer whales that prey on sea lions also falls. The population changes in otter, urchin and kelp rise, fall, and rise, respectively, as expected, although the changes are too small to show up in the table. When harvesting is increased to 2.2, the pressure on pollock is too great for the species to survive and pollock become extinct in the region.

The data from Table 1 are used to estimate a relation between all nine species steady-state populations and pollock harvests. In all cases, a linear function provided the best fit, and the relation between the steady state population of species i, $i = 1, \ldots, 9$, and harvested pollock, h, is given by

$$n_i(h) = \hat{a}_i + \hat{b}_i \cdot h \tag{6}$$

Coefficients in (6) for the nine species are displayed in Table 2.[13] Substituting (6) for each species into (4) yields a measure of DNB for the Alaskan ecosystem:[14]

$$-h^2 \sum_{i=1}^{9} \left(\frac{\hat{b}_i}{\hat{a}_i} \right)^2 \tag{7}$$

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[12] For brevity, the period-by-period populations are not presented. Convergence of the populations to their steady state values tends to be smooth for long-lived species and possibly oscillatory for short-lived species.

[13] Although steady-state populations turn out to be linear in harvests, the plant and animal objective functions and population update equations used in the simulations are non-linear.

[14] That (7) is determined from GEEM and is an argument in the consumer's utility function implies that only feasible ecosystem states are available to choose among.

Table 1 Steady state populations and harvests

h	n_l	n_2	n_3	n_4	n_5	n_6	n_7	n_8	n_9
Harvest	Phyto.	Zoo.	Herring	Pollock	Sea Lion	Kelp	Urchin	Otter	K. whale
0	42.22223	210.2426	4.518834	5.140773	0.153157	1076.92	10.7692	0.050631	0.008445
0.25	42.22222	210.2719	4.519448	4.784487	0.14992	1076.92	10.7692	0.050631	0.008319
0.5	42.22221	210.3031	4.520077	4.455347	0.146836	1076.92	10.7692	0.050631	0.008199
0.75	42.2222	210.3361	4.520721	4.15262	0.143913	1076.92	10.7692	0.050631	0.008085
1	42.22219	210.371	4.521376	3.875218	0.141154	1076.92	10.7692	0.050631	0.007977
1.25	42.22218	210.4076	4.52204	3.621774	0.138559	1076.92	10.7692	0.050631	0.007876
1.5	42.22217	210.4457	4.52271	3.390724	0.136127	1076.92	10.7692	0.050631	0.007781
1.75	42.22216	210.4853	4.523386	3.180389	0.133852	1076.92	10.7692	0.050631	0.007692
2	42.22215	210.5261	4.524064	2.98905	0.131727	1076.92	10.7692	0.050631	0.007609
2.15	42.22214	210.5512	4.524472	2.882657	0.130522	1076.92	10.7692	0.050631	0.007561
2.2	42.22214	210.5518	4.516809	0	0.106822	1076.92	10.7692	0.050631	0.007407

Another useful property of GEEM and DNB is that they can be related to resilience of the ecosystem. According to Carpenter et al. (2001), resilience has two ecological meanings: (i) the magnitude of disturbance an ecosystem can withstand and still persist (Holling 1973; Gunderson and Holling, 2001), and (ii) the time taken for a disturbed ecosystem to return to its initial state (Pimm 1984). Regarding (i), h is the magnitude of disturbance and the value of h that causes pollock extinction is the measure of resilience. In the extreme, if the disturbance causes a complete collapse of the ecosystem such that all species populations are driven to zero, then $s = N$, the number of species lost. Regarding (ii), after a harvesting disturbance flips the ecosystem to a new steady state, and then the disturbance is removed ($h = 0$), GEEM yields the number of periods that pass before the ecosystem returns to the pre-disturbance state.

4 Efficient allocation

In this section an efficient allocation is derived by having the social planner choose optimum economic and ecological variables that characterize a steady-state. As indicated above the pollock population, n_4, is harvested, and both the sea otter population, n_8, and the killer whale population, n_9, provide ecosystem services. The social planner maximizes (1) subject to (2), (3), (5), (6) and (7). The Lagrangian associated with the planner's problem is given by[15,16]

$$\begin{aligned}L = {}&U\left[h, x, \hat{a}'_8 + \hat{b}_8 \cdot h, \hat{a}_9 + \hat{b}_9 \cdot h, -h^2 \cdot \sum_{i=1}^{9} \left(\frac{\hat{b}_i}{\hat{a}_i}\right)^2\right] + \lambda_h \left[H\left(l_h, \hat{a}_4 + \hat{b}_4 \cdot h\right) - h\right] \\ &+ \lambda_x [X(l_x) - x] + \lambda_\ell [\bar{l} - l_h - l_x]. \end{aligned} \tag{8}$$

