A new adaptive system approach to predator–prey modeling

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Abstract

A computable general equilibrium approach can effectively model adaptive ecological systems, and here it is applied to a predator–prey system. Features of the model include: (1) predators and prey maximize net energy intake by responding to energy expenditures for capturing prey and for avoiding capture; (2) the expenditures are determined system-wide by the interaction of all predators and prey; (3) predator consumption is negatively related to its expenditures on prey; (4) prey biomass given up to predators is negatively related to the predator's expenditure owing to predation risk; (5) when there is but one prey species, the steady-state predator consumption and expenditure are independent of the prey density because any advantage of a larger prey density is competed away by the predators; (6) when there are two prey species, the steady-state predator consumptions and expenditures are not independent of the densities, because there are many combinations of consumptions and expenditures that yield a steady state, and the combinations are differentiated by prey densities; (7) no a priori assumptions are made about functional responses, and the functional response observed depends on whether the prey consumption is allowed to vary and on the numerical response of the predator; (8) functional and numerical responses tend to be negatively related; (9) predator switching behavior depends on the relative expenditures for the prey species, and the predator may specialize in one prey or switch gradually between prey; (10) population difference equations depend on individual net energies and not on aggregated species parameters, while oscillations in a population depend on average lifespan.
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Keywords: Predator–prey; Functional response; Optimum foraging; Switching; Optimization

1. Introduction

In adaptive systems individuals process information about their environment and then alter their behavior according to some objective (Hraber and Milne, 1997). Ecological systems are clearly adaptive because individual plants and animals act *as if* they have objectives and they alter their behavior in response to environmental changes. Moreover, the individual behaviors lead to population dynamics that are often the cause of the environmental changes. This circularity under-

scores the importance of linking individual behavior with population dynamics, and doing so in a way in which natality, mortality and predation rates and functional and numerical responses directly follow from the individual behavior.

General equilibrium analysis is an effective means of modeling adaptive systems, because individuals are assumed to have objectives and they respond to environmental factors beyond their individual control, yet the factors are determined by the aggregate behavior of all individuals. In economics, general equilibrium has been referred to as the most important development in economics in the twentieth century (Sandler, 2001). The origins of general equilibrium theory date back to the French economist Walras (1954) working

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in the late 1800s, although the modern conception of the theory was formulated by Leontief (1941) in an input–output framework, and in a more general framework by Arrow and Debreu (1954) and others in the 1950s. The input–output framework is restricted to linear production technologies, and consumers and producers in the economy do not exhibit maximizing behavior and, therefore, do not form an adaptive system. These limitations provided impetus for the more general, non-linear framework of Arrow and Debreu who rigorously proved the existence of prices and quantities such that demands of many consumers who maximize utility are equal to supplies from many producers who maximize profit. Moreover, the relations that describe the economic system are sufficiently complete to determine the values of its variables: each relation represents a balance of forces, and a relation that is out of balance sets in motion forces that tend to restore the balance (Arrow, 1968).

The theory moved to application with computational algorithms developed by Scarf (1967) and others in the 1960s, and with improvements in computer technology. Early applications were presented by Shoven and Whalley (1973, 1974). Today, computable general equilibrium (CGE) models are widely used by government agencies and industry. They utilize data on consumer and firm characteristics to evaluate how the feedback effects of tax, trade or environmental policies impact prices, wages and employment (Shoven and Whalley, 1992; Ginsburg and Keyzer, 1997). Computers allow much detail and complexity so that geographic regions with thousands of representative consumers and firms are included.

These notions about system relations in economics apply well to ecological systems, and this paper applies a modified CGE approach to predator–prey relationships. Predator–prey relationships are chosen because they contain key elements that drive ecosystem outcomes, and, therefore, can be building blocks for larger, ecosystem-wide CGE models. The immediate purpose of this paper is to demonstrate that the CGE approach explains a fairly wide range of standard, and some not so standard, ecological outcomes. The ultimate purpose of developing a CGE ecosystem model is two-fold: (1) to identify the relations, grounded in individual behavior, that are sufficient to describe the broad workings of an ecosystem, and (2) to integrate the model with a CGE economic model

so that the reciprocal impacts between economies and ecosystems can be measured.

The starting point in the CGE approach is to postulate that both predator and prey individuals optimally forage to maximize incoming net energy. Optimizing behavior underpins adaptive system models, and the goal is to derive hypotheses with respect to animal behavior (Bernstein et al., 1999). Maximization entails weighing the benefits of energy gained from consumed biomass against the costs of energy lost to predators and respiration, and to the energy expenditures for capturing prey. These expenditures are central in the CGE approach. They result from the collective behaviors of individual predators and individual prey, yet any one individual has an inconsequential impact on the expenditures. Roughly, the larger the predator density engaged in intraspecific interference competition for prey, and the smaller the prey density, the greater are the predator energy expenditures. The energy expenditures are signals that the predators and the prey respond to in foraging optimally, and that prey respond to in balancing food intake with predation risk (Luttbeg and Schmitz, 2000). The predator and prey responses are the forces that restore balance by driving the system toward a steady state.

Specifically, each time period is specified to be a reproductive cycle, and for simplicity both predator and prey are assumed to have the same length cycle. In each time period the CGE calculations yield the energy expenditures and the optimum consumptions of the individual predator and prey. At the end of each time period, the expenditures and consumptions are used to calculate predator and prey net energies and respirations, and in turn these net energies and respirations are inserted into difference equations that adjust the populations. Because the net energies and respirations can change across periods, the approach is an example of a structural dynamic model. Bendoricchio and Jørgensen (1997) refer to structural dynamic models as a promising stage of ecological modeling because they can simulate changes in ecosystem structure. There is a distinction, however, between the adaptive approach herein and structural dynamic models that use ascendancy (Ulanowicz, 1980), or Bendoricchio and Jørgensen's exergy, or other objectives as goal functions: the latter assume the ecosystem maximizes an objective, whereas the former assumes each individual maximizes an objective, in this case net energy.

In future work it would be interesting to determine whether maximization at the individual level leads to maximization for the overall system.

The within-period CGE calculations coupled with the end-of-period dynamics also are used to study functional and numerical responses. Functional responses track the consumption of the predator as a function of prey density, and numerical responses track the change in predator density as a function of prey density (Smith, 1996). Because both densities and consumption rates are determined within the model, the functional response is determined within the model and not specified a priori as is usually done in predator–prey systems. The results show how the predator's functional response depends on the prey's functional response and on both species numerical responses. If the numerical responses are suppressed, which is appropriate for isolating the short-term functional response, then a Holling (1959) type II response follows. This type II response is not due to variable search times and fixed handling times that are not separated out in the model, nor is the response destabilizing (Murdoch and Oaten, 1975).

A second prey species is added to the model and switching behavior is examined. Switching depends on the different energy expenditures for prey species that the predator confronts, and if members of two prey species are consumed, then the marginal energy gain/marginal energy expenditure ratios are equal across the prey species (Stephens and Krebs, 1986). Because the ratios depend on the energy expenditures that, in turn, depend in part on species densities, the ratios vary with density changes so that predator switching occurs, in varying degrees, as the relative costs of the prey change.

To apply the model, simulations are used for the in-period CGE calculations and the end-of-period population adjustments. In each period all individuals are maximizing net energy and the biomass flows between predators and prey are balanced, and if the populations converge over periods, then a steady state is attained. The simulations use real data from a marine ecosystem in the Eastern Bering Sea off Alaska.

The CGE approach in which individual entities are the basic unit is consistent with the object-based approaches described by Parrot and Kok (2002); however, unlike the object-based work where individuals follow simple behavioral rules, here the individuals

make optimal predation choices in each period and their choices change with changing prey conditions. Parrot and Kok introduce a detailed description of each animal's physiological state as well as considerable detail about the animal's environment. In the end, the animals still follow rules, although the rules are defined over an infinite set of alternatives and designed to minimize the animal's energy expenditures. The optimization approach herein does not contain detailed physiological states, but the animals choose from an infinite set of alternatives and by optimizing net energy they are continually balancing energy expenditures and nutritional requirements.

2. Predator and prey behavior in CGE

In each time period or reproductive cycle, predators optimally forage by consuming a net-energy maximizing quantity of prey biomass. In foraging models, the length of the time period is often left unspecified, and a reproductive cycle is probably longer than what is usually envisioned. With a long time period some of the detailed strategic behaviors of predator and prey are being omitted, so the behavior herein must be thought of as that which results from pursuing a long-term objective. A shorter time period could be used but would not add significantly to the points made below.

Hannon (1973, 1976) introduced a formal statement of net energy maximization, although he envisioned maximization at the species or trophic level as opposed to the individual level, and he did not investigate dynamics of multiple species. Members of the predator species are assumed identical, and a representative predator's net energy is given by:

$$R_d = [e_y - e]x_d - r_d(x_d) - \beta_d \qquad (1)$$

where subscripts d and y refer to predator and prey, and where the e terms are in energy units per biomass units (kcal/kg) and the x is biomass flow (kg/unit time), making R_d power units (Watts). The predator chooses its consumption, x_d, and each unit of biomass consumed contains e_y units of energy, where e_y is the energy content in a unit of prey biomass. The e is the total energy expenditure over the time period for locating, attacking and handling units of prey biomass. Unlike other optimum foraging models, locating, attacking and handling prey are not separated out, but

combined into one activity. If they were separated then there would be separate energy expenditure for each activity. This would complicate the model and whether or not the additional insights are worth the complication is left for future research. Following Gurney and Nisbet (1998), respiration is divided into two parts: (1) the function $r_d(x_d)$ is respiration or energy lost to the atmosphere that depends on biomass consumed and includes feces, locomotion, and reproduction, and (2) β_d is resting metabolic rate that is independent of x_d.

