Biology as a Source of Non-convexities in Ecological Production Functions

John Tschirhart

Abstract   Generating ecological production functions, including harvest yield functions, is a high priority research area. Most yield functions used in economics and ecology rely on convexity properties of species growth functions, but convexity is shown here to depend on whether realistic biology is incorporated. Optimizing behavior by individual organisms is connected with species population dynamics in order to derive growth functions in a general equilibrium ecosystem model. Non convexities are shown to be an inherent property of the growth functions owing to familiar biological processes including predator-prey and competitive relations, predator satiation and prey substitution. The growth functions generate yield functions that are problematic for management, because they exhibit kinked average revenue curves, discontinuous marginal revenue curves, and knife edge optimum effort levels where a small increase above the optimum effort can rapidly deplete the stock. These phenomena can be explained entirely by the underlying biological processes.

Keywords   Ecological production function · Non convexity · Ecology/economy integration · Growth functions · Multi species · Animal behavior · Predator/prey · Satiation · Yield functions

1 Introduction

How ecosystem services contribute to human well being is becoming a principal question in resource economics (Bateman et al. 2011). One of the greatest challenges to finding an answer is integrating economic valuation functions with ecological production functions (National Research Council 2005); generating the latter functions has become a high priority research area (United States Environmental Protection Agency 2009). An important subset of ecological production functions are harvest or yield functions. They are familiar to economists

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because they are central in renewable resource models; for example in fisheries, harvest functions are needed to determine sustainable yields that balance ecological and social goals. In fact, Roughgarden (1998) states that for managers: "the most important product for fishery scientists to deliver is a process-based "production function" for a fishery…" (p. S161)

Harvest functions are derived from species growth functions that in ecology typically are the starting point in dynamic population models. A crucial property of growth and harvest functions is their convexity, and whether the feasible combinations of inputs (human harvesting effort) and outputs (biomass yields) form a convex set. In most of the economics literature, harvesting models employ simple growth functions, especially the logistic growth function, in which the technology is convex. Convexity is convenient because efficient allocation mechanisms are obtainable using a price system; non-convexities are inconvenient because resource allocation mechanisms in most non-convex environments are poorly understood (Dasgupta and Mäler 2004). The purpose here is to examine convexity properties of species growth functions that are explicitly or implicitly used in the ecological and economic literature, and to show how convexity depends on whether realistic biology is incorporated.

Although most growth and yield functions employed in economics are convex, a notable exception is the case of critical depensation (Clark 1976; Dasgupta and Mäler 2004). Also most models apply to a single species in a single patch, although Smith (2004) explores growth and yield functions for multiple patches and discusses implication of nonconvexities. Multi-species models based on Lotka (1925) and Volterra (1926) are the cornerstone of species relationship theory, and they have been used in economics albeit sparingly (Tschirhart 2009). The underlying growth functions in Lotka-Volterra (LV) models are often convex. Additionally, the models rely on species-level interactions; hence, they are macro in scale with little recognition of micro behavior by individual animals. Consequently, the biology that may give rise to any non convexities is not discernable.

An alternative to single and multi-species LV models is to connect optimizing behavior by individual organisms with species population dynamics from which growth functions can be derived. In ecology, most studies employing optimum foraging ignore population dynamics and most studies of population dynamics ignore optimum foraging (Abrams 1999). But there are models that connect individual optimization and species dynamics, and they have been linked to general equilibrium economic models to show how economic and ecological systems are jointly determined (Eichner and Pethig 2005, 2009; Finnoff and Tschirhart 2008). Following this connected approach, a general equilibrium ecosystem model (GEEM) is used below to derive growth functions. Non convexities are shown to be an inherent property of the growth functions owing to familiar biological processes including predator-prey and competitive relations, predator satiation and prey substitution.[1] The growth functions generate yield functions that are problematic for management, because they exhibit kinked average revenue curves, discontinuous marginal revenue curves, and knife edge optimum effort levels where a small increase above the optimum effort can rapidly deplete the stock. These phenomena can be explained entirely by the underlying biological processes.[2]

Developing yield functions that admit more detailed biological processes is important, too, because ecological systems that contain harvested species may cease to function in the same manner after one or more species' populations are reduced (Redford and Feinsinger 2001). As demonstrated with GEEM, animal behavior that determines diet selection and

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[1] Eichner and Pethig (2003) employ individual behavior to derive difference equations for species growth, and they find that satiation is 'highly consequential' for species dynamics.

[2] Similarly, Swallow et al. (1990) show how biophysical processes create non convexities in timber harvest functions.

underpins growth functions changes with changes in predator and prey densities, which then modifies the growth functions upon which harvest management is based.[3]

In the following section familiar properties of single species growth functions are reviewed, followed by properties of LV models in Sect. 3. Section 4 is a brief discussion about incorporating animal behavior into developing growth functions, and a theory of one approach to incorporation is in Sect. 5. Section 6 is an application of the theory for an Alaskan marine food web, followed by concluding remarks in Sect. 7.

2 Single Species Growth Functions

To fix ideas and notation, start with the familiar single-species logistic growth and a standard Shaffer harvest production function:

$$\dot{N} = F(N) - H(E, N) = rN(1 - N/K) - qEN \tag{1}$$

$F(N)$ is the growth function, $H(E, N)$ the harvest function, N is the population density, r is the birth minus mortality rate and K is the carrying capacity. The last term is harvest as a function of human effort, E, and species density, where q is a catchability coefficient. Using the growth function and constant harvests, the production function can be constructed showing harvest as a function of effort (Hartwick and Olewiler 1998). Both population growth as a function of density and harvest as a function of effort are strictly concave, symmetric shapes, and the production set is convex.

There are numerous other forms for single species growth (May and Oster 1976). For example, there is the discrete Beverton and Holt (1957) stock recruitment curve:

$$N^{t+1} - N^t = N^t \left[\frac{r}{1 + \frac{r-1}{K} N^t} - 1 \right] \tag{2}$$

that yields a strictly concave function although not perfectly parabolic as with the logistic, and a production function similar to the logistic. Another form from Moran (1950), Ricker (1954) and other authors is:

$$N^{t+1} - N^t = N^t \left[e^{r(1-N^t)} - 1 \right] \tag{3}$$

which plots as in Fig. 1. For values of $r < 2$ both growth and production functions are strictly concave, whereas for $r > 2$ the growth function only exhibits non convexity. For the growth functions in (1–3) $d(F(N)/N)/dN < 0$, or per capita growth is decreasing which is a feedback that controls the population (Clark 1976). As density increases with Beverton-Holt the decreasing per capita growth never reaches minus one and the population does not go to zero. This is referred to as compensatory growth. For the growth functions in (1) and (3), however, per capita growth reaches minus one at high densities, and the population goes to zero. This stronger feedback is referred to as overcompensatory (Clark 1976).

Single species growth functions for which $d(F(N)/N)/dN > 0$ over a range of $N \in [0, N']$ where $N' < K$ are said to be depensatory. Over this range the growth function is non-convex as shown in the top left panel of Fig. 2, and it generates multiple harvest equilibriums.