The first-order conditions listed in Appendix A can be rearranged to establish:

Proposition 1 *The efficient allocation is characterized by*

$$\frac{U_h}{U_x} + \frac{U_{n_8}}{U_x} \cdot \hat{b}_8 = -\frac{U_{n_9}}{U_x} \cdot \hat{b}_9 + \frac{U_s}{U_x} \cdot 2 \cdot h \cdot \sum_{i=1}^{9} \left(\frac{\hat{b}_i}{\hat{a}_i}\right)^2 + \frac{X_l}{H_l} - \frac{X_l}{H_l} \cdot H_{n_4} \cdot \hat{b}_4 \cdot \tag{9}$$

Equation (9) represents the rule for the efficient allocation of pollock harvests. The left side captures the benefits from additional harvesting. The first term, U_h / U_x, is the consumer's marginal willingness to pay for food in terms of the aggregate consumption good, and the second term $U_{n_8} \cdot \hat{b}_8 / U_x$, is the marginal benefit from the increased ecosystem service provided by a larger sea otter population that follows

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[15] We restrict our attention to interior solutions. The question of optimal extinction is beyond the scope of the present paper.

[16] It is worth mentioning that our problem (8) is compatible with the optimal steady state problem (OSSP) of Carlson et al. (1991).

Table 2 Estimation of the parameters $\hat{a}_i$ and $\hat{b}_i$

Species i		$\hat{a}_i$ (t-stat)	$\hat{b}_i$ (t-stat)	R^2
1	phyto	42.22 (40982440)	–0.01005 (–55)	0.997
2	zoo	210.23 (62621)	0.145 (61)	0.998
3	herring	4.519 (232982)	0.003 (179)	0.999
4	pollock	5.004 (96.6)	–1.038 (–26)	0.988
5	sea lion	0.152 (427)	–0.0105 (–38.7)	0.995
6	kelp	1076.9 (1×10^{13})	-5×10^{-10} (–8.5)	0.901
7	urchin	10.769 (2×10^{13})	-1×10^{-10} (–42)	0.997
8	otter	0.0506 (3×10^{8})	6.8×10^{-9}(62)	0.998
9	kw	0.0084 (612)	–0.00041 (–39)	0.995

the smaller pollock population.[17] The right side captures the costs caused by the changes in ecosystem services through increased harvesting. The positive first term (recall, $\hat{b}_9 < 0$ from Table 2) represents a cost from the loss of killer whale ecosystem services as their population falls. Thus, increased anthropogenic intervention via harvesting that reduces pollock populations lowers killer whale populations and raises otter populations as the community adjusts toward a new steady state, and these population changes have opposite impacts on utility. However, in moving to their new steady state populations, both killer whales and sea otter are moving away from their natural steady states and both are incurring a cost to consumers through the fall in naturalness given by the positive second term on the right side of (9). The final two terms represent the harvesting costs: X_l/H_l is the direct marginal labor cost and $-X_l \cdot H_{n_4} \cdot \hat{b}_4 / H_l$ displays the indirect labor cost (recall, $\hat{b}_4 < 0$ from Table 2) that emerges since harvesting reduces the pollock population and thus harvesting becomes more labor intensive. This last term is equivalent to the marginal stock effect in bioeconomic fishery models (e.g., Clark 1976).

To obtain more specific results parametric functions will be used. The utility function U is assumed to be additive separable:

$$U(h, x, n_8, n_9, s) = \beta \cdot h + V(x) + W(s) + v_8 \cdot n_8 + v_9 \cdot n_9 \tag{1a}$$

where V takes a logarithmic form

$$V(x) = \alpha \cdot \ln x \tag{1b}$$

and W is a root function

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[17] Essentially, a smaller pollock population means sea lions must pay higher energy prices for their prey, sea lion net energy falls and their population falls, Similarly, the killer whales that prey on sea lions experience a population decline after they start paying a higher energy price for sea lions. But when the energy price killer whales pay for sea lions rises, individual whales switch to capturing more of the relatively cheaper otter (Killer whale switching behavior has been documented by Estes et al. 1998.). There follows a short run drop in otter owing to an ecological "functional response" by the killer whales, but then a long run rise in otter owing to fewer killer whales and this is referred to in ecology as a "numerical response." Interestingly, the functional response has parallels with economic price effects, and the numerical response has parallels with economic income effects. An advantage of the general equilibrium approach over extant ecological approaches is that, in one model, switching behavior, functional responses and numerical responses are all tracked and explained by individual behavior.

$$W(s) = \varphi \cdot \sqrt{s}. \tag{1c}$$

In (1a)–(1c) α, β, φ and v are parameters reflecting the benefits of the aggregate consumption good, food from harvested pollock, and ecosystem services. The production function is assumed to have constant returns to scale, i.e.,

$$x = l_x, \tag{2a}$$

and the harvesting function takes the following form (as proposed by Schaefer 1957):

$$h = \mu \cdot l_h \cdot n_4, \tag{3a}$$

where μ is a productivity parameter.