The first-order necessary condition for maximizing (1) over x_d is:

$$\frac{\partial R_d}{\partial x_d} = e_y - e - \frac{dr_d(x_d)}{dx_d} = 0 \qquad (2)$$

that states to maximize net energy the individual forages to the point where the marginal energy gained from a unit of consumption ($e_y - e$) equals the marginal energy lost to respiration ($dr_d(x_d)/dx_d$). If the second derivative of (1) is negative, then combining it with (2) provides sufficient conditions for a maximum. For specificity, a power functional form is used for variable respiration: $r_d(x_d) = \alpha_d x_d^{\eta}$ where α_d is a species specific constant. Thus, the second-order condition is for a maximum is:

$$\frac{\partial^2 R_d}{\partial x_d^2} = -\eta(\eta - 1)\alpha_d x_d^{(\eta-2)} < 0 \qquad (3)$$

To satisfy (3) the simplest form for the power function is used so $\eta = 2$. In this case condition (2) can be used to solve for the predator's consumption as a function of the energy expenditure:

$$x_d(e) = \frac{(e_y - e)}{(2\alpha_d)} \qquad (4)$$

Hence, $dx_d(e)/de < 0$ implying that the predator's consumption is negatively related to its energy expenditure. Expenditure e is central to the behavior in the model and it clearly must be nonnegative. Because e is determined by intra and inter species competitions as explained below, the following definitions will be useful:

> For the predator, a *competitive state* is said to prevail when $e > 0$, and a *noncompetitive state* is said to prevail when $e = 0$. Also, when $e = 0$ the predator is *satiated* and consumption is $e_y/(2\alpha_d)$ from (4).

Satiation occurs when the prey is essentially free to the predator, and the predator's consumption is at its maximum possible value. When satiated the predator does not consume more because the energy gain from addition consumption is outweighed by the energy loss to respiration.

Using the same variable respiration form for the prey, a representative member of the prey species is assumed to maximize net energy given by:

$$R_y = [e_0 - e^p]x_y - \alpha_y x_y^2 - \beta_y - e_y[1 + t(e)]g(x_y) \qquad (5)$$

The first term three terms on the right side of (5) carry the same meaning as for the predator in (1), except the prey is obtaining biomass and energy from whatever species it preys on. (If this is a plant, predation is on the sun and e_0 is the energy photosynthesized per unit of plant biomass.)

The fourth term is energy lost to the predator. (Of course, if an animal is captured and consumed by a predator, it is no longer available to study. For this reason, the predation should be thought of as the average loss over members of the prey species.) The e_y is the energy embodied in a unit of prey biomass that also appears in the predator's income term in (1). The function $g(x_y)$ is the quantity of biomass each prey individual is willing to supply to predators rather than not consuming its own prey. That is, in maximizing (5), the prey would prefer to supply zero biomass to the predator because outflows reduce net energy. However, the prey can supply zero biomass only if it demands zero biomass from its own prey in the sense that to capture its own prey, the prey is subjected to predation risk. Assuming the more the prey feeds on its own prey, the more it is exposed and the more biomass it supplies to predators, and assuming $g(x_y)$ is differentiable, then $dg(x_y)/dx_y > 0$.

The term t in (5) is additional energy expenditure by the prey. A prey individual loses energy to a predator equal to $e_y g(x_y)$ when it is attacked and captured. Also, regardless of whether or not it is captured, the prey loses energy to the atmosphere by avoiding or attempting to avoid attack. This energy lost to antipredator behavior is represented by t. Studies suggest that the antipredator loss is greater when the risk of capture is greater (Lima, 1998). If the risk is positively related to the energy that the predator spends to search for,

attack and handle the prey, then we can justify writing the function $t = t(e)$, and assuming differentiability, $dt(e)/de > 0$. The first and second-order sufficient conditions for a maximum of (5) are:

$$\frac{\partial R_y}{\partial x_y} = e_0 - e^p - 2\alpha_y x_y - e_y[1 + t(e)]\frac{dg(x_y)}{dx_y} = 0$$

$$\text{(6)}$$

$$\frac{\partial^2 R_y}{\partial x_y^2} = -2\alpha_y - e_y[1 + t(e)]\frac{d^2 g(x_y)}{dx_y^2} < 0 \qquad \text{(7)}$$

Whether (7) is satisfied depends on the form of the prey's biomass supply function. Again to obtain specific results, a power form is used so that $g(x_y) = \delta_y x_y^\mu$ where δ_y is a species specific constant. Tschirhart (2000) shows that in order for the predator to exhibit a positive functional response, it must be that $0 < \mu < 1$. Again the simplest form is used so $\mu = 1/2$. In this case, (7) becomes:

$$\frac{\partial^2 R_y}{\partial x_y^2} = -2\alpha_y + \frac{1}{4}e_y[1 + t(e)]\delta_y x_y^{-3/2} \qquad \text{(8)}$$

which is negative provided

$$x_y > \left\{\frac{e_y[1 + t(e)]\delta_y}{8\alpha_y}\right\}^{2/3} \qquad \text{(9)}$$

In numerous simulations using real data and species-specific parameters taken from the literature, (9) has been satisfied invariably.

Although a closed form solution for the prey's consumption cannot be obtained, the prey's biomass supply function, $g(x_y) = \delta_y x_y^{1/2}$, can be substituted into (6), and using the implicit function theorem and the second-order condition it is easy to show that the prey's supply is a function of both predator's and prey's energy expenditures:

$$\delta_y x_y(e^p, e)^{1/2} \qquad \text{(10)}$$

Moreover, comparative static analysis (Varian, 1992) shows:

$$\frac{\partial \delta_y x_y(e^p, e)^{1/2}}{\partial e} < 0 \quad \text{and} \quad \frac{\partial \delta_y x_y(e^p, e)^{1/2}}{\partial e^p} < 0 \qquad \text{(11)}$$

or the prey's consumption is negatively related to both its energy expenditure on its own prey and the

predator's energy expenditure. The intuition for the latter is that if the predator is expending more on capturing prey, then the prey is expending more to escape and is less willing to forage owing to predation risk. As a result the greater the predator's expenditure on capturing prey, the less willing is the prey to risk supplying biomass to the predator. This negatively sloped supply curve is a significant departure from economic models (Tschirhart, 2003).

The predators are engaging in intraspecific, interference competition for the prey, and the intensity of this competition determines the energy expenditure, e. The equilibrium value for the energy expenditure is a system-wide indicator of scarcity much the same as a monetary expenditure is in an economic market. The energy expenditure plays a role similar to the "food item edibility" in Parrot and Kok (2002) where predators consume prey according to its "delectability and distance."

The energy expenditure is determined by a biomass balance equation in which the sum of all predators' consumptions equals the sum of all preys' biomass supplies. Because all predators and prey in a species are assumed identical, then using (4) and (10) and letting N_d and N_y be the density of predators and prey, respectively, the biomass balance equation is:

$$N_d x_d(e) = N_y \delta_y x_y(e^p, e)^{1/2} \qquad \text{(12)}$$

To complete the CGE equations, there must be a biomass balance equation between the prey and its prey to determine the prey's energy expenditure, e^p, from its predation. Let N_{yy} be the population of the prey's prey species and write:

$$N_y x_y(e^p, e) = N_{yy} g(x_{yy}) \qquad \text{(13)}$$

N_{yy} and $g(x_{yy})$ are assumed to be fixed implying that the prey's available food source is constant. In modeling an entire ecosystem, this assumption can be relaxed and all species are predators, prey or both and no biomass resources are constant (Tschirhart, 2000, 2002).

The CGE calculations consist of solving the four Eqs. (2), (6), (12) and (13), for the four variables: e, e^p, x_y, and x_d. Equilibrium is defined as the state wherein each member of both the predator and prey species are processing energy efficiently by maximizing their net flows, and there is biomass balance between the
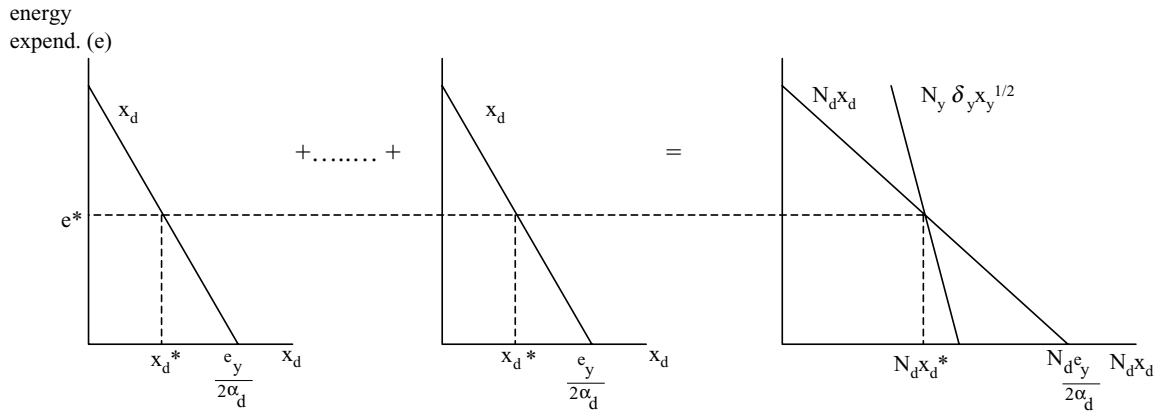
Fig. 1. Determining energy expenditure. The two leftmost graphs are representative predators' consumptions as functions of energy expenditure as given by (4) in the text. The predators takes e^* as a signal of the cost of a unit of prey and chooses quantity x_d^*. All identical predators do the same and their consumptions are summed to form the total consumption function in the rightmost graph. According to Eq. (12), the intersection of the total consumption function and the total biomass supply function given by (10) summed over all prey individuals determines the energy expenditure e^*. This is the sense in which e^* is determined by the actions of all predators and prey but is beyond the control of any one individual; that is, an individual is one of many and has a negligible effect on the total curves.

predator and prey and the prey and its prey. The population densities are fixed in each time period when the CGE is calculated, although they are updated between periods as shown below. The densities are important in determining the energy expenditures via (12) and (13) as shown in Fig. 1. The CGE calculations yield the consumptions and expenditures within any given period as functions of the parameters; that is,

$$e = e(N, \alpha, \beta, \delta_y), e^p = e^p(N, \alpha, \beta, \delta_y),$$
$$x_y = x_y(N, \alpha, \beta, \delta_y) \text{ and } x_d = x_d(N, \alpha, \beta, \delta_y) \quad (14)$$

where arguments are vectors: $N = (N_d, N_y, N_{yy})$, $\alpha = (\alpha_d, \alpha_y)$ and $\beta = (\beta_d, \beta_y)$.