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[3] Over time harvested fish stocks undergo changes in individuals' sizes, ages and fertility (Murphy 1967; Borisov 1978; Garrod 1988), because harvesting induces artificial selection that impedes natural selection and causes rapid evolution of commercial stocks (Edeline et al. 2007). Such artificial selection can dramatically lower yields and calls for an evolutionary approach to management that incorporates more biological behavior (Law 2000).
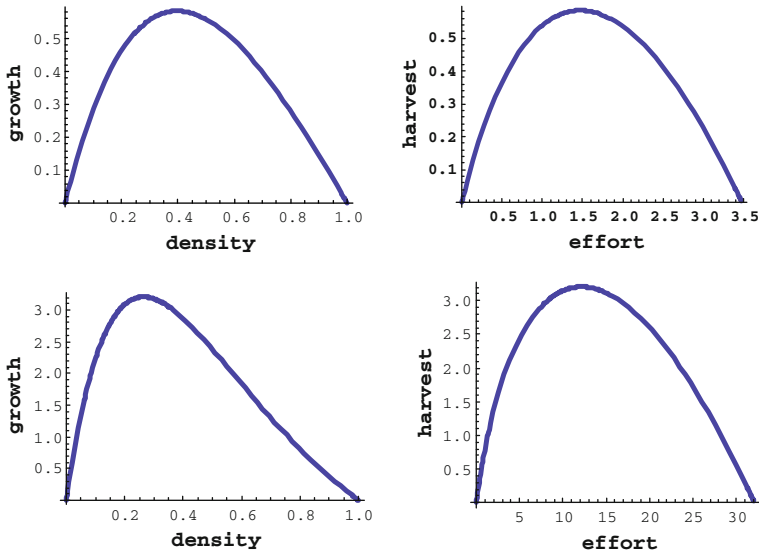
Fig. 1 Growth and production functions for $\dot{N} = N[e^{r(1-N)} - 1]$ with $r = 1.5$ in the *top panels* and $r = 3.5$ in the *bottom panels*. The harvest function is qEN with $q = 1$
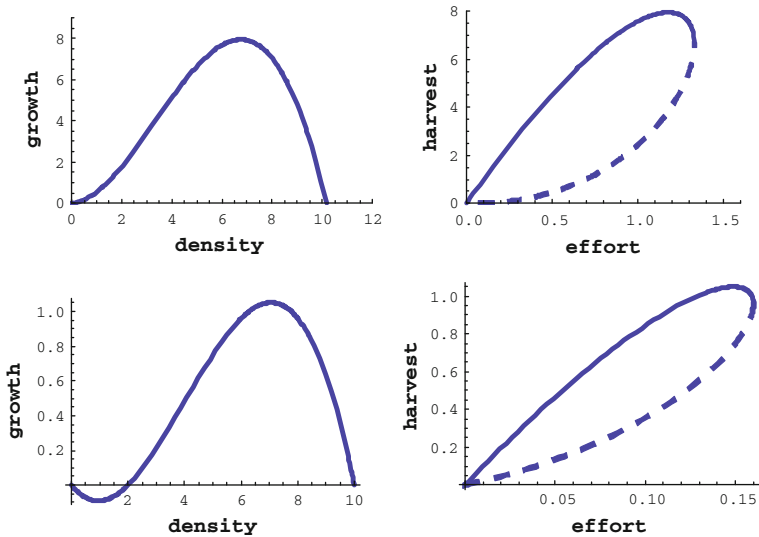

Fig. 2 Growth and production functions for depensation in the *top two panels* for the growth function $.1(.5N(10N - N^2) + .8N$, and critical depensation ((4) in the text) in the *bottom two panels* with $r = 0.2$, $K_o = 2$, and $K = 10$. The harvest function is qEN with $q = 1$

Critical depensation refers to growth functions that exhibit an Allee effect implying there is some positive minimum population below which the species will become extinct. A common justification for an Allee effect is difficulty finding mates at small densities, although other justifications are offered such as the need for a minimum group size to rear offspring or feed. There are many functional forms for Allee effects (Boukal and Berec 2002), including the one used in Clark's classic work (1976):

$$\dot{N} = rN(N/K_o - 1)(1 - N/K) \tag{4}$$

Function (4) is shown in the bottom left panel of Fig. 2; for densities below $N = K_o = 2$ the species is doomed to extinction. The growth curve is strictly convex for densities $2 \leq N \leq 4$. The dashed curves in both right panels represent unstable equilibrium harvests and correspond to the strictly convex portions of the growth curves in the left panels. The curves in both systems exhibit hysteresis, and the critical depensation system exhibits irreversibility (Clark 1976).

3 Growth Functions in Two-Species Lotka-Volterra Models

Single-species models collapse the ecosystem into the single parameter K; they do not account for the myriad ways that species interact within ecosystems. Adding a second species to the modeling admits more biological realism. Relationships between interacting species are categorized by how the species impact one another. Predator-prey (predator gains, prey loses) and competition (all species lose) receive the most attention. Ecological models of these relations usually contain two or three species, rarely are they extended to many species, and they start with a population-growth function for each species. A simple structure for the LV predator-prey model is:

$$\begin{aligned} \dot{N} &= rN(1 - N/K) - bPN \\ \dot{P} &= aPN - dP \end{aligned} \tag{5}$$

where N and P are the prey and predator densities, respectively.[4] The prey has self-limiting growth dictated by the logistic form and d is a predator mortality rate (in each other's absence prey would grow to K and the predator would decline to zero). Terms a and b are rates of change due to the interactions. The interaction, PN, is called mass action, a notion borrowed from chemistry that the force between two reactants is proportional to their masses. In essence, an amount of biomass, bNP, is taken from the prey species of which aNP is captured by the predator species. The rate at which predators capture prey is bN and is called the functional response. In (5) the functional response, which is refereed to as a Holling Type I response, is linear in prey density.

To generate a growth curve from (5), the procedure is to harvest the predator at a constant effort in the LV equations. As long as effort is not too large, we obtain prey and predator equilibriums as functions of E. These are steady states, and for constant E the same harvest can be taken each period without changing the prey and predator densities. But this means that the harvest is the growth which yields a function of P for a growth curve, and a function of E for the harvest production curve.

Formally, the procedure is as follows. Define

$$\begin{aligned} \tilde{G}(N, P) &= \dot{N} = rN(1 - N/K) - bPN \\ \tilde{F}(N, P) &= \dot{P} = aPN - dP \end{aligned} \tag{6}$$

and setting $\tilde{G}(N, P) = \tilde{F}(N, P) = 0$ will yield no-harvesting equilibrium values $N^{**} > 0$ and $P^{**} > 0$ for a predator and prey coexistence state. Now append the functions in (5) by harvesting the predator using again the Shaffer harvest function and define the new functions:

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[4] In the original LV equations, the prey growth rate in the predator's absence was exponential instead of self limiting as in (5). The original model predicted continuing oscillations and behavior based on initial conditions. Adding self-limiting growth is more realistic and leads to stability and behavior independent of initial conditions.
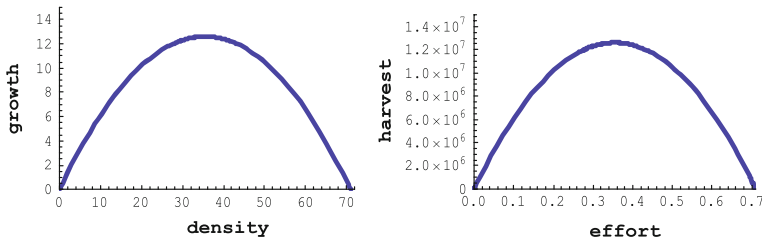
Fig. 3 Growth and harvest *curves* for LV equations and Holling Type I functional response. Taken from Ragozin's and Brown's system: $\dot{N} = N(c - dN) - \beta PN$ and $\dot{P} = P(a - bN) - \alpha PN$ with parameters: $a = 36$, $b = .88 \times 10^{-8}$; $c = .35$; $d = .35 \times 10^{-8}$; $\alpha = .35 \times 10^{-8}$; $\beta = .12 \times 10^{-8}$. For easier reading, all units on both axes in the left panel have been divided by 1×10^6. The harvest function is qEN with $q = 1$

$$G(N, P; E) = rN(1 - N/K) - bPN$$
$$F(N, P; E) = aPN - dP - qEP \tag{7}$$

Setting $G(N, P; E) = F(N, P, E) = 0$ will yield the steady state or equilibrium prey and predator densities as functions of effort:

$$N^*(E) \quad \text{and} \quad P^*(E) \tag{8}$$

Using (8), harvest or $qEP^*(E)$ can be plotted as a function of effort which is done below for specific LV equations. Inverting $N^*(E)$ yields

$$E(N^*) \tag{9}$$

and using (9) in $P^*(E)$ we get $P^*(E(N^*))$ which can be inverted to obtain

$$N^*(P^*) \tag{10}$$

Substituting (10) into $\tilde{F}(N, P)$ from (6) yields growth, $\tilde{F}(N^*(P), P)$, that can be plotted as a function of P which is also done below.

Economists have used the LV predator-prey model with Type I functional response in which either the predator, prey, or both are harvested (Hannesson 1983; Ragozin and Brown 1985; Wilen and Brown 1986; Ströbele and Wacker 1991; Hartwick and Olewiler 1998; Brown et al. 2005), or neither is harvested but the predator density is controlled (Tu and Wilman 1992). For (5), the classic LV predator prey equations with Holling Type I response yields growth and harvest functions similar to the single-species logistic growth function. Ragozin and Brown (1985) modify system (5) by giving the predator self-limiting growth; the growth and harvest production functions are shown in Fig. 3. Both the growth and production functions exhibit well-behaved, parabolic curves and the technology is convex.

In three leading ecology journals from 1996 to 1999, of the 45 papers published on predator-prey relations, 27% of them used a Holling Type I linear response (Skalski and Gilliam 2001). However, the type I response omits important predator activities; in particular, real responses will depend on how predators expend time to capture and handle prey, and whether they are satiated. Consumption of prey per predator cannot rise without limit in proportion to the prey density. To account for this consider:

$$\dot{N} = rN(1 - N/K) - b(N)P$$
$$\dot{P} = cPb(N) - dP \tag{11}$$

where $b(N)$ is the functional response (Berryman 1992). Two popular extensions of the Type I response are the Holling Type II and Type III:

$$\text{(II) } b(N) = \frac{mN}{a + N} \quad \text{and} \quad \text{(III) } b(N) = \frac{mN^2}{a^2 + N^2} \tag{12}$$

where m is a maximum attack rate and a is a half-saturation constant ($b(a) = m/2$). In papers from the three leading ecology journals, 69% used a Holling Type II response which exhibits decreasing marginal consumption of prey per predator.[5] Using Type II, adding predator harvests, and rewriting (11) gives:

$$\dot{N} = rN \left(1 - \frac{N}{K}\right) - \frac{mPN}{a + N}$$
$$\dot{P} = \frac{cmN}{a + N} - dP - EP \tag{13}$$

Depending on the parameter values, coexistence of the predator and prey populations is either unattainable or attainable with either a stable steady state or with limit cycles. Interestingly, larger values of the prey carrying capacity, *ceteris paribus*, lead to the limit cycles, a phenomena referred to as the paradox of enrichment. Using an example from Gurney and Nisbet (1998), Fig. 4 shows the growth and harvest functions for two values of prey carrying capacity in the upper and lower panels, with all other parameters in (13) the same. Gurney and Nisbet (p. 163) derive the range of prey carrying capacities that produce stability with no harvesting, $E = 0$. Adding harvesting simply adds another source of mortality in (13), and the authors' range for stability can be written in terms of effort for a fixed carrying capacity:

$$\frac{cm(K - a)}{K + a} - d \leq E \leq \frac{cmK}{K + a} - d \tag{14}$$

For example, in the upper panels in Fig. 4, $K = .7$ and (14) becomes $-.188 \leq E \leq .106$ so that any positive level of effort less than .106 will yield stability. This is illustrated in the upper right panel. Alternatively, in the lower panels $K = 2$ and stability requires $.067 \leq E \leq .233$. In the bottom left panel the linear effort line represents the smallest constant harvest, $E = .067$, that yields stability, while in the bottom right panel the dashed (solid) curve represents effort values that yield oscillatory (stable) behavior. Thus the system in the upper panels is stable in the absence of harvesting, whereas the system in the lower panels is unstable without harvesting, and can only be stabilized if effort levels are at least .067. In effect, harvesting can offset instability owing to the paradox of enrichment.

Another extension of the LV equations introduces diet selection into the dynamics by adding a second prey species (e.g., Fryxell and Lundberg 1998). Consider a one predator-two prey system where the predator consumes quantities of one or both prey species. The predator's functional response is given by the fraction term in the last line of (15):

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[5] In economics, Bulte and Damania (2003) use the Holling Type II functional response in the prey equation; however, the predator equation exhibits logistic growth without the response. Under open access, they find that if there are multiple equilibria, heavier predator harvesting can increase the prey density. Bulte (2003) uses the Holling Type III functional response in an open access poaching model and finds multiple equilibria and unexpected changes in species densities.
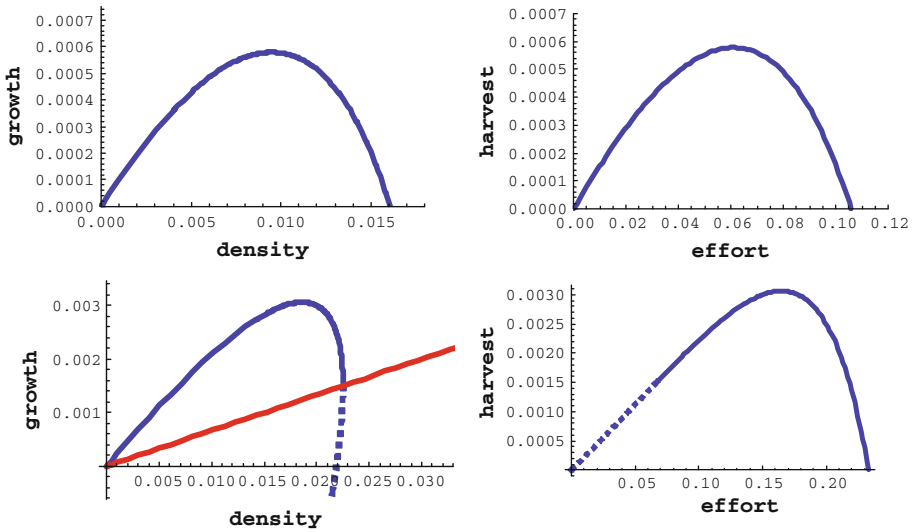
Fig. 4 Growth and harvest *curves* for Holling Type II functional response. Parameters are from Gurney and Nisbet for the system given by (13) sans the effort term. In all figures, $r = d = c = .1$, $a = 1$, $m = 5$, and in the *top panels* $K = .7$ and in the *bottom panels* $K = 2$. Harvest is qEN with $q = 1$