Using (1a), (1b), (1c), (2a), (3a) and (5) the efficiency condition (9) can be rearranged to read

$$h^2 + h \cdot \left[\frac{\hat{a}_4 \cdot \left(2 \cdot \bar{l} \cdot \mu \cdot \hat{b}_4 - 1\right)}{\hat{b}_4 \cdot \left(\bar{l} \cdot \mu \cdot \hat{b}_4 - 1\right)}\right] + \frac{\hat{a}_4^2 \cdot \bar{l} \cdot \mu - \frac{\hat{a}_4 \alpha}{\beta - c}}{\hat{b}_4 \cdot \left(\bar{l} \cdot \mu \cdot \hat{b}_4 - 1\right)} = 0, \tag{9a}$$

where $c \equiv \varphi \cdot \sqrt{\sum_{i=1}^{9} \left(\hat{b}_i / \hat{a}_i\right)^2} - v_8 \cdot \hat{b}_8 - v_9 \cdot \hat{b}_9$. Then applying Viète's rule we obtain:

Table 3 Comparative static results

Shocks	dh	dl_h	dl_x	dx
d$\alpha > 0$	–	–	+	+
d$\beta > 0$	+	+	–	–
d$\varphi > 0$	–	–	+	+
d$v_8 > 0$	+	+	–	–
d$v_9 > 0$	–	–	+	+
d$\mu > 0$	+	+	–	–
d$\hat{a}_1 > 0$	+	+	–	–
d$\hat{a}_2 > 0$	+	+	–	–
d$\hat{a}_3 > 0$	+	+	–	–
d$\hat{a}_4 > 0$	?	?	?	?
d$\hat{a}_5 > 0$	+	+	–	–
d$\hat{a}_6 > 0$	+	+	–	–
d$\hat{a}_7 > 0$	+	+	–	–
d$\hat{a}_8 > 0$	+	+	–	–
d$\hat{a}_9 > 0$	+	+	–	–
d$\hat{b}_1 > 0$	+	+	–	–
d$\hat{b}_2 > 0$	–	–	+	+
d$\hat{b}_3 > 0$	–	–	+	+
d$\hat{b}_4 > 0$	?	?	?	?
d$\hat{b}_5 > 0$	+	+	–	–
d$\hat{b}_6 > 0$	+	+	–	–
d$\hat{b}_7 > 0$	+	+	–	–
d$\hat{b}_8 > 0$	?	?	?	?
d$\hat{b}_9 > 0$	+	+	–	–

$$h = -\frac{\hat{a}_4 \cdot \left(2 \cdot \bar{l} \cdot \mu \cdot \hat{b}_4 - 1\right)}{2 \cdot \hat{b}_4 \cdot \left(\bar{l} \cdot \mu \cdot \hat{b}_4 - 1\right)} \pm \sqrt{\left[\frac{\hat{a}_4 \cdot \left(2 \cdot \bar{l} \cdot \mu \cdot \hat{b}_4 - 1\right)}{2 \cdot \hat{b}_4 \cdot \left(\bar{l} \cdot \mu \cdot \hat{b}_4 - 1\right)}\right]^2 - \frac{\hat{a}_4^2 \cdot \bar{l} \cdot \mu - \frac{\hat{a}_4 \alpha}{\beta - c}}{\hat{b}_4 \cdot \left(\bar{l} \cdot \mu \cdot \hat{b}_4 - 1\right)}} \quad (9b)$$