3. Dynamic population adjustments

Densities change according to the success of the individuals in acquiring net energy. Referring to the predator's net energy in (1), the variable respiration term includes energy devoted to reproduction, and in steady state when populations are unchanging, the variable respiration is defined to include exactly that energy needed for the individual to reproduce itself once over its lifetime. Because net energy can also be used for reproduction, it follows that in steady state net

energy is zero. Therefore, if individuals in the species have positive (zero, negative) net energy in a CGE this period, there is more (the same, less) energy available for reproduction, and next period their population will increase (remain the same, decrease). When all individuals have zero net energy, a steady state is attained.

Using this reasoning, we can show that densities change according to discrete population update equations that follow from the individuals' objective functions. First, consider the predator. In steady-state it must be the case that births equals deaths in each time period, and if s_d is the lifespan of the representative predator, then the total number of births and deaths must be N_d/s_d. Dividing the totals by N_d yields the per capita steady-state natality and mortality rates:

$$\frac{1}{s_d} \quad (15)$$

The predator's maximum net energy in a period is given by $R_d(x_d(N, \alpha, \beta, \delta_y), e(N, \alpha, \beta, \delta_y)) = R_d(\cdot)$ which is obtained by substituting (14) into the predator's net energy objective function. In a steady state, $R_d(\cdot) = 0$. As explained above, by the definitions of the terms in (1), reproduction energy is contained in the variable respiration. Let $v_{d,ss}$ be the steady-state variable respiration and let $\rho v_{d,ss}$ be the proportion of this variable respiration devoted to

reproduction. Thus, in steady state the energy given by $\rho v_{d,ss}$ yields a per capita natality rate of $1/s_d$. Next, suppose the predator is not in steady state and that $R_d(\cdot) \neq 0$ and variable respiration is v_d. Assuming that the proportion of $R_d(\cdot)$ that is available for reproduction is the same as the proportion of variable respiration available for reproduction, the energy now available for reproduction is $\rho[R_d(\cdot) + v_d]$. Finally, assuming that reproduction is linear in available energy, then it follows that if $\rho v_{d,ss}$ yields a per capita natality rate $1/s_d$, then $\rho[R_d(\cdot) + v_d]$ yields a per capita natality rate of:

$$\left(\frac{1}{s_d}\right) \frac{[R_d(\cdot) + v_d]}{v_{d,ss}} \tag{16}$$

The change in density is obtained by multiplying the current period's density by the difference between the natality and mortality rates, where the latter rate is assumed independent of energy available for reproduction. Therefore, using (16), the density adjustment equation is:

$$
\begin{aligned}
N_d^{t+1} &= N_d^t + N_d^t \left[\frac{1}{s_d} \frac{R_d(\cdot) + v_d}{v_{d,ss}} - \frac{1}{s_d}\right] \\
&= N_d^t + N_d^t \frac{1}{s_d} \left[\frac{R_d(\cdot) + v_d}{v_{d,ss}} - 1\right]
\end{aligned} \tag{17}
$$

Expression (17) reduces to the steady state if $R_d(\cdot) = 0$ (in which case $v_d = v_{d,ss}$), because the bracketed term is zero. Alternatively, $R_d(\cdot) > (<)0$ implies that $v_d > (<)v_{d,ss}$, in which case density increases (decreases).

For the prey species, in steady state the births must equal deaths *plus* any individuals lost to predation. The mortality rate is $m = (1 - P(s_y))/s_y$ where $P(s_y)$ is the predation in each period for an individual that lives s_y periods. Mortality can be written:

$$
\begin{aligned}
1 - P(s) &= 1 - p - p(1 - p) - p(1 - p)^2 \\
&\quad - p(1 - p)^3 - \cdots - p(1 - p)^{s-1}
\end{aligned} \tag{18}
$$

where each period p is the percentage of the prey taken from what is remaining of the prey from previous periods. Therefore, summing (18), the mortality rate is $m = (1 - p)^{s_y}/s_y$. In steady state, the natality rate equals the mortality rate plus the predation rate, so the

natality rate is $m + p$ or

$$\frac{p + (1 - p)^{s_y}}{s_y} \tag{19}$$

Using (19) instead of (15) as the steady-state natality rate, the density update equation becomes

$$N_y^{t+1} = N_y^t + N_y^t \left[p + \frac{(1 - p)^{s_y}}{s_y}\right] \left[\frac{R_y(\cdot) + v_y}{v_{y,ss}} - 1\right] \tag{20}$$

When the representative prey solves (5) for x_y, then $\delta_y x_y^{1/2}$ is the optimum amount of biomass supplied by a representative individual prey in each period. Therefore, $p = \delta_y x_y^{1/2}/w_y$ is the predation rate on this prey where w_y is the prey weight so that p is in percent of an individual.

There are no fixed parameters in the update equations other than the lifespans. Update Eqs. (17) and (20) show that population changes are linked to foraging behavior through the individuals' objective functions. Moreover, in non steady state, the terms in (17) and (20) (i.e., $R_i(\cdot)$, v_y and p) will change period to period depending on the consumptions and supplies of the predator and prey species. Changing values of $R_i(\cdot)$, v_y and p are sometimes referred to as environmental noise. Models that concentrate on a single species account for environmental noise by adding a random number to birth rates (Stephan and Wissel, 1999). The general equilibrium approach used here replaces the random variable with terms that are determined within the model.

The predator–prey adaptive system creates forces that move individuals from positive or negative net energy to zero net energy and to a steady state. For example, suppose the system is not in steady state and individuals in the prey species have positive net energy in period one so that their density increases in period two via (20). This increase lowers the predators' energy expenditures for consuming the prey, because the prey is more abundant. Therefore, predators' consumptions increase by (4), the prey supplies of biomass to the predators increase, and prey' net energies decrease which places downward pressure on prey density in period three via (20). In addition, in period two the energy expenditure incurred by prey for consuming their own prey increases as there is more intraspecific competition for their own prey when

their density increases in period two. This movement of energy expenditure also reduces the prey net energy as they demand less of their own prey and this too places downward pressure on density in period three via (20). (If the prey species begins with negative net energy in period one, the energy expenditures move in the opposite directions, and again the species moves toward zero net energy and a steady state.)

4. Functional and numerical responses

Functional response of the predator is determined by individual behaviors of both predator and prey, and behaviors underpinning Holling type I, II and III responses have been documented. Type I, II and III responses imply that the number of prey taken per predator is linear in prey density, is increasing at a decreasing rate in prey density, or is increasing at an increasing then decreasing rate in prey density, respectively. The usual approach in predator–prey models is to assume a priori one of the three types of responses; however, an a priori assumption can be restrictive if the behaviors can change owing to interactions between or changes in the populations.

The CGE approach determines consumptions and densities of both the predator and the prey; therefore, tracking functional responses is first a matter of deciding what is the appropriate response to track. Four cases are identified here. Functional response refers to the short-term consumption response of the predator to varying prey densities so it is appropriate to fix the predator density (Murdoch and Oaten, 1975). But fixing the predator density can be done with or without fixing the prey consumption. Case (i) is defined as having the prey consumption (x_y) fixed. Case (ii) is defined as having the prey consumption vary in such a way that total prey consumption is fixed; that is, $N_y x_y$ is fixed. Studies that do not account for prey consumption do not specify whether case (i) or case (ii) is being analyzed. Case (ii) may come closer to an appropriate measure for functional response than case (i) if the important measure is the biomass available to the predator. In case (i) the number of prey is the measure of availability, regardless of how available the prey is to the predator. In case (ii) the measure of availability is the product of the number of prey and their consumption; and because prey consumption accounts for the prey's predation risk, it is providing a proxy for how exposed the prey are to the predator.

If numerical response is of interest, then obviously the predator density must be allowed to change; but the functional response can be measured after the predator density is allowed to change over one or few periods versus change until a steady state is reached. Again, both possibilities are considered in cases (iii) and (iv), respectively. The numerical responses addressed here are due to reproduction only, immigration and emigration are not considered, although multiple patches would be an interesting extension of the CGE approach.

The predators' total consumptions in each period are given by the left side of (12). If the within period equilibrium values for consumption from (14) are substituted into (12) and then (12) is solved for predator consumption, the functional response is given by the identity:

$$x_d(N) \equiv \frac{N_y}{N_d} \delta_y x_y(N)^{1/2} \tag{21}$$

where only the vector of densities are shown in the consumption functions and other parameter arguments are suppressed. The Holling type response of the predator is determined by the signs of $\partial x_d / \partial N_y$ and $\partial^2 x_d / \partial N_y^2$. For case (i), the predator density and the prey consumption are held constant at $\bar{N}_d$ and $\bar{x}_y$, respectively, so that $x_d(N)$ is linear in N_y and

$$\frac{\partial x_d}{\partial N_y} = \frac{\delta_y}{\bar{N}_d} \bar{x}_y^{1/2} \quad \text{and} \quad \frac{\partial^2 x_d}{\partial N_y^2} = 0 \tag{22}$$

Thus, case (i) yields a type I functional response, provided the predator is unsatiated. If the prey density is large enough, the predator expenditure will be zero and a non-competitive state exists in which case the predator is satiated, $\partial x_d / \partial N_y = 0$, and a flat functional response attained.