$$\dot{N}_1 = r_1 N_1 (1 - N_1/K_1) - \frac{\alpha \beta_1 N_1}{1 + \alpha(\beta_1 h_1 N_1 + \beta_2 h_2 N_2)} P$$

$$\dot{N}_2 = r_2 N_2 (1 - N_2/K_2) - \frac{\alpha \beta_2 N_2}{1 + \alpha(\beta_1 h_1 N_1 + \beta_2 h_2 N_2)} P \qquad (15)$$

$$\dot{P} = cP \frac{e_1 \alpha \beta_1 N_1 + e_2 \alpha \beta_2 N_2}{1 + \alpha(\beta_1 h_1 N_1 + \beta_2 h_2 N_2)} - dP - EP$$

Only the predator is being harvested, both prey growths are self limiting with logistic growth, c converts the rate of prey consumption to a rate of predator reproduction, and e_i, h_i, and β_i are the energy content of prey i, the handling time or the time it takes for the predator to subdue and consume a unit of prey i, and the probability of attack against prey i, $i = 1, 2$, respectively. There are multiple steady states including non existence for the predator and one or both prey, although at least on prey must exist for predator existence. Under some conditions (i.e. parameter sets that allow coexistence of predator and both prey), the system in (15) shows for the predator a smooth, strictly concave growth curve and a convex harvest technology similar to the single-species model in Fig. 1.

4 On Modeling Behavior

A substantial portion of bioeconomic modeling employs the single species growth functions, and a substantial portion of ecological modeling employs the LV equations. With the exception of the depensation model, growth and harvest functions derived from the single species and LV approaches exhibit convexity properties that are convenient for analysis, at least for some parameter ranges. The issue here is whether the exhibited properties represent enough real organism behavior to be relied on for creating trustworthy bioeconomic harvest policies. In this section, some reasons for suspecting that the models are less than behaviorally

complete are indicated, followed in the next section by an alternative modeling approach that relies more on individual behavior.

Clearly, extending the single-species models to two and three species LV models admits more biological detail; what is less clear is the behavior that underlies the details. Ecosystem properties ultimately are determined by individual organism behavior, but LV equations begin at the species population level which can mask individual behavior. As Eichner and Pethig (2006) state:

> "Choosing populations as basic endogenous variables amounts to disregarding the transactions of individual organisms, fails to identify the types and scales of those transactions and does not answer the question as to how the interaction of individual organisms translates into population changes." (p. 280)

The LV models that introduce functional responses and diet choices in (13) and (15) define the response as the predator per-capita consumption of the two prey. In contrast, ecological foraging theory, which does not employ LV equations and does not produce dynamic population adjustments, assumes individuals behave as if they maximize energy, or fitness (Stephens and Krebs 1986). Individual predator maximization ought to produce the predator's demand functions for prey that are the individual's consumption. In other words, the demand functions from optimal foraging should be the functional responses. But demand functions should depend on parameters observable to the predator, in particular, the energy profitability of searching for and consuming prey items.[6] Functional responses in LV equations contain prey densities which in many cases are not observable to the predator. In fact, in Holling (1959) original experiments that defined Type I, II and III responses, the predators were blindfolded students who preyed on sandpaper discs laid out on tables, so the students were unaware of prey densities. Obviously, functional responses that depend on densities are very convenient because they can be inserted into the LV equations to produce population dynamics. But as descriptions of real choice behavior they are at best proxies.

Implicit in (15) and in similar models, is that the predator is an optimal forager, and this can be accomplished by maximizing the functional response. (See e.g., Gleeson and Wilson 1986.) But there are two problems with this approach. First, it again requires that the predator can observe the parameters in the response including densities. Second, the response is defined to be the predator's consumption of (or demand for) prey, but ideally the form of the demand function should be determined from the predator's optimization problem. The LV equation approach, however, is to assume the form of the response at the outset. In effect, the functional response is treated as a formula to be maximized instead of being the result of a maximization process.

5 An Optimization Approach with Dynamics

5.1 An Economic Example

Before exploring a more behaviorally oriented approach to derive growth and yield functions, consider the following simple, stylized economic model of a perfectly competitive industry. The point will be to derive a growth function for the number of firms in the industry. Although growth functions are not examined in economic models, the strictly convex shape of the curve

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[6] Stephens and Krebs (1986) cover foraging theory in depth. Individual predators optimize fitness by maximizing net energy intake over times spent in various feeding grounds. Species densities do not enter the problem; in fact, optimal foraging theory typically does not investigate dynamics.

derived follows from familiar entry and exit conditions and a commonly used profit function that is strictly-concave in output.

Assuming all firms are identical and price takers regardless of the number of firms, write profit as:

$$\pi = (p - c)q - q^2 - F \tag{16}$$

where q is quantity, F is a fixed cost, p is the initial price that prevails when there are a small number of firms in the industry, and c is a deviation from the price that responds to the number of firms. The idea is that starting with one firm, $n = 1$, the price is p and the price does not change as the number of firms grows until some competitive threshold is reached at which time firm competition causes the price to deviate from p by c. The conditions for equilibrium in the industry can be written:

$$\partial\pi/\partial q = p - c - 2q \le 0, \quad q\partial\pi/\partial q = 0, \quad q \ge 0$$
$$nq \le D, \quad c(D - nq) = 0, \quad c \ge 0 \tag{17}$$

where D is a fixed market demand. The conditions define the number of firms at which competition will impact price. When $q < D/n$, $c = 0$ and the firms are not competing to supply their share of D so price remains p. But when $c > 0$, $q = D/n$ and firms compete to supply their share and more firms will drive down price through increases in c. (The reason for introducing c and not changing p directly will become apparent below in the ecological interpretation.)

Following Smith (1969), entry of new firms, or growth, is assumed to depend linearly on profit. In discrete terms and using t for the time period, the growth is:

$$G(n) = n^{t+1} - n^t = gn^t\pi \tag{18}$$

where g is a growth constant. The shape of the growth curve will depend on the signs of

$$\partial G/\partial n = g\{n\partial\pi/\partial n + \pi\} \quad \text{and} \quad \partial^2 G/\partial n^2 = g\{n\partial^2\pi/\partial n^2 + 2\partial\pi/\partial n\} \tag{19}$$

where the time superscript is dropped.

Case 1: $q > 0, nq < D \rightarrow c = 0$ and $\hat{q} = p/2$ where the hat notation indicates the optimum. Because $\hat{q}$ is independent of n, π is also independent so that $\partial G/\partial n = g\pi$ and $\partial^2 G/\partial n^2 = 0$. Moreover, substituting $\hat{q}$ into π yields $\partial G/\partial n = g[p^2/4 - F] > 0$. The last inequality is assumed to hold otherwise profit is never positive and there can be no growth.