To see how the efficient allocation responds to changes in the parameters α, β, φ, v_8, v_9, $\hat{a}_i$, $\hat{b}_i$ and μ comparative static results are listed in Table 3. It is interesting to observe that the sign $\mathrm{d}h$ = sign $\mathrm{d}l_h$ = –sign $\mathrm{d}l_x$ = –sign $\mathrm{d}x$. Obviously, the opposite signs of the labor inputs follow directly from the labor constraint (5). The same signs of $\mathrm{d}x$ and $\mathrm{d}l_x$ come from (2a) and sign $\mathrm{d}h$ = sign $\mathrm{d}l_h$ displays the property that harvesting is an increasing function of labor. To see that, rearrange (3) accounting for $n_4 = \hat{a}_4 + \hat{b}_4 \cdot h$ to $h = \frac{\mu \cdot l_h \cdot \hat{a}_4}{1 - \mu \cdot l_n \cdot \hat{b}_4} \equiv H(l_n)$ and differentiation yields $\frac{\mathrm{d}h}{\mathrm{d}l_n} \equiv H_l = \frac{\mu \cdot \hat{a}_4}{\left(1 - \mu \cdot l_n \cdot \hat{b}_4\right)^2}$. Having this in mind the results of Table 3 conform to intuition. Increasing the preference parameter of the aggregate consumption good, $\mathrm{d}\alpha > 0$, calls for an increase of the efficient amount of the consumption good, $\mathrm{d}x > 0$ and calls for driving back the harvesting of pollock, $\mathrm{d}h < 0$, because additional labor is used in the production process, $\mathrm{d}l_x > 0$, which is absent for harvesting, $\mathrm{d}l_h < 0$. Vice versa, increasing the preference parameter of food yields an efficient allocation that is characterized by a higher level of harvesting and a lower level of the consumer good. Moreover, an increase in the preference parameter of naturalness and the flow of ecosystem services, i.e., of φ, results in a reduction of harvesting such that the naturalness of the ecosystem is better preserved. Since the sea otter population benefits from harvesting, increasing the preference parameter v_8 calls for an extension of pollock harvesting.

Table 3 also provides the comparative static effects of the GEEM-generated steady-state parameters $\hat{a}_i$ and $\hat{b}_i$. Increases in $\hat{a}_i$ for all species except pollock lead to increases in the efficient harvesting. For changes in $\hat{b}_i$, consider that $\hat{b}_i$ measures the sensitivity of the ith species' population to harvesting. For phytoplankton, sea lions, kelp and sea urchins, $\hat{b}_i < 0$ and harvesting decreases their populations and decreases DNB; therefore, an increase in $\hat{b}_i$ makes these species less sensitive to harvesting and harvesting is increased. Alternatively, $\hat{b}_i > 0$ for zooplankton and herring and harvesting increases their populations from the natural steady state and decreases DNB. An increase in $\hat{b}_i$ makes these species more sensitive to harvesting; therefore, harvesting is reduced to lessen the divergence from the natural DNB.

For pollock, sea otter and killer whales, the comparative statics for $\hat{a}_4$, $\hat{b}_4$, $\hat{b}_8$ and $\hat{b}_9$ are more involved because of their additional impact either through the harvesting function or through the non-consumptive ecosystem services. For killer whales, an increase in the negative value of $\hat{b}_9$ makes them less sensitive to harvesting so increased harvesting has less of an impact on the killer whales contribution to DNB and to the benefits from whale watching. Therefore, harvesting is increasing in $\hat{b}_9$. However, sea otter populations benefit from more harvesting so while increased harvesting decreases DNB, it increases the benefits of otter watching, and the change in harvesting with respect to $\hat{b}_8$ is ambiguous. Lastly, the change in harvesting with respect to $\hat{a}_4$ and $\hat{b}_4$ are also ambiguous. This follows because increased harvesting reduces DNB and the naturalness of the entire community, but increased harvesting also increases the benefits from consuming fish.

5 Market failure and correction

In this section competitive markets are introduced. There is a competitive market for harvest with price p_h, a competitive market for the aggregate consumption good with price p_x and a competitive market for labor with price p_ℓ. In addition to these prices we introduce a tax on harvesting pollock, τ, and a standard on harvesting pollock, σ, that are set by a fishery manager. As a necessary condition for a competitive equilibrium of the market economy the representative consumer, the production firm and the harvesting firm solve optimization problems as specified by the Lagrangians (10), (11) and (12), respectively:

$$L^C = U[h, x, n_8, n_9, s] + \gamma_c[\phi - p_h h - p_x x], \tag{10}$$

$$L^X = p_x x - p_\ell l_x + \gamma_x[X(l_x) - x], \tag{11}$$

$$L^H = (p_h - \tau) \cdot h - p_\ell l_n + \gamma_h \left[H\left(l_h, \hat{a}_4 + \hat{b}_4 \cdot h \right) - h \right] + \gamma_s[\sigma - h] + \gamma_b\left[\bar{h} - h\right] \tag{12}$$

where ϕ is a lump sum transfer of profits and of the tax revenue to the representative household.

Three remarks are in order with respect to the consumer's and the harvesting firm's problems. First, the representative consumer is assumed to have no control over the ecosystem; in particular, species populations are beyond his influence. Therefore, he takes the level of the population densities of the sea otters, n_8, and killer whales, n_9, and the state of the ecosystem, s, as exogenously given and exhibits Nash-like behavior responding to the prevailing levels of n_8, n_9 and s. Second, the fishery is not a common property resource and the harvesting firm has sole property rights over the fishery.[18] Sole ownership yields efficient harvesting in standard one-species bioeconomic models. The owner is assumed to not account for the affect of harvesting on other species. Third, the harvesting firm faces an biological upper bound on harvesting, $\bar{h}$, at which the pollock population becomes extinct. Initially, the firm is assumed to choose a harvest below the biological upper bound so that the last constraint in (12) is inactive.