For case (ii), $x_y(N)$ is not constant so that from (21):

$$\frac{\partial x_d}{\partial N_y} = \frac{\delta_y}{\bar{N}_d} \left[N_y \frac{x_y^{-1/2}}{2} \frac{\partial x_y}{\partial N_y} + x_y^{1/2} \right] \tag{23}$$

Because total prey biomass consumed is constant in case (ii), write:

$$N_y x_y(N_y) \equiv k \tag{24}$$

and differentiating yields

$$\frac{\partial x_y}{\partial N_y} = -\frac{x_y}{N_y} \tag{25}$$

Substituting (25) into (23) and using (24) gives:

$$\frac{\partial x_d}{\partial N_y} = \frac{\delta_y}{\bar{N}_d} \frac{x_y^{1/2}}{2} = \frac{\delta_y k^{1/2}}{2\bar{N}_d} N^{y(-1/2)} > 0 \tag{26}$$

and

$$\frac{\partial^2 x^d}{\partial N_y^2} = -\frac{\delta_y k^{1/2}}{4\bar{N}_d} N_y^{-3/2} < 0 \tag{27}$$

Taken together (26) and (27) imply that x_d is strictly concave in N_y which implies a type II functional response. Again, saturation is attained when the prey density becomes large enough to drive the predator expenditure to zero.

In optimal foraging models, a type II response most often results from a fixed handling time (Jeschke et al., 2002). Since handling time is not separated out here from searching, attacking, digesting and so on, there must be another explanation for the type II response. Consider that stability in this model depends on how energy expenditures respond to population changes, because changes in energy expenditures change net energies, and reproduction depends on the net energies. Thus, if the predator population increases then the predators' expenditure on prey ought to increase owing to intraspecific competition, and the preys' energy loss ought to increase owing to more predation risk (in addition to increased energy loss accompanying the increased biomass loss). These expected relationships between populations and expenditures are what provide expected, and stable, population dynamics. As indicated above, $0 < \mu < 1$ is necessary to obtain the expected relationships. A $\mu < 1$ (it is 1/2 in (21)) drives the strictly concave shape of the functional response. Thus, the type II functional response can be traced to intraspecific competition and predation risk. This result is consistent with Sih (1984) who examines how risk impacts feeding behavior, and with recent evidence showing that risk predation yields a type II response in the field (Abramsky et al., 2002).

For cases (iii) and (iv), both predator density and prey consumption are allowed to vary. The difference is that for case (iii) the predator density is allowed to adjust over one or a few reproductive cycles, whereas

in case (iv) the predator density adjusts to a steady state. No analytical results can be obtained for case (iii), because the system is in transition. For case (iv), a steady state implies that net energy for the predator is zero. Therefore, setting (1) to zero, using (2), and recalling that $r_d(x_d) = \alpha_d x_d^2$, the steady-state expenditure and consumption of the predator are:

$$e = e_y - 2\sqrt{\alpha_d \beta_d} \quad \text{and} \quad x_d = \left(\frac{\beta_d}{\alpha_d}\right)^{1/2} \tag{28}$$

Thus, if the predator population is allowed to adjust to its steady state, the functional response of the predator is constant and independent of the prey density. The independence can be explained as follows. Suppose from the steady state the prey density increases. Initially the predators are better off because their expenditure on prey decreases and they each consume more. But this means greater net energy for each predator, that in turn leads to increased predator density and greater predator competition that causes their expenditures to rise. Eventually, rising expenditures reduce consumptions, and predator net energies and densities fall until consumption and expenditure return to their initial levels, net energies return to zero, and predator density stabilizes. The predator population, by increasing its numbers, competed away the advantage of a larger prey density.

There will be a numerical response in case (iv) that can be obtained by rewriting (21) as:

$$N_d \equiv \frac{N_y}{x_{d,ss}} \delta_y x_y(N)^{1/2} \tag{29}$$

where $x_{d,ss}$ is the steady-state value of predator consumption that does not vary with N_y. Following the same procedure used to obtain (26) and (27), we can obtain from (29):

$$\frac{\partial N_d}{\partial N_y} = \frac{\delta_y k^{1/2}}{2x_{d,ss}} N_y^{-1/2} > 0 \tag{30}$$

and

$$\frac{\partial^2 N_d}{\partial N_y^2} = -\frac{\delta_y k^{1/2}}{4x_{d,ss}} N_y^{-3/2} < 0 \tag{31}$$

The predator's numerical response, when its population is allowed to attain a steady state for each prey density, is a strictly concave function of the prey density. This implies a numerical response curve shaped like a type II functional response.

5. Switching behavior

To examine predator-switching behavior, a second prey is introduced. Following (1) and (5), the net energies for representative members of the predator and two prey species are:

$$R_d = [e_{y1} - e^1]x_{d1} + [e_{y2} - e^2]x_{d2} - \alpha_d[x_{d1} + x_{d2}]$$
$$- 0.5\alpha_d[x_{d1}x_{d2} + x_{d1}^2 + x_{d2}^2] - \beta_d \qquad (1')$$

$$R_{y1} = [e_{01} - e^{p1}]x_{y1} - \alpha_{y1}x_{y1}^2 - \beta_{y1}$$
$$- e_{y1}[1 + t(e^1)]x_{y1}^{1/2} \qquad (5')$$

$$R_{y2} = [e_{02} - e^{p2}]x_{y2} - \alpha_{y2}x_{y2}^2 - \beta_{y2}$$
$$- e_{y2}[1 + t(e^2)]x_{y2}^{1/2} \qquad (32)$$

where numbers 1 and 2 have been added to subscripts d and y and superscript p to distinguish prey one from prey two. The functional form for the variable respiration of the predator given by third and fourth terms in (1') is important, because the degree of switching will depend on it. The quadratic form used here is reasonably general and allows the predator to specialize in consuming one species only, or to substitute between the two prey in a continuous fashion, which is more likely (Baalen et al., 2001). The functional form also can be estimated given enough consumption data.

The predator–prey biomass balance equations become:

$$N_d x_{di}(e_i) = N_{yi}\delta_{yi}x_{yi}(e^{pi}, e_i)^{1/2}, \quad i = 1, 2 \qquad (33)$$

The biomass balance equations between prey one and its prey, and between prey two and its prey are given as:

$$N_{y1}x_{y1}(e^{p1}, e_1) = N_{y,y1}g(x_{y,y1}) \qquad (13')$$

$$N_{y2}x_{y2}(e^{p2}, e_2) = N_{y,y2}g(x_{y,y2}) \qquad (34)$$

The predator chooses x_d^1 and x_d^2 to maximize (1'). To allow for the possibility that the predator specializes in only one prey species, Kuhn–Tucker optimality conditions with respect to the ith prey, $i = 1, 2$, $i \neq j$,

are:

$$\frac{\partial R_d}{\partial x_{di}} = e_{yi} - e^i - \alpha_d - 0.5\alpha_d[x_{dj} + 2x_{di}] \leq 0$$
$$x_{di}\frac{\partial R_d}{\partial x_{di}} = 0 \qquad \text{and} \qquad x_{di} \geq 0 \qquad (35)$$

Together, these three conditions imply that if the predator consumes the ith prey so that $x_{di} > 0$, then the marginal energy gained per biomass unit consumed (e_{yi}) equals the sum of marginal energy loses to locating, attacking and handling (e^i) and to marginal respiration. Alternatively, if the marginal energy gained is less than the sum of the energy losses, the ith prey is not consumed because it does not provide the predator with at least as much energy as it costs (Stephens and Krebs, 1986). If both prey types are consumed, then the marginal gain/marginal loss ratios are equal across the prey species:

$$\frac{e_{y1}}{e^1 + \alpha_d + 0.5\alpha_d[x_{d2} + 2x_{d1}]}$$
$$= \frac{e_{y2}}{e^2 + \alpha_d + 0.5\alpha_d[x_{d1} + 2x_{d2}]} \qquad (36)$$

Because the ratios in (36) depend on the energy expenditures, e^i and e^j, their magnitudes change with changing densities in which case the predator may exhibit switching behavior by consuming more of one prey and less of the other.

If both prey are consumed in positive quantities, then the two derivatives in (35) can be used to solve for the predator's consumptions as functions of the energy expenditures:

$$x_{d1} = \frac{[1 + \alpha_d][e_{y1} - e^1] - 0.5\alpha_d[e_{y2} - e^2]}{1 + 1.75\alpha_d + \alpha_d^2},$$
$$x_{d2} = \frac{[1 + \alpha_d][e_{y2} - e^2] - 0.5\alpha_d[e_{y1} - e^1]}{1 + 1.75\alpha_d + \alpha_d^2} \qquad (37)$$

The consumption of either prey item depends on the energy expenditures on both prey. As expected, the consumption of the ith prey is negatively related to the expenditure on the ith prey; however, the consumption of the ith prey is positively related to the expenditure on the jth prey. The magnitude of the terms in (37) indicate that the negative affects are more important than the positive affects for equal expenditure changes.