Case 2: $q > 0, c > 0 \rightarrow \hat{q} = D/n$ and $\hat{c} = p - 2D/n$. Substituting $\hat{q}$ and $\hat{c}$ into (19) yields:
$\partial G/\partial n = g\{-D^2/n^2 - F\} < 0$ and $\partial^2 G/\partial n^2 = gD^2/n^3 > 0$.

The result is a growth curve that is positively sloped and linear over small n and negatively sloped and strictly convex over large n. The top left panel in Fig. 5 displays the shape, although Fig. 5 is derived below for a species instead of an industry, so for an industry the density on the horizontal axis would be the number of firms, n. Also, the shape of the strictly convex portion depends on the signs $\partial\hat{c}/\partial n > 0$ and $\partial^2\hat{c}/\partial n^2 < 0$; or if c is interpreted as a measure of competition, then competition is strictly concave in c. These features carry over in the following ecological model.
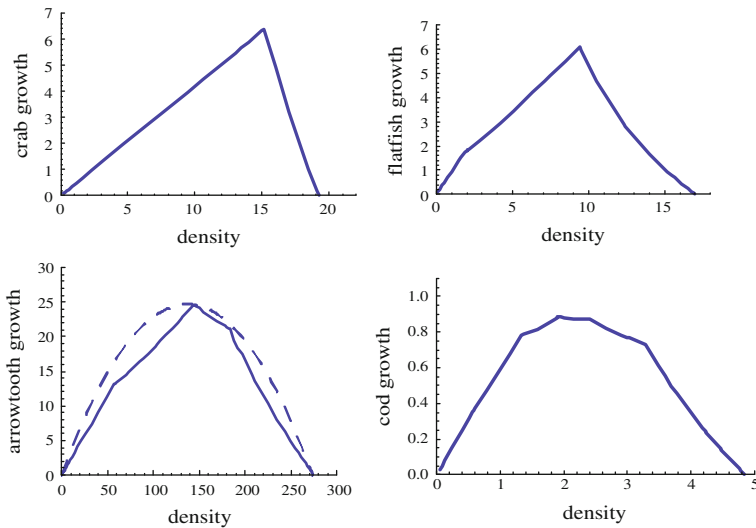
Fig. 5 Growth *curves* for crabs, flatfish, arrowtooth flounder and Pacific cod that have one, two, three and five prey species in the model, respectively. *Bottom left panel* also shows an approximate logistic *curve*. One unit of density is I individuals per km^2 of surface water where $I = 100$ for crab, 1,000 for flatfish, 1 for arrowtooth and 100 for cod

5.2 Predator Optimization

Returning to ecological growth functions, consider one predator and one prey species and assume all individuals are identical within a species. The prey is indexed by 1 and the predator by p. The objective functions of representative individuals in each species and a feasibility condition are:

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\begin{aligned}
R_1 &= (e_0 - e_{10})x_{10} - f_1(x_{10}) - b_1 - e_1 y_1(x_{10}) \\
R_p &= (e_1 - e_{p1})x_{p1} - f_p(x_{p1}) - b_p \\
N_p x_{p1} &\le N_1 y_1(x_{10})
\end{aligned}
\tag{20}
$$

In the prey objective function on the first line, the first term on the right side is the inflow of energy to an individual in the prey species from its own prey (the prey's prey is not being modeled here). The choice variable or demand is x_{10} which is the biomass consumed by the prey. The e_0 is the energy embodied in the biomass of a unit of the prey's prey, and e_{10} is the energy spent capturing the unit. This latter energy is essentially an energy cost or price; there is one price in each predator and prey relation.

The second and third terms in the prey objective function represent respiration energy lost to the atmosphere. Following Gurney and Nisbet (1998) respiration is divided into a variable component, f_1, that depends positively on biomass consumption ($\partial f_1/\partial x_{10} > 0$) and includes reproduction, maintenance, defending territory, etc., and a fixed component or basal metabolism, b_1. The fourth term is the outflow of energy to the predator species 2. The e_1 is the embodied energy in a unit of prey biomass and y_1 is the biomass the prey is "willing" to supply to the predator in species 2. The biomass supply function depends on the prey individual's demand, because the more the individual feeds, the more it is exposed and the more biomass it is "willing" to supply to predators. This tradeoff between foraging gains and losses is a result of predation risk (Lima 1998).

The second line in (20) is an individual predator's objective function and the terms have similar interpretations as in the prey objective function. Note the predator's objective function is analogous to the firm's objective function given by (16). The predator chooses an optimum biomass to consume of the prey species, x_{p1}. The marginal cost of searching for and capturing a unit of that biomass is e_{p1}. The predator is assumed to be a top predator so there is no predation term as there is in the prey objective function. The third expression in (20) is a feasibility condition; the total biomass consumed by all individuals in the predator species cannot exceed the total biomass all individuals in the prey species are willing to lose to predation.

Initially, to make this model as similar as possible to two-species LV models, the prey is assumed to not solve a maximization problem so x_{10} is fixed. Therefore, also fixed is the supply of an individual prey to predators, $y_1(x_{10})$. This is comparable to a predator-prey LV model since the predator consumes the prey, but the prey does not consume its own prey. The prey is basically passive for now. (Bringing in the prey's prey, and the prey's prey's prey, etc. is straightforward in the GEEM framework (Tschirhart 2000, 2004).)

The Kuhn-Tucker conditions for a predator maximum are:

$$\partial R_p/\partial x_{p1} = e_1 - e_{p1} - \partial f_p/\partial x_{p1} \leq 0$$
$$[\partial R_p/\partial x_{p1}]x_{p1} = 0 \qquad x_{p1} \geq 0 \tag{21}$$
$$N_p x_{p1} - N_1 y_1 \leq 0$$
$$e_{p1}[N_p x_{p1} - N_1 y_1] = 0 \quad e_{p1} \geq 0 \tag{22}$$

The conditions imply that if the predator consumes a positive quantity, $x_{p1} > 0$, then the marginal energy gained from a unit of prey biomass equals the marginal energy lost to searching for the unit of prey biomass plus the marginal energy lost to variable respiration. Alternatively, if the derivative is negative at the optimum, the predator consumes zero. The derivative is negative if $e_1 \leq e_{p1}$; thus a necessary condition for the predator to consume at all is that the energy in a unit of prey biomass exceeds the energy search cost.

Condition (22) implies that if the predator's marginal cost of searching is positive, then the biomass demanded by the predator equals that supplied by the prey. Alternatively, if the predators' demand is less than what the prey is willing to supply, then the energy price to the predator is zero, or $e_{p1} = 0$. The case of demand less than supply is important. Essentially it is saying that the predators are satiated, because even though the marginal cost of predation is zero, they are not consuming all that the prey is willing to supply. The idea is rather simple. Satiation, as will be seen below, occurs when the predator/prey density ratio is relatively small so there is abundant prey available per predator and the predators satiate themselves. The cost term then is a way to measure satiation, when it is zero there is satiation in the prey, when it is positive the predator is not satiated. The larger is e_{p1} the less the predator consumes. (Of course, searching is never zero or costless, but we could define a minimum cost that is some positive value and subtract it from e_1 without changing the main points.)