Maximizing the Lagrangians (10)–(12) and rearranging the first-order conditions yields:

$$\frac{U_h}{U_x} - \tau - \gamma_s = \frac{X_l}{H_l} - \frac{X_1}{H_1} \cdot H_{n_4} \cdot \hat{b}_4, \tag{13}$$

that characterizes the market allocation under regulation by the fishery manager. Comparing (9) and (13), there is a source for inefficiency in the laissez-faire economy when the tax rate is zero and the harvest standard is absent ($\tau = \sigma = 0$). The harvesting firm ignores the ecosystem externalities stemming from the impact of harvesting on ecosystem services, more specifically the impact on the sea otter population, on the killer whale population and on the naturalness of the ecosystem. Because the fishery is not a common property resource, this inefficiency is not the usual open access problem; instead it is a result of the ecosystem externalities.

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[18] In fact, the pollock fishery was a regulated open access fishery until 1999 at which time a system similar to individual quotas was set up.

A price setting (tax) or quantity setting (standard) approach can be used to achieve the efficient allocation. Proposition 2 shows how to close the inefficiency gap using a tax. With a positive tax, τ, the fishery manager is collecting the natural resource rents in the fishery.[19]

Proposition 2 *Set* $p_x = \lambda_x, p_l = \lambda_l, p_h = \lambda_h \cdot \left(1 - H_{n_4} \cdot \hat{b}_4\right) + \tau$, $\sigma = 0$ *and*

$$\tau = \frac{U_{n_8}}{U_x} \cdot \hat{b}_8 + \frac{U_{n_9}}{U_x} \cdot \hat{b}_9 - \frac{U_s}{U_x} \cdot 2 \cdot h \cdot \sum_{i=1}^{9} \left(\frac{\hat{b}_i}{\hat{a}_i}\right)^2, \tag{14}$$

then a competitive general equilibrium is attained and the pertinent allocation is efficient.

To prove Proposition 2 observe that the first-order conditions of the Lagrangians (10)–(12) are listed in the second column of Table 4. When the prices and the tax rate as specified in Proposition 2 are inserted into column 2 of Table 4 it is straightforward to show that these conditions are in accordance with column 1 of Table 4 that characterizes the efficient allocation. From (14), we infer that τ reflects the social costs of reducing ecosystem services through marginal increases of harvesting.

In lieu of a tax, the fishery manager can set a standard to recover the efficient allocation. Denote h^* as the efficient level of pollock harvesting from the social planner's problem.[20]

Proposition 3 *Set* $p_x = \lambda_x$, $p_l = \lambda_l$, $p_h = \lambda_h \cdot \left(1 - H_{n_4} \cdot \hat{b}_4\right) + \gamma_s$, $\tau = 0$ and $\sigma = h^*$, *then a competitive general equilibrium is attained and the pertinent allocation is efficient.*

Next we consider again the parametric functions (la), (lb), (1c), (2a) and (3a). Note that from (3a), labor in the fishery can be written as $l_h = h/\mu \cdot n_4$. Thus, even in the absence of any regulation, the harvesting firm in solving (12) would not set harvesting at the biological upper bound, because as the fish population approaches zero, labor approaches infinity. In fishery models, extinction is more likely on the ecological side if there is some positive minimum population below which the species cannot successfully reproduce. The pollock species fits this case: from table 1 extinction occurs if $\bar{h} \geq 2.2$, or about 1.3 metric tons. On the economic side, extinction is more likely given open access, a low harvesting cost and a high market price for fish (Hartwick and Oleweiler 1998). Extinction does not occur here because harvesting cost becomes prohibitively high when there are few fish in the sea.[21]

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[19] Observe that in case of $\sigma = 0$ the constraint $h \geq \sigma$ is weakly binding which implies that $\gamma_s = 0$. In addition, since we assume an interior solution of the social planner's optimization problem, it can be shown that for the prices and the tax rate specified in Proposition 2 the constraint $h \leq \bar{h}$ is also weakly binding such that $\gamma_b = 0$.

[20] In case of the standard it can be shown that $\gamma_s = \frac{U_{n_8}}{U_x} \cdot \hat{b}_8 + \frac{U_{n_9}}{U_x} \cdot \hat{b}_9 - U_s \cdot 2 \cdot h \cdot \sum_{i=1}^{9} \left(\frac{\hat{b}_i}{\hat{a}_i}\right)^2$. The proof of Proposition 3 follows along the same lines as the Proof of Proposition 2.