If the prey densities are held constant, then steady-state values for predator density and consumptions and expenditures for the prey can be obtained by solving five equations that include (33), (1′) set to zero, and the first derivatives of (1′) with respect to the consumptions set to zero. For $i, j = 1, 2, i \neq j$ these steady-state values are:

$$x_{di} = \frac{(2\beta_d/\alpha_d)^{1/2} N_{yi} x_{yi}}{\sqrt{(N_{y1}x_{y1})^2 + N_{y1}x_{y1}N_{y2}x_{y2} + (N_{y2}x_{y2})^2}}$$

$$e^i = e_{yi} - \alpha_d$$

$$- \frac{\sqrt{\beta_d/\alpha_d} \left\lfloor N_{yi}x_{yi}\sqrt{2} + N_{yi}x_{yi}\sqrt{0.5} \right\rfloor}{\sqrt{(N_{y1}x_{y1})^2 + N_{y1}x_{y1}N_{y2}x_{y2} + (N_{y2}x_{y2})^2}}$$

$$N_d = \sqrt{2\left(\frac{\alpha_d}{\beta_d}\right)\left[(N_{y1}x_{y1})^2 + N_{y1}x_{y1}N_{y2}x_{y2} + (N_{y2}x_{y2})^2\right]} \qquad (38)$$

In the one-prey model the consumption and expenditure were independent of the prey densities in steady state, but this result does not hold with two prey species. As with one prey, in steady state the predator is earning zero net energy at some combination of consumptions and expenditures. If a prey density increases, the predator population still competes away the advantage of that larger prey density through reproduction that drives up their expenditures. But with two prey there are infinitely many combinations of consumptions and expenditures that the system can move to that will yield zero net energy for the predators. The combination realized depends on the prey densities. From (38), the predator's consumption of the jth prey increases (decreases) with permanent increases in the density of the jth (ith) prey.

6. Simulations

Initially, Steller sea lions (*Eumetopias jubatus*) and killer whales (*Orcinus orca*) in the Eastern Bering Sea are the predator and prey, respectively, although walleye pollock (*Theragra chalcogramma*) are also included as prey for the sea lions. The pollock are a groundfish that support one of the largest fisheries in the world. To examine killer whale switching behavior, sea otters (*Enhydra lutris*) also are introduced as

an alternative prey for the killer whales, as well as sea urchins (*Strongylocentrotus* sp.) as prey for the otter.

The killer whale and Steller sea lion objective functions are given by (1) and (5). Parameters in (1) and (5) were either gathered from published sources or estimated by calibration using population and consumption data. Resting metabolic rates (β terms), embodied energies (e^i terms) and weights are the parameters available in published sources. Table 1 lists the data used to construct the parameters. (For details on the data sources, see Finnoff and Tschirhart, 2003.) Unlike standard population models in which estimated parameters represent aggregated behavior (Hassell et al., 1976), the parameters gathered or calibrated here are for individuals. Individual parameters are more readily interpretable, easier to obtain and avoid some of the problems inherent in fitting discrete population models (Morris, 1990).

To obtain the variable respirations (α terms) and the biomass balance parameters (δ terms), data on populations and biomass consumptions for pollock, sea lions and killer whales are needed. Consider the sea lions as an example of gathering the data. Steller sea lions are an endangered species, and current and historical population estimates are readily available. For easier computer computations, all species' populations were converted to population units, and then divided by the square kilometers of surface area of the EBS (1,300,000) to obtain the population units per square kilometer. The biomass consumption of sea lions was taken from experiments in which the daily caloric requirement of sea lions was measured (Rosen and Trites, 2000). The caloric value was converted to a biomass flow by dividing it by the number of calories embodied in a kilogram of pollock. A complication arises because in the wild sea lions are known to eat octopus and squid and other fish species besides pollock. Because only pollock are in the model, only the sea lion intake of pollock was reflected in their biomass consumption. Using studies (SAFE, 2000, Appendix D) that estimate 76% of the sea lion diet in the wild is fish, of which 60% is pollock, yields the result of $2663 \, \text{kg year}^{-1}$ of pollock.

One way to calibrate the model, and the approach taken here, is to assume the data is from a time period in which the system was in a steady state. In 1966 the Steller sea lion population had not yet begun its precipitous decline that has marked recent decades,

Table 1
Initial variables and parameters

	Pollock	Steller sea lion	Killer whale	Sea otter	Urchin
Populations (N_i)	(i) 6.16215 units km^{-2}; 1 unit = 1000 individuals	(ii) 0.096154 km^{-2}; 1 unit = 1 individuals	(iii) 0.007723 units km^{-2}; 1 unit = 0.1 individuals	(iv) 0.050631 units km^{-2}; 1 unit = 100 individuals	(v) 10.7692 units km^{-2}; 1 unit = 1×10^7 individuals
Biomass flow (x_{ij})	(vi) 7440 kg unit^{-1} year^{-1}	(vii) 2663 kg year^{-1}	(viii) 486.6 kg unit^{-1} year^{-1} (Steller) 28.3 kg unit^{-1} year^{-1} (otter)	(ix) 255500 kg unit^{-1} year^{-1}	(x) 330000 kg unit^{-1} year^{-1}
Embodied energy (e_i) (kcal kg^{-1})	(xi) 1128	(xii) 2000	(xiii) NA	(xiv) 1810	(xv) 717
Resting metabolic rate (β_i)	(xvi) 1247688 kcal unit^{-1} year^{-1}	(xvii) 731326 kcal year^{-1}	(xviii) 130356 kcal unit^{-1} year^{-1}	(xix) 32193000 kcal unit^{-1} year^{-1}	(xx) 67732500 kcal unit^{-1} year^{-1}
Weight (w_i)	(xxi) 1000 kg unit^{-1}	(xxii) 250 kg	(xxiii) 399.6 kg unit^{-1}	(xxiv) 2800 kg unit^{-1}	(xxv) 87600 kg unit^{-1}
Predation (δ_{ij})	0.274052	2.67741	NA	0.021365	20.4214
Variable respiration (α_i) (kcal year^{-1})	0.019220	0.234413	0.548144	4.9318×10^{-4}	0.101000

and the pollock commercial fishery was small relative to the latter 1970s and beyond; therefore, the system was assumed to be in a steady state in 1966. This seems reasonable because the sea lion and pollock populations were not changing significantly, and for the killer whales there is little else that can be said owing to scant data.

The sea lions', killer whales' and pollocks' 1966 consumptions and densities were substituted into (12) to obtain the biomass balance parameters, δ_y. The variable respiration parameters, α, for sea lions and killer whales were obtained by substituting the 1966 densities and consumptions, along with the resting metabolic rates and embodied energies, into expressions (1) and (5) set to zero and into first-order conditions (2) and (6), and solving for the α terms and the energy expenditures. Setting (1) and (3) to zero implies that the system was in steady state. (Assuming a steady state is not necessary for calibration. For example, if the sea lion population was falling from 1966 to 1967, then net energy, or (5), would be set to a negative number that would yield an R_y that, when substituted into the population update equation, (20), accounts for the fall.)

Running the simulations comprises two steps: first, for the CGE calculations, start with initial densities for the two species and use the two first-order conditions ((2) and (6)) and the two balance Eqs. (12) and (13) to solve for the two consumptions (x_d and x_y) and two expenditures (e and e^p). In the second step, substitute the consumptions and expenditures into the net energy objective functions ((1) and (5)) to obtain the optimum net energies, and use these net energies to adjust the densities according to (17) for killer whales and (20) for the sea lions. Then return to step one with the new densities. Each set of two steps comprises a 1 year time period. If the densities converge over time, because the net energies move to zero, then a steady state is obtained. If the initial densities are (are not) steady-state densities, then the adjustments in the second step are (are not) zero.

6.1. Results 1—populations and lifespans

Initially only the one prey model is simulated so there are no sea otter or sea urchin until Results 5 below. The steady-state consumptions and densities are listed in Table 1. In the first simulation the initial den-

sity of the sea lions (killer whales) was shocked by 20% below (above) its steady state value, and then steps one and two were repeated until the system returned to steady state. This is shown in panel (a) of Fig. 2. Convergence was smooth and required about 20 years to return to steady state, although most of the convergence took place in the first 10 years.

Predator–prey dynamics often exhibit oscillations in the laboratory and field, and in familiar Lotka–Volterra models oscillations depend on the values of the fixed, aggregated parameters that describe the population interactions. In difference Eqs. (17) and (20) the lifespans of the predator and prey are the only fixed parameters outside the CGE equations. Short lifespans are more typical in species of smaller individuals with rapid reproduction that are likely to exhibit more oscillatory behavior. To demonstrate, the same simulation was rerun with lifespans halved and again with lifespans cut by 95%. The results are shown in panels (b) and (c) of Fig. 2. The halved lifetimes yield damped oscillations, and the severely reduced lifespans yield chaotic oscillations.

6.2. Results 2—the role of competition

A second simulation illustrates the importance of competition in the model, and shows in accordance with (28) that a predator's steady-state consumption and expenditure are independent of prey densities. With the data in Table 1 there are two predator–prey relationships that can be used to demonstrate competitive affects: killer whale/sea lion and sea lion/pollock. For variety, the latter will be used in this simulation.