Each time period, for constant densities, conditions (21) and (22) are sufficient to solve for an x_{p1} and e_{p1}. A simple comparative statics exercise reveals that:

$$\partial e_{p1}/\partial N_1 < 0 \quad \text{and} \quad \partial e_{p1}/\partial N_p > 0 \tag{23}$$

Increased prey density decreases the predator's search cost, and increased predator density increases the predator's search cost (owing to more interference competition).

In each time period, the optimum net energy is found by substituting the x_{p1} and e_{p1} into the predator's net energy function in (20). The predator density growth is assumed to depend on the optimum net energy earned in the period, similar to the way that industry growth in

the economic example depended on the firms' profits. The idea is the optimum net energy is what determines the foraging success of the individuals, and therefore determines their reproduction success or fitness. That fitness depends on maximizing net energy is consistent with natural selection (Pennycuick 1979).

The difference equation for population updating is derived as follows. In steady-state it must be the case that births equals deaths in each time period, and if s_p is the lifespan of the representative predator, then the total number of births and deaths must be N_p/s_p. Dividing the total by N_p yields the per capita steady-state birth and death rates:

$$1/s_p \tag{24}$$

The predator's maximized net energy in period t is given by

$$\hat{R}_p^t(x_{p1}^t(e_{p1}^t(\bar{N}^t)),\ e_{p1}^t(\bar{N}^t)) = \hat{R}_p^t(\cdot) \tag{25}$$

which is obtained by substituting the predator's consumption and energy cost into its net energy objective function in (20), and where $\bar{N}^t = \left(N_1^t, N_p^t\right)$. Consistent with the optimization problem, marginal search cost in (25) is written as a function of the densities and consumption as a function of the marginal search cost. The problem has obvious similarities to a competitive economic market in that the individual predator has no control over the price, or marginal search cost, and takes it as given; at the same time the price is being determined by the actions of all predators.

Reproduction requires energy and, by the definitions of the terms in (20), that energy is contained in the variable respiration f_p. Let f_p^{ss} be the steady-state variable respiration, and let vf_p^{ss} be the proportion of this variable respiration devoted to reproduction. Thus, in steady state the energy given by vf_p^{ss} yields a per capita birth rate of $1/s_p$ from (24). Next, suppose the predator species is not in steady state and let variable respiration be f_p. Assuming that the proportion of $\hat{R}_p^t(\cdot)$ that is available for reproduction is the same as the proportion of variable respiration available for reproduction, the energy available out of steady state for reproduction is $v\left[\hat{R}_p^t(\cdot) + f_p\right]$. Finally, assuming that reproduction is linear in available energy, then it follows that if vf_p^{ss} yields a per capita birth rate $1/s_p$, then $v\left[\hat{R}_p^t(\cdot) + f_p\right]$ yields a per capita birth rate of:

$$(1/s_p)\left[\hat{R}_p^t(\cdot) + f_p\right]\Big/ f_p^{ss} \tag{26}$$

Growth is obtained by multiplying the current density by the difference between the birth and death rates, where the latter rate is assumed to be independent of energy available for reproduction. Therefore, using (26), the density-dependent, growth equation is:

$$\begin{aligned}
N_p^{t+1} - N_p^t &= N_p^t\left[\frac{1}{s_p}\frac{\hat{R}_p^t(\cdot) + f_p}{f_p^{ss}} - \frac{1}{s_p}\right] \\
&= N_p^t\frac{1}{s_p}\left[\frac{\hat{R}_p^t(\cdot) + f_p}{f_p^{ss}} - 1\right]
\end{aligned} \tag{27}$$

Expression (27) reduces to the steady state if $\hat{R}_p^t(\cdot) = \hat{R}_p^{tss}(\cdot) = 0$ (in which case $f_p = f_p^{ss}$), because the bracketed term is zero. Alternatively, $\hat{R}_p^t(\cdot) > (<)\,0$ implies that $f_p > (<)f_p^{ss}$, in which case density increases (decreases).

5.3 Predator Growth Curve

Finally the growth curve can be derived. Since the curve is $N_p^{t+1} - N_p^t$ as a function of N_p^t, the shape of the curve can be ascertained from the derivatives of $N_p^{t+1} - N_p^t$ with respect to N_p^t. Let $\Delta N = N_p^{t+1} - N_p^t$ and omitting the time superscript for brevity, substitute into (27) for $\hat{R}_p^t(\cdot)$ from (20) and (25) to get:

$$\Delta N_p = N_p \frac{1}{s_p} \left[\frac{(e_1 - e_{p1}(\bar{N}))x_{p1}(e_{p1}(\bar{N})) - f_p(x_{p1}(e_{p1}(\bar{N}))) - b_p + f_p(x_{p1}(e_{p1}(\bar{N})))}{f_p^{ss}} - 1 \right]$$

$$= N_p \frac{1}{s_p} \left[\frac{(e_1 - e_{p1}(\bar{N}))x_{p1}(e_{p1}(\bar{N})) - b_p}{f_p^{ss}} - 1 \right] \tag{28}$$

The first two derivatives, after dropping the function arguments, are:

$$\frac{\partial \Delta N_p}{\partial N_p} = \frac{1}{s_p} \left[\frac{(e_1 - e_{p1})x_{p1} - b_p}{f_p^{ss}} - 1 \right] + \frac{N_p}{s_p f_p^{ss}} \frac{\partial e_{p1}}{\partial N_p} \left[(e_1 - e_{p1})\frac{\partial x_{p1}}{\partial e_{p1}} - x_{p1} \right] \tag{29}$$

$$\frac{\partial^2 \Delta N_p}{\partial N_p^2} = \frac{N_p}{s_p f_p^{ss}} \left[\left[(e_1 - e_{p1})\frac{\partial x_{p1}}{\partial e_{p1}} - x_{p1} \right] \frac{\partial^2 e_{p1}}{\partial N_p^2} - \left(\frac{\partial e_{p1}}{\partial N_p} \right)^2 \frac{\partial x_{p1}}{\partial e_{p1}} \right]$$

$$+ \frac{2}{s_p f_p^{ss}} \left[(e_1 - e_{p1})\frac{\partial x_{p1}}{\partial e_{p1}} - x_{p1} \right] \frac{\partial e_{p1}}{\partial N_p} \tag{30}$$

The slope of the predator growth function is given by (29), and the concavity or convexity is determined by the sign of (30).

Expression (29) has a clear interpretation. The first term on the right side is the per capita growth or the growth contributed by one individual. The second term is a loss in growth attributable to *all* the competing individuals. (The second term is negative by (23), downward sloping predator demand, $\frac{\partial x_{p1}}{\partial e_{p1}} < 0$, and $e_1 \geq e_{p1}$ otherwise the prey is not consumed from (21) and (22).) When an individual joins the population, it adds to the competition among the predators, which is measured by the increase in the marginal search cost of predation, $\partial e_{p1}/\partial N_p$. The increased cost implies less consumption for each predator and lower net energy for reproduction. Less consumption is the predator's version of a stock externality. Adding another means more offspring are produced, but at the same time raises the cost of predation to all predators which results in less offspring produced. Which effect dominates? Since the second term contains N_p, the larger (smaller) the population the more the negative (positive) effect will dominate, or the greater the likelihood that the growth function is negatively (positively) sloped. However, without specific functional forms the sign of (29) is indeterminate.