[21] Realistically, in numerous fisheries the target species has not become extinct, but the fisheries have been depleted to the point of near collapse, and 69% of the world's major fish species are in decline (McGinn 1998).

Table 4 Pareto efficiency and markets

Column	Row	Efficiency 1	Markets 2
Consumption	1	$\frac{U_h}{U_x}+\frac{U_{n_8}}{U_x}\hat{b}_8+\frac{U_{n_9}}{U_x}\hat{b}_9-\frac{U_s}{U_x}2h\sum_{i=1}^{9}\left(\hat{b}_i/\hat{a}_i\right)^2=\frac{\lambda_h}{\lambda_x}\cdot\left(1-H_{n_4}\hat{b}_4\right)$	$\frac{U_h}{U_x}=\frac{p_h}{p_x}$
Production	2	$\frac{\lambda_x}{\lambda_l}=\frac{1}{X_l}$	$\frac{p_x}{p_l}=\frac{1}{X_l}$
Harvesting	3	$\frac{\lambda_h}{\lambda_l}=\frac{1}{H_l}$	$\frac{p_h-\tau-\gamma_s-\gamma_b}{p_l\cdot\left(1-H_{n_4}\hat{b}_4\right)}=\frac{1}{H_l}$

In the absence of the standard ($\sigma = 0$), for the parametric functions harvesting can be calculated as[22]

$$h=-\frac{\hat{a}_4\cdot\left(2\cdot\bar{l}\cdot\mu\cdot\hat{b}_4-1\right)}{2\cdot\hat{b}_4\cdot\left(\bar{l}\cdot\mu\cdot\hat{b}_4-1\right)}\pm\sqrt{\left[\frac{\hat{a}_4\cdot\left(2\cdot\bar{l}\cdot\mu\cdot\hat{b}_4-1\right)}{2\cdot\hat{b}_4\cdot\left(\bar{l}\cdot\mu\cdot\hat{b}_4-1\right)}\right]^2-\frac{\hat{a}_4^2\cdot\bar{l}\cdot\mu-\frac{\hat{a}_4\alpha}{\beta\cdot(1-\tau)}}{\hat{b}_4\cdot\left(\bar{l}\cdot\mu\cdot\hat{b}_4-1\right)}} \tag{13a}$$

Total differentiation of (13a) yields the expected result that harvesting is decreasing in the tax rate. Combining (13a) and (9b) yields the efficient tax rate in the parametric version of the model

$$\tau=\frac{c}{\beta}=\frac{1}{\beta}\cdot\left(\varphi\cdot\sqrt{\sum_{i=1}^{9}\left(\frac{\hat{b}_i}{\hat{a}_i}\right)^2}-v_8\cdot\hat{b}_8-v_9\cdot\hat{b}_9\right) \tag{14a}$$

Expression (14a) shows the determinants of the efficient tax rate. The tax rate is decreasing in the preference parameters for food, β, and for otter, and increasing in the preference parameters for ecosystem services, ϕ, and for killer whales.[23] In the absence of the tax rate ($\tau = 0$) the ecosystem externalities can be corrected by the standard $\sigma = h^*$ where h^* is specified in (9b). It is interesting to observe that the comparative statics with respect to the efficient allocation, more specifically with respect to the efficient harvesting, can be transferred to the harvest standard such that column 2 of Table 3 (dh) is identical to the comparative static effect of increases in a specific parameter on the efficient standard (dσ).

Finally, we present a numerical example based on the parameter values $\alpha = 0.5$, $\varphi = 1.5, \beta = \mu = v_8 = v_9 = \bar{l} = 1$. Figure 2 shows harvesting, utility and naturalness as functions of the tax rate. While harvesting is decreasing and convex and naturalness is increasing and concave in the tax rate, the welfare function attains a maximum at $\tau = 0.6972$ which is the efficient tax rate from (14a). In the laissez-faire economy the harvesting rate is about 2.0313, but taking ecosystem services into account the efficient harvesting rate is 1.3347 that is reached at the efficient tax rate. The divergence from the natural state under the laissez-faire economy is $s = -0.8905$, and the divergence under efficient harvesting is $s = -0.3845$. The former (latter)

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[22] To eliminate the degree of freedom in prices we choose harvest as numeraire and set $p_h = 1$.

[23] The tax rate can be negative if the preference parameter for a larger killer whale population dominates all other effects. This seems highly unlikely and is not found to be the case in the empirics.