The results are shown in Fig. 3 in which the sea lion density, consumption of pollock, energy expenditure on pollock and the pollock density are tracked for 31 years. Initially all values are set to their steady state levels and this is maintained for the first 4 years as shown by the horizontal lines. In year 5 the pollock density is shocked upward and held there for the duration of the simulation. Greater pollock resources cause the sea lion expenditure on pollock to fall as there is less intra species competition among the sea lions. In this example, the expenditure falls all the way to zero indicating a noncompetitive state is attained. The sea lions respond to the lower expenditures by increasing consumption according to (11), and with expenditure at zero the sea lions reach satiation. For the next 10
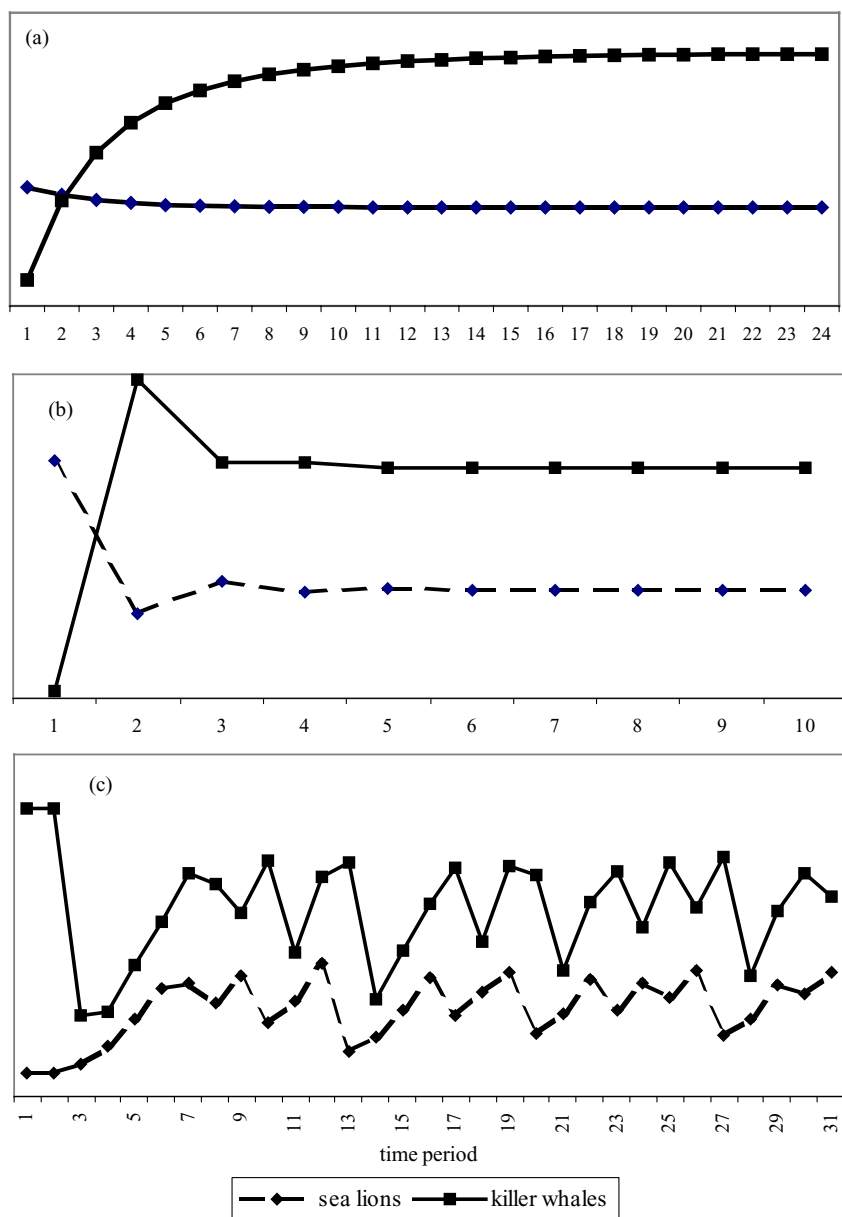
Fig. 2. Densities and lifespans post shock. Panel (a) shows the convergence of sea lion and killer whale densities to their steady-state levels following initial 20% shocks to the steady-state levels. Panel (b) and (c) are similar except that the average lifetime of both species are reduced by 50 and 95%, respectively. Densities are rescaled to fit on the same graph.

years the expenditures remain at zero and the consumptions remains at satiation. The greater consumption and lower expenditure increases each sea lion's net energy above the steady state value of zero, and with more energy available for reproduction the sea

lion density increases by (20). As long as the sea lion expenditure is zero, they continue to earn positive net energy and their population grows. Around year 14, however, the sea lion density becomes so large that intra species competition resumes which begins to drive
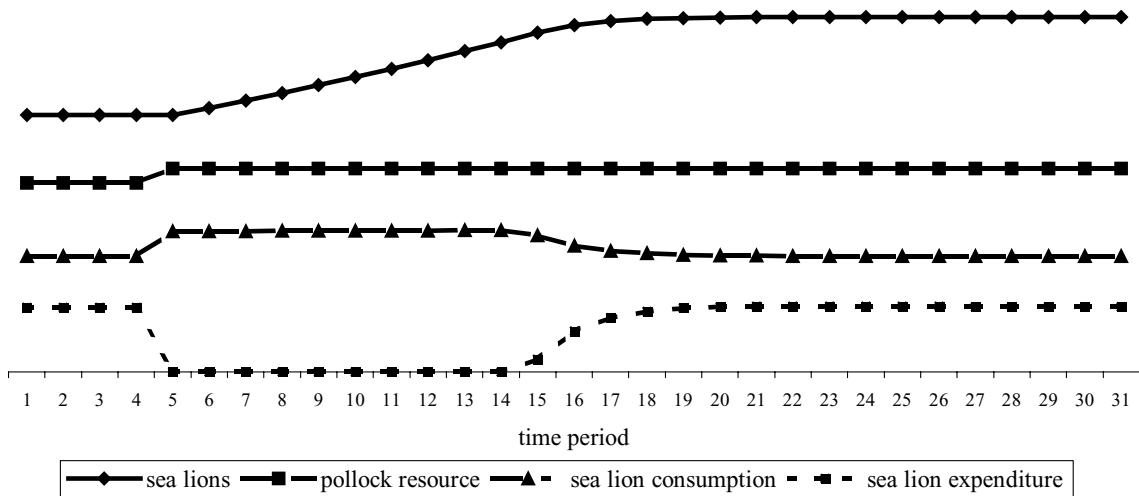
Fig. 3. Consumption and expenditure. A one time permanent increase in the sea lions' prey (pollock) leads to both an initial lower sea lion expenditure on pollock and an increase in consumption. But as the sea lions' numerical response leads to permanent increase in density, their expenditure and consumption return to the original levels owing to competition over the greater pollock density.

the expenditure above zero. The greater expenditure causes consumption to start decreasing, and both variables continue these trends for about 6 years until they return to their steady-state levels. At that time the sea lion net energies return to zero and the density levels off to a new steady state that reflects the permanent increase in pollock. Essentially, the sea lions enjoyed the benefit of more pollock, but in competing for that benefit their functional response led to a numerical response that increased the sea lion density until the benefit to the individual completely dissipated.

The forces that drive the sea lions to zero net energy are fundamental to competition. Eqs. (2), (6), (12) and (13), along with the difference Eqs. (17) and (20), generate these forces in the model. During the first 4 years in Fig. 3 the first four equations are active in each year's calculations. However, when the pollock resource is increased via (19) and the sea lion expenditure on pollock drops to zero in the noncompetitive state, the sea lion consumption of pollock is less than what the pollock are willing to supply. Thus, the left side of (13) is less than the right side, and this equation is eliminated from the yearly calculations. Eqs. (2), (6) and (12) are used to determine e, x_y and x_d while $e^p = 0$. When the sea lion population begins to increase via (20) and e^p turns positive, all four equations are used again to determine e, x_y, x_d and e^p in each year. The sequence of events is also shown in Fig. 4

using individual and aggregate sea lion consumption curves and an aggregate pollock supply curve.

6.3. Results 3—varying pollock resources

The killer whale and sea lion populations are limited by the fixed amount of pollock biomass resource available to the prey. To illustrate the dependency of both predator and prey densities on the pollock biomass, a simulation was run wherein the sea lion and killer whale start at steady state densities in 1970, and then are allowed to adjust to an arbitrarily changing pollock density up through year 2000. The results shown in panel (a) of Fig. 5 show changes in the sea lion density following the changes in the pollock density, and the changes in the killer whale density following the changes in the sea lion density, both with lags from 1 to 6 years.

A second simulation was run wherein the pollock population was forced to follow the actual estimated populations for the years 1970–2000 (Witherell, 2000). As shown in panel (b), the sea lion and killer whale densities follow the pollock density with lags when the pollock experienced a 7-year downturn after 1973. The pollock experienced a heavy recruitment year in 1981 after which the population went through a series of oscillations, perhaps due in part to commercial fishing, although it never returned to
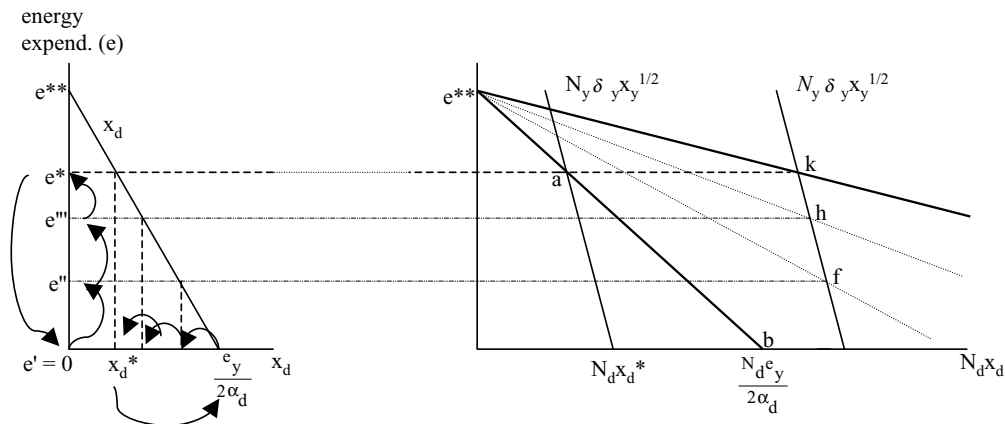
Fig. 4. Steady-state consumption independent of prey density. The left graph is for a representative sea lion, the right graph is all sea lions and all pollock. Initially the sea lions are in steady state with the energy expenditure by sea lions at e^* and the consumption of each individual at x_d^*. The energy expenditure is determined by the intersection of the total consumption and total supply curves at point a. There is a permanent increase in the pollock which moves the supply curve rightward from $N_y \delta_y x_y^{1/2}$ to $N_y \delta_y x_y^{1/2}$. Expenditure drops to zero at point b, because the new total supply curve exceeds the initial total consumption curve at all positive expenditures. Sea lions now earn positive net energy and the population increases which pivots the total consumption curve about point e^{**} as new individual consumption curves are added to the initial curve, $e^{**}b$. It eventually begins to intersect the new total supply curve moving through points f, h and finally k, each intersection yielding a greater expenditure. When it returns to k, steady state is restored because sea lions earn zero net energy and their population ceases to grow. To the individual sea lion the whole process appears as a shifting energy price for which it changes its maximum consumptions indicated by the arrows in the left graph.

the lower densities of the 1970s. The sea lions and killer whale densities increased with a lag following the heavy recruitment year of the pollock; however, neither density experienced the oscillations.