The sign of (30) is also indeterminate without specific functional forms. The first term on the right side is positive, but the second term is negative. The positive first term requires:

$$\partial^2 e_{p1}/\partial N_p^2 < 0 \tag{31}$$

which follows from a comparative static exercise on (21) and (22) for $x_{p1} > 0$ and $e_{p1} > 0$. Again, the greater is N_p, the more likely the first term dominates yielding a strictly convex growth curve. Inequality (31) along with $\partial e_{p1}/\partial N_p > 0$ have a sensible interpretation. Recalling that e_{p1} is a measure of competition, the implication is that competition increases with population growth but at a decreasing rate. (This was true for the economic example

provided above.) For example, when a second predator is added to a lone predator the increase in competition is greater than when an eleventh predator is added to a group of ten predators.

Although the signs of (29) and (30) are indeterminate generally, for the case of predator satiation they are determinate if we assume no Allee effect at very small predator densities.[7] Assuming satiation exists at small densities (which simulations using real data bear out below), then $e_{p1} = 0$ and $\partial e_{p1}/\partial N_p = 0$. Substituting these values into (29) and (30) yields:

$$\partial \Delta N_p/\partial N_p = \text{ constant } \text{ and } \partial \Delta^2 N_p/\partial N_p^2 = 0 \qquad (32)$$

Per capita predator growth is constant and growth is linear in density.

To get definitive signs for the non satiation case, we will assume that the form of the variable respiration is:

$$f_p(x_{p1}) = rx_{p1} + rx_{p1}^2 \qquad (33)$$

where r is a constant scaling factor. Power functions arise often in ecology, and the first term in (33) is included for generality; the scaling in both terms is assumed to be the same for ease in finding numerical solutions. Using (33) in (21) and (22) and assuming that the solution yields positive values for x_{p1} and e_{p1}, we obtain:

$$x_{p1} = y_1 \frac{N_1}{N_p} \text{ and } e_{p1} = e_1 - r - 2ry_1 \frac{N_1}{N_p} \qquad (34)$$

Substituting these values into (29) and (30) yields

$$\partial \Delta N_p/\partial N_p < 0 \text{ and } \partial \Delta^2 N_p/\partial N_p^2 > 0 \qquad (35)$$

implying that the non satiation section of the growth curve is negatively sloped and strictly convex. The satiation case in (32) applies to lower predator densities while the non satiation case in (35) applies to higher predator densities. The top left panel of Fig. 5 illustrates an example of the resulting growth function. The function is linear from the origin to a density of about 15, and strictly convex from 15 to the carrying capacity.

System (20) can be extended to two prey by adding consumption of a second prey, x_{p2}, with its associated energy search cost, e_{p2}, expanding the predator's variable respiration to a quadratic form, and adding an objective function for the second prey and another market clearing condition:

$$R_1 = (e_0 - e_{10})x_{10} - f_1(x_{10}) - b_1 - e_1 y_1(x_{10})$$
$$R_2 = (e_0 - e_{20})x_{20} - f_2(x_{20}) - b_2 - e_2 y_2(x_{20})$$
$$R_p = (e_1 - e_{p1})x_{p1} + (e_2 - e_{p2})x_{p2} - r(x_{p1} + x_{p2}) - .5r(x_{p1}^2 + x_{p2}^2 + x_{p1}x_{p2}) - b_p$$
$$N_p x_{p1} \leq N_1 y_1(x_{10}), \quad N_p x_{p2} \leq N_2 y_2(x_{20}) \qquad (36)$$

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[7] Christiaans et al. (2007) include Allee effects in a model that also derives growth curves based on individual optimization, although their individuals are analogous to utility maximizing human consumers as opposed to profit maximizing firms used here. In some cases they derive a growth curve like that in the bottom right panel of Fig. 2, but their curve is developed from micro principles instead of assumed as in most bioeconomic work.

Following the same procedures used to obtain (29), the slope of the predator growth curve can be derived:

$$\partial \Delta N_p / \partial N_p = \frac{1}{s_p} \left[\frac{\{(e_1 - e_{p1})x_{p1} + (e_2 - e_{p2})x_{p2}\} - b_p}{f_p^{ss}} - 1 \right.$$
$$+ \frac{N_p}{s_p f_p^{ss}} \left[\frac{\partial e_{p1}}{\partial N_p} \left[(e_1 - e_{p1})\frac{\partial x_{p1}}{\partial e_{p1}} + (e_2 - e_{p2})\frac{\partial x_{p2}}{\partial e_{p1}} - x_{p1} \right] \right.$$
$$\left. \left. + \frac{\partial e_{p2}}{\partial N_p} \left[(e_1 - e_{p1})\frac{\partial x_{p1}}{\partial e_{p2}} + (e_2 - e_{p2})\frac{\partial x_{p2}}{\partial e_{p2}} - x_{p2} \right] \right] \right] \quad (37)$$

In comparing (37) to its single prey counterpart in (29), there are now cross-price effects in that changes in the marginal search cost for one prey can impact demand for both prey. Because $\partial x_{pi} / \partial e_{pj} > 0$, $i, j = 1, 2, i \neq j$, the predator treats the prey as substitutes. Moreover, the presence of a substitute prey increases the likelihood that the growth curve will be positively sloped over greater densities. For example, suppose at very low predator densities a predator is satiated in both prey, and, owing to increased competition, as the populations grows satiation turns to non satiation first for prey one and then for prey two. For densities where the predator is non satiated for prey one but satiated for prey two, the last term in (37) drops out because $\partial e_{p2} / \partial N_p = 0$. The remaining middle term on the right side is similar to the negative term in (29) except that in (37) there is the additional cross price effect that is positive.

6 Empirical Examples

6.1 Predator Consumption and Growth Curves

Shapes of growth functions will depend on the specific predator species and the number and characteristics of the prey species. By way of example we construct a GEEM for an eighteen component marine food web off Alaska displayed in Fig. 6. In food webs species are often aggregated into components (Solow and Beet 1998), and here each component is either a single species or a composite of multiple species. The model is age structured only for pollock which accounts for two components: adult and juvenile. Earlier versions of this Alaskan model with fewer components have been described elsewhere (Finnoff and Tschirhart 2003a,b, 2008).[8] GEEM uses real data on species densities, consumptions and the physiological parameters described above for ecosystems comprised of plants, invertebrates, fish and mammals. There are sixteen predators in Fig. 6, nine of which pursue multiple prey. Prey selection by predators change with relative densities and at some densities certain prey may be eliminated completely from the diet as in Owen-Smith and Mills (2008).