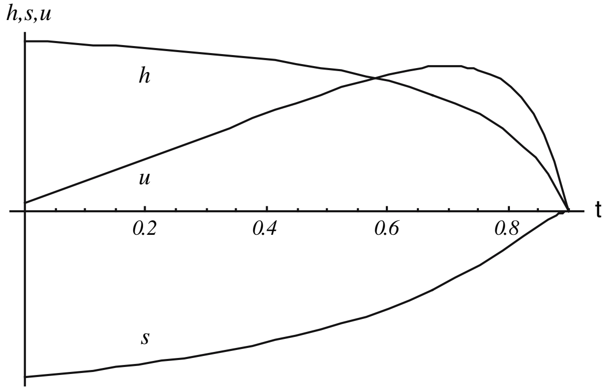

Fig. 2 Numerical example showing harvesting (h), welfare (u) and naturalness (s) as functions of the tax rate t. The vertical axis is rescaled for each variable

divergence is largely comprised of drops in the pollock, sea lion and killer whale populations of about 42.14% (27.69%), 14.03% (9.22%) and 9.91% (6.51%), respectively.

6 Conclusion

An integrated economic/ecological model is presented that includes two common ecosystem services, consumptive use of a fish species and non-consumptive use of popular observable species, and a third service that is likened to the naturalness of the entire ecosystem. There is a tradeoff between consumptive use and maintaining the ecosystem in a natural state, although consumptive use of fish can increase or decrease the popular species depending on their position in the food web, and thereby add to or detract from the non-consumptive service. The third service is made operational by introducing DNB that relates harvesting to the divergence of the ecosystem from its natural state. Using GEEM, DNB can be quantified for various harvest levels, including levels that would drive the fish species to extinction. By including all species, DNB accounts not only for how the loss of high profile species diminishes naturalness, but also how lower profile species such as phytoplankton or sea urchins contribute to naturalness.

Economically efficient levels of the three ecosystem services are analytically derived, and they are compared to the levels delivered by competitive markets. The unregulated markets do not account for ecosystem externalities, and either taxes or standards are needed to regain the efficient solution. Higher taxes reduce harvesting and the benefits of consuming fish, they increase the benefits of observing killer whales but decrease the benefits of observing sea otter, and they increase the naturalness of the ecosystem.

Our static optimization model does omit important dynamic issues concerning the path of utility, profits and naturalness during transition periods, and the stability properties of the steady states. For example, optimum steady state harvests may be lower or higher than those found here if during transition optimum harvests were higher or lower, respectively. Although we cannot analytically prove the stability properties of the ecosystem modeled here, in numerous GEEM simulations where populations were disturbed by 20% or more from harvesting or natural steady states, the system returned to steady state. There is debate among ecologists regarding whether ecosystems achieve steady states and whether they are unique. The idea of succession wherein young ecosystems evolve toward a unique steady state, such as when a field with many young saplings eventually becomes a forest with a few large, dominant trees, has given way to recognizing that systems continually undergo shocks and switch between different steady states, possibly experiencing hysteresis (Holling et al. 1995; Perrings 1998; van Kooten and Bulte 2000). GEEM could be used to generate alternative steady-state populations for DNB under changing ecosystem conditions. For example, the phytoplankton populations described below are dependent on temperature and available nutrients (Leviton 1982), and these conditions can be incorporated into GEEM in a manner described in Tschirhart (2002) for a terrestrial system. Of course, values for DNB that change with weather or other abiotic phenomena would complicate the human problem, requiring policies that respond to the changing conditions. This complication is not addressed in this paper, and we leave a dynamic economic model for future research.

Implementing the efficient solution for a real economy would require placing values on the ecosystem services. Marketed commodities such as harvested fish species can be valued using market prices. Species such as killer whales and sea otter also can be valued in cases where they are marketed as observable species and people pay to view them. But all these species contribute to welfare by more than their market values because of their role in maintaining natural biodiversity. Contingent valuation methods designed to obtain existence values (Loomis and white 1996) have been used to ferret out contributions of individual species to welfare, but typically the methods are not applied to collections of species that make up biodiversity. Studies that consider the value of all amenities of an ecosystem along the lines of Conrad (1997) are promising.

Regardless of whether monetary values can be obtained, and the abstract economy presented, our approach provides a framework for thinking about how economies and ecosystems are interconnected. The Alaskan example is fairly simple, yet it portrays a complex assortment of competing interests that arise around natural resource use. The harvesting firms and some consumers may view the ecosystem primarily as a source of fish, the tourism industry and visitors to Alaska may view the ecosystem primarily as a source of wildlife recreation, and other households may view the ecosystem primarily as a source of wilderness related values. All these competing interests will intensify as human populations and their consumption levels rise, yet the stocks of natural resources remain bounded from above. Integrated economic/ecological models are needed to help sort out these competing interests.