The lack of oscillations for the sea lions and killer whales is related to the intra-species sea lion competition for pollock. After the heavy recruitment year in 1981, sea lion competition for pollock was reduced to the noncompetitive state where the sea lion energy expenditures on pollock were zero. The zero expenditure continued through year 2000. Consequently, as explained above, the sea lions enjoyed positive net energy every year following 1981 and their population grew uninterrupted. That the pollock population went through oscillations did not matter as long as it remained large enough to hold the sea lion energy expenditure at zero.

In actuality, Steller sea lion populations continued their decline after 1981 despite the greater pollock numbers. The causes of the decline are not fully understood, but several hypotheses have emerged (SEIS, 2001). Prior to 1990 possible factors contributing to the decline included commercial harvesting, entanglement in fishing gear, subsistence hunting, inten-

tional shooting, and nutritional stress owing to the decline of Pacific herring that are an energy rich prey species. Since 1990 possible factors contributing to the continued decline include nutritional stress owing to commercial harvesting of prey species, particularly pollock, increased predation by killer whales, and a climate regime shift causing warmer ocean temperatures. These factors are beyond the scope of the predator prey model developed here, although they could be incorporated into the CGE approach.

6.4. Results 4—functional and numerical responses

Simulations were run for the four cases of functional and numerical responses described above. For a single prey, starting in each case with a steady-state sea lion density of $N_4 = 0.2$, the sea lion density was changed in increments in the interval $0.05 < N_4 < 5.0$ while the killer whales consumption and density were tracked. Fig. 6 displays the killer whale functional (top panel) and numerical responses (bottom panel) that are labeled for the four cases. Roughly, there is a negative relation between the two responses: the more
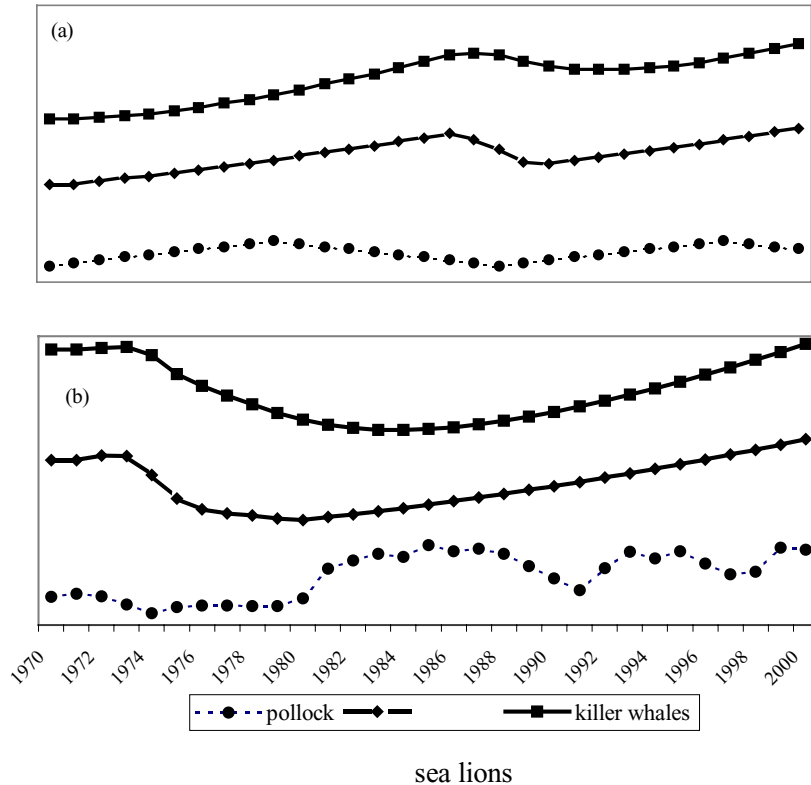
Fig. 5. Varying resource. Killer whale and sea lion densities are responding in a lagged fashion to changes in the pollock density. Panel (a) shows smooth artificial changes in pollock, and panel (b) shows actual estimates of pollock densities.

the killer whale density is allowed to adjust to yield a larger numerical response, the less is the functional response. This is a result of the additional competition that ensues when the killer whale density increases. Case (iv) is the extreme where the killer whale density is allowed to attain a steady state for each new sea lion density, and the result harkens back to Fig. 3. That is, the killer whales increase in population until all the advantage of a larger sea lion population is competed away and each whale consumes the same as they did before the sea lion population increased.

For case (i) the killer whales exhibit a type I response until saturation, and in case (ii) the killer whales exhibit type II response until saturation. Because sea lion consumption is held fixed in case (i), as the sea lion density increases the total biomass available to the whale increases linearly and whale consumption follows suit by (22). That type I response may be unrealistic for killer whales and sea lions is a reflection of increasing the sea lion density

without changing the sea lion consumption which is also unrealistic. As sea lion numbers increase, given a fixed amount of fish resource, the consumption per sea lion ought to decrease. This decrease is allowed to occur in case (ii). Although type II responses is intuitively appealing, in many models it can be desta-bilizing (Murdoch and Oaten, 1975). Here type II re-sponse is consistent with stability. Basset et al. (1997) also find type II response stabilizing, although the source of stability involved predators (grazers) that overharvested one patch before moving to another.

6.5. Results 5—two prey and switching behavior

Fig. 7 shows the results of a simulation in which the pollock resource was varied based on actual es-timates of pollock as done above in Results 3. The killer whale consumptions and expenditures for sea li-ons and sea otter are displayed for 31 years. Regard-ing the sea lions, the expenditures on them initially

one killer whale annual
consumption in numbers
of sea lions

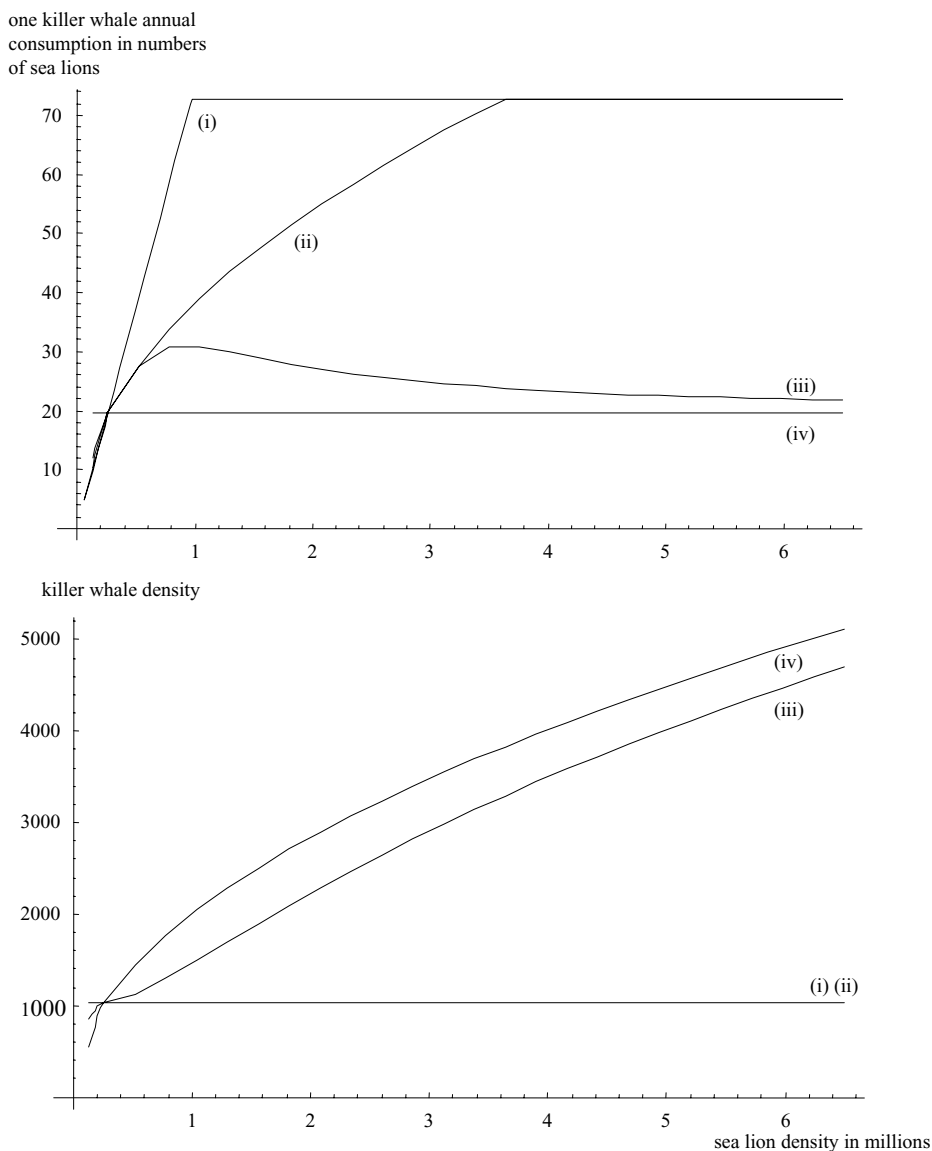killer whale density

sea lion density in millions

Fig. 6. Functional and numerical responses. There is a tradeoff between the functional and numerical responses. The greatest functional response (curve (i)) occurs within periods (intragenerational) when there is no numerical response. When there is a numerical response (intergenerational), the functional response is smaller (case (iii)) or possibly zero (case (iv)).

went up in response to a fall in the sea lion population, but after about 5 years as the sea lion population slowly increases over time (Fig. 5), the expenditure on them slowly decreases, and the representative killer whale slowly consumes more. This behavior where the predator responds to the expenditure on a prey item is in keeping with (37).