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Appendix A

Derivation of the comparative static results of Table 3: The starting point of the comparative static analysis is (9a) which is rearranged to

$$h^2 \cdot \left[\hat{b}_4 \cdot \left(\bar{l} \cdot \mu \cdot \hat{b}_4 - 1\right)\right] + h \cdot \left[\hat{a}_4 \cdot \left(2 \cdot \bar{l} \cdot \mu \cdot \hat{b}_4 - 1\right)\right] + \hat{a}_4^2 \cdot \bar{l} \cdot \mu - \frac{\hat{a}_4 \alpha}{\beta - c} \equiv A = 0 \tag{A1}$$

Implicit differentiation of (A.1) with respect to the parameter $\theta = \alpha, \beta, \varphi, v_8, v_9, \mu, \hat{a}_i, \hat{b}_i$ yields

$$\frac{\mathrm{d}h}{\mathrm{d}\theta} = -\frac{A_\theta}{A_h}. \tag{A2}$$

We restrict our attention to parameter constellations which satisfy the second-order condition $A_h < 0$. Differentiation of A with respect to $\theta = \alpha, \beta, \varphi, v_8, v_9, \mu, \hat{a}_i, \hat{b}_i$ we obtain

$$A_\alpha = -\frac{\hat{a}_4}{\beta - c}, \quad A_\beta = \frac{\hat{a}_4 \alpha}{(\beta - c)^2} > 0, \quad A_\varphi = -\frac{\hat{a}_4 \alpha}{(\beta - c^2)} \cdot \sqrt{\sum_{i=1}^{9} \left(\hat{b}_i / \hat{a}_i\right)^2} < 0,$$

$$A_{v_8} = \frac{\hat{a}_4 \alpha}{(\beta - c)^2} \cdot \hat{b}_8 > 0, \quad A_{v_9} = \frac{\hat{a}_4 \alpha}{(\beta - c)^2} \cdot \hat{b}_9 < 0, \quad A_\mu = h^2 \hat{b}_4 \bar{l} + 2h \hat{a}_4 \hat{b}_4 \bar{l} + \hat{a}_4^2 \bar{l} = n_4^2 \bar{l} > 0,$$

$$A_{\hat{a}_i} = \frac{\hat{a}_4 \alpha}{(\beta - c)^2} \cdot \frac{\varphi}{\sqrt{\sum_{i=1}^{9} \left(\hat{b}_i / \hat{a}_i\right)^2}} \cdot \frac{\hat{b}_i^2}{\hat{a}_i^3} > 0 \qquad \text{for } i = 1,2,3,5,6,7,8,9,$$

$$A_{\hat{a}_4} = 2\bar{l}\mu n_4 - \frac{\alpha}{\beta - c} + \frac{\alpha}{(\beta - c)^2} \cdot \frac{\varphi}{\sqrt{\sum_{i=1}^{9} \left(\hat{b}_i / \hat{a}_i\right)^2}} \cdot \frac{\hat{b}_4^2}{\hat{a}_4^2},$$

$$A_{\hat{b}_i} = -\frac{\hat{a}_4 \alpha}{(\beta - c)^2} \cdot \frac{\varphi}{\sqrt{\sum_{i=1}^{9} \left(\hat{b}_i / \hat{a}_i\right)^2}} \cdot \frac{\hat{b}_i}{\hat{a}_i^2} = -\operatorname{sign} \hat{b}_i \qquad \text{for } i = 1,2,3,5,6,7,$$

$$A_{\hat{b}_4} = h \cdot \left(\bar{l}\mu n_4 - h\right) - \frac{\alpha}{(\beta - c)^2} \cdot \frac{\varphi}{\sqrt{\sum_{i=1}^{9} \left(\hat{b}_i / \hat{a}_i\right)^2}} \cdot \frac{\hat{b}_4}{\hat{a}_4} > 0,$$

$$A_{\hat{b}_8} = -\frac{\hat{a}_4 \alpha}{(\beta - c)^2} \cdot \left[\frac{\varphi}{\sqrt{\sum_{i=1}^{9} \left(\hat{b}_i / \hat{a}_i\right)^2}} \cdot \frac{\hat{b}_8}{\hat{a}_8^2} - v_8\right],$$

$$A_{\hat{b}_9} = -\frac{\hat{a}_4 \alpha}{(\beta - c)^2} \cdot \left[\frac{\varphi}{\sqrt{\sum_{i=1}^{9} \left(\hat{b}_i / \hat{a}_i\right)^2}} \cdot \frac{\hat{b}_9}{\hat{a}_9^2} - v_9\right] > 0,$$

which establishes the second column of Table 3, The derivation of the comparative statics with respect to l_h, l_x and x is sketched in the text.

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