Regarding the sea otter, the trend appears counter-intuitive, but it also is in keeping with (37). The ot-ter experienced a small but sharp fall in density (not shown) around period five after which there was a small but steady increase in density for the remaining periods. The expenditures tracked this trend inversely in Fig. 7, with expenditures initially rising sharply but
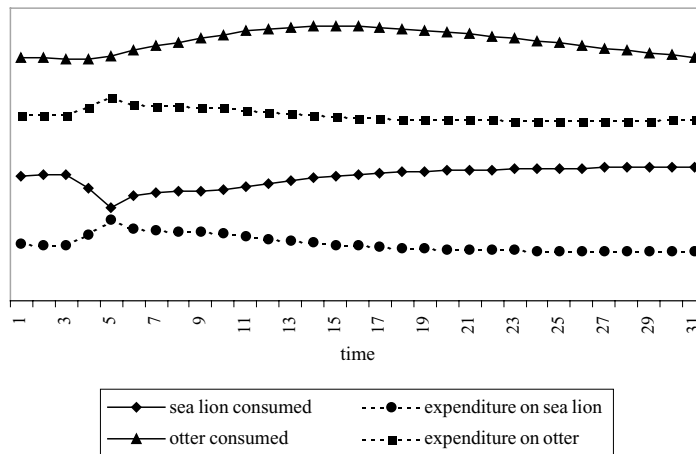
Fig. 7. Killer whale consumption and expenditures. The killer whale consumption of sea lions is inversely related to the killer whale expenditure on sea lions. The same would hold true for the killer whale and sea otters in the absence of the sea lions, but with the sea lions as a second prey, the consumption of otter decreases when the expenditure on them is relatively flat, because the expenditure on sea lions is decreasing making them relatively more attractive as prey.

then slowly falling. The killer whale consumption of otter responded as expected for about the first fourteen periods by inversely tracking the expenditure, but then it began to directly track the expenditure for the remaining periods. In other words, as killer whale expenditures on otter fell, the consumption also fell. The reason is the indirect effects from the falling sea lion expenditure. Expenditures on both otter and sea lion were falling, and the former encourages more otter consumption, but the latter encourages less otter consumption and more switching to sea lion. In this case, the latter affect dominated.

If field observations uncovered an increase in the otter populations at the same time that killer whales consumed fewer otter, the result would appear at odds with expected functional response behavior. Yet, if further investigation revealed that killer whales had switched to alternative prey, the observations would be fully consistent with a model based on optimizing behavior in which the predator responds to *relative* expenditures.

6.6. Results 6—two prey and functional and numerical responses

Using the same simulation as in Results 5, functional and numerical responses for both prey were recorded for 30 years and displayed in Fig. 8. Several points are noteworthy. Starting with the sea otter, the lower left panel shows a negatively sloped functional response for the first 4 years. During this period the falling sea otter density is accompanied by a falling whale density (lower right panel) but a rising per capita whale consumption (lower left panel). The falling otter density caused a rise in the killer whale expenditure on otter; nevertheless the representative killer whale consumed more otter because the expenditure on sea lions was also rising (see Fig. 7). With both expenditures rising, the otter became *relatively* less costly and switching from sea lions to otter occurred as can be seen in the falling functional response for sea lions in the upper left panel during the same period. The switching is taking place when the sea lion density is falling, a phenomena that has been suggested in field observations (Estes et al., 1998).

Switching in the reverse direction from sea otter to sea lions takes place from about year 15–25. During this time there are increasing functional (type II) and numerical responses for sea lions and a falling functional response for sea otter. While the killer whale density is increasing, the consumption per whale is decreasing. The killer whales expenditures for both prey are decreasing, but otter are becoming relatively more costly and the whales are switching to sea lions.
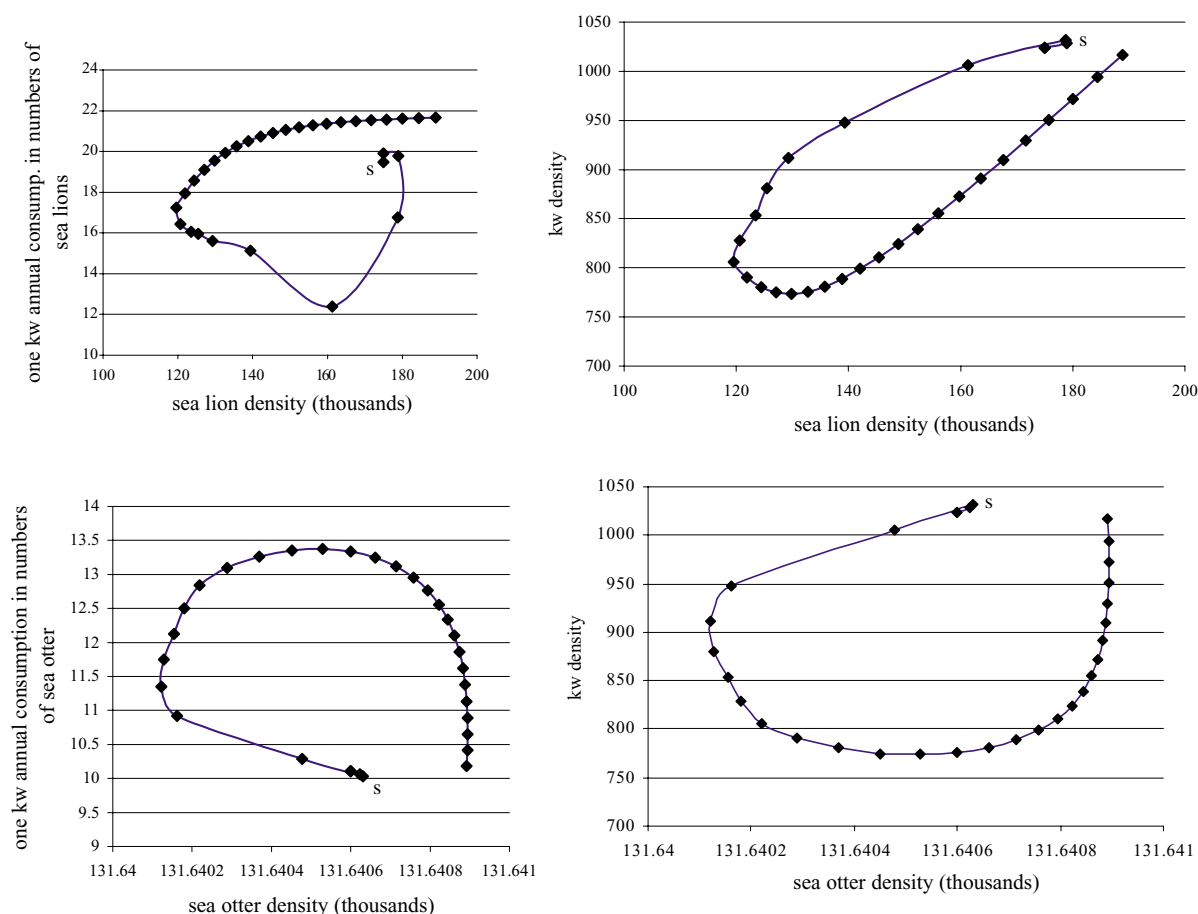
Fig. 8. Killer whale functional and numerical responses with two prey. A representative killer whale's consumption of sea lions and sea otter over time starting at point s in all panels. Negatively sloped segments can be explained by switching behavior and the interaction of the two responses.

During the final 5 years consumption of otter is decreasing although the otter density is virtually stationery. The reason is that the expenditure on otter is rising. The increased expenditure is not due to shrinking prey density, but rather to an increasing predator density that leads to greater intraspecific competition among the killer whales.

Years 6–10 show a negatively sloped functional response for sea lion. During this time, the killer whale expenditures for both prey are decreasing even though the sea otter density is increasing only slightly and the sea lion density is actually falling. The falling killer whale density and the slackening of intraspecific competition for prey explain the decreasing expenditures.

7. Conclusion

The CGE model offers an alternative approach to modeling predator–prey relationships that is based on individuals behaving efficiently by maximizing their net energy intake, and then using that net energy for reproduction. In this way the model bridges individual behavior and population dynamics. Comparing the results of the CGE to the extant literature is complicated by the very different CGE framework, but most of them have parallels to results scattered throughout more conventional dynamic predator–prey, predation risk, switching, optimum foraging and functional response models. Because the CGE approach accounts for a wide variety of results in one model, it may

be useful for following key variables in large, complicated ecosystems. If this proves true, then when humans cause changes to these systems, intentional or otherwise, the system responses can be predicted. CGE economic models, for example, are used to assess the impacts of government taxes or tariffs on prices, quantities, firm profits and consumer incomes. Similarly, with a CGE ecosystem model, myriad human actions can be assessed for their impact on functional and numerical responses and species populations (see for example, Finnoff and Tschirhart, 2003). To be useful in this regard, a CGE ecosystem model must include enough species and functional groups to capture the system's essential features. To be credible, a CGE ecosystem model must yield results that are in keeping with known ecosystem responses and species behaviors. Although the model herein included only five species, it can be extended to incorporate numerous species and numerous predator–prey relationships. At the same time it is based on individual behavior and produces the above results suggesting it is ecologically credible.

There are many ways in which the model can be extended. Three important extensions include: first, introducing abiotic resources such as carbon and nitrogen that would cycle endogenously; second, introducing age-structured populations that would allow for more accurate biomass and energy flows and population updating; and third, introducing spatial aspects to allow individuals to move among patches according to the relative net energies available across patches, thus describing an ideal free distribution (Fretwell and Lucas, 1970). Even with these additions, however, the model is not useful for capturing many of the intricate details of ecosystem functioning, or the bewildering array of strategies practiced by species in the pursuit of fitness. But such detail may be of secondary importance if the question is how broad ecosystem functions are being impacted by widespread interference with natural systems.

Acknowledgements

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