In deriving growth curves, all predators and prey are active in that no prey species consumption is held constant as was done in the partial equilibrium analysis for (20). A growth curve for species k is derived by holding its density constant at any level below its carrying capacity, and then simulating the system to allow all other species to reach a steady state. Then the system is run for one more period and the density change in species k is recorded as the growth. The four panels in Fig. 5 show the growth curves for four predators: crab (a

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[8] Other applications of GEEM include foodwebs for the Neus River estuary (Finnoff and Tschirhart 2010), an unprecedented California rodent invasion (Kim et al. 2007), and cattle grazing and elk harvesting on US rangelands (Hussain and Tschirhart 2010).
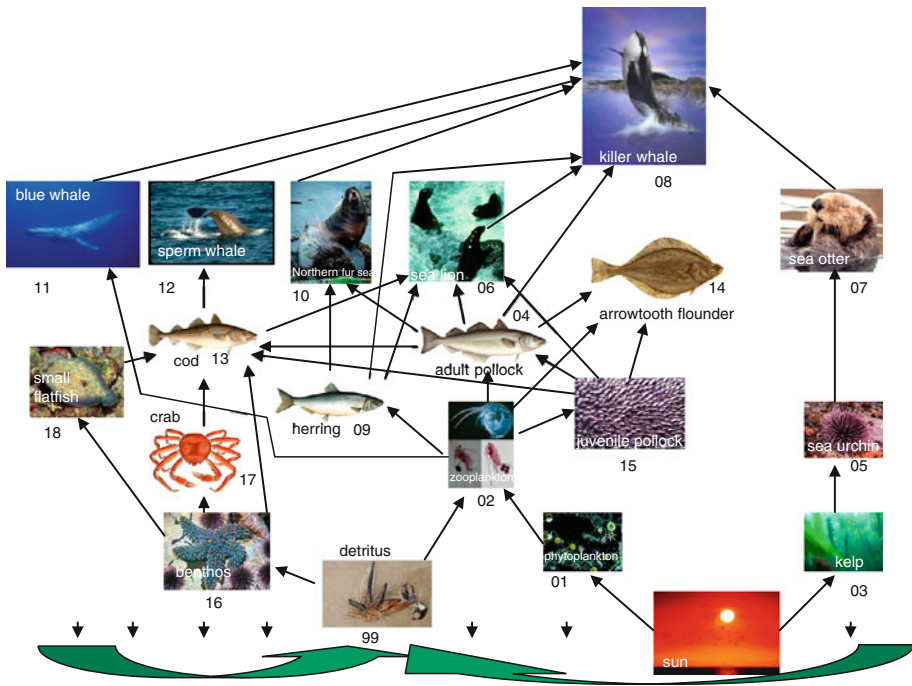
Fig. 6 Food web of an Alaskan near-shore and off-shore marine ecosystem

composite of snow and king crabs), flatfish (a composite of yellowfin sole, flathead sole and Alaska plaice), arrowtooth flounder and Pacific cod.

All curves begin with a linear segment from the origin where the predators are satiated in all their prey. Then the curves move into piecewise-connected, strictly convex segments. Each connection point corresponds to a density where the predator transitions from predator saturation to non saturation in one of its prey. The crab, flatfish, flounder and cod have one, two, three and five connection points, respectively, corresponding to their number of prey as shown in the food web in Fig. 6. Kuhn-Tucker conditions can be used to explain the order of prey over which the predator transitions from being saturated to non saturated as its density increases. For example, arrowtooth (index 14, see Fig. 6) consume adult and juvenile pollock and zooplankton, and the non saturation order is adult pollock ($N_{14} = 58$), juvenile pollock ($N_{14} = 146$) and zooplankton ($N_{14} = 183$). For small arrowtooth densities to the left of $N_{14} = 58$ the following Kuhn-Tucker conditions apply:

$$N_{14}x_{1402} < N_{02}d_{0214}(x_{0201} + x_{0299})^{.5} \Rightarrow e_{1402} = 0$$
$$N_{14}x_{1404} < N_{04}d_{0414}(x_{0402} + x_{0415})^{.5} \Rightarrow e_{1404} = 0 \qquad (38)$$
$$N_{14}x_{1415} < N_{15}d_{1514}x_{1502}^{.5} \Rightarrow e_{1415} = 0$$

$$e_{02} - r_{14} - .5r_{14}(2x_{1402} + x_{1404} + x_{1415}) = e_{1402} = 0$$
$$e_{04} - r_{14} - .5r_{14}(2x_{1404} + x_{1402} + x_{1415}) = e_{1404} = 0 \qquad (39)$$
$$e_{15} - r_{14} - .5r_{14}(2x_{1415} + x_{1402} + x_{1404}) = e_{1415} = 0$$

Conditions (38) imply that arrowtooth demands for all three prey, zooplankton (02), adult pollock (04) and juvenile pollock (15), are less than what these prey species are willing to

supply at the prevailing levels of predation risks. Accordingly the energy costs to arrowtooth are all zero. Arrowtooth satiation in zooplankton implies from the first expression in (39) that the individuals consume zooplankton biomass to the point where the marginal respiration cost of consuming more biomass equals the marginal energy gain, e_{02}. The second two expressions are similar for adult and juvenile pollock prey. Along the linear segment in the lower left panel of Fig. 5, the consumptions of both pollock prey (not shown) are equal and greatly exceed consumption of zooplankton, because pollock energy content exceeds that of zooplankton. Individual arrowtooth in this range are earning positive net energy and arrowtooth density is increasing as per (27). With increasing arrowtooth density, the left sides of (38) are increasing while the right sides change very little, and eventually the left side of the adult pollock expression is the first to become equal to its right side. At this point, arrowtooth is no longer satiated in adult pollock and e_{1404}, the energy cost of consuming adult pollock, turns positive along the first strictly convex segment in the lower left panel. Thus, adult pollock is the first prey item for which the arrowtooth become non satiated, and the reason is related to the density and consumption of adult pollock. Generally, a prey species with higher density and consumption, the latter which means higher predation risk, will be further up in the prey ordering for which the predator becomes non satiated.

The points of connection between segments in the growth curves correspond to substantial predator substitution. Consider for example the cod consumption patterns in Fig. 7 where the cod growth curve is reproduced and below it are the individual cod's consumptions of its five prey as indicated. For low cod densities below $N_{13} = 0.58$ where intraspecific competition is minimal, the individual cod are satiated in crab, adult and juvenile pollock and flatfish, and do not prey on benthos at all. Benthos are the least nutritious in terms of energy content, and with no competition for the other species, the marginal energy gain from consuming benthos is less than the marginal energy loss to respiration and cod predators. Beginning at $N_{13} = 0.58$, the cod density is sufficiently high to generate intraspecific competition for juvenile pollock which drives positive the energy cost of consuming juveniles. In the bottom panel then, each cod substitutes away from the costly juvenile to the 'free' adult pollock, crab and flatfish. Although the decreased kg consumption of juvenile exceeds the increased kg consumption of adult pollock, crab and flatfish combined. Generally, as densities increase across Fig. 7 after the point at which the predator is no longer satiated in all prey (e.g., $N_{13} = 0.58$), consumption totaled over all prey species is decreasing simply because at least one energy cost is increasing, and the others are constant at zero.

At $N_{13} = 1.35$, the greater cod density generates intraspecific competition for crab and the cod substitute away from crab, and continue to substitute away from juvenile, to the remaining free species, adult pollock and flatfish. Moreover, cod begin to feed on benthos. Benthos are now desirable prey because total cod consumption is smaller; therefore, the marginal energy loss to respiration and predation has fallen below the marginal energy gain from consuming benthos. At $N_{13} = 1.90$ and $N_{13} = 2.45$, intraspecific competition for adult pollock and flatfish commence, respectively, and again the cod substitute away from these prey. Finally, at $N_{13} = 3.25$ intraspecific competition for benthos commences, and the cod are no longer satiated in any prey. There is no more substitution and the cod consumptions of all prey decrease proportionately. Alternatively, from the other direction if cod density is started at its carrying capacity and forced to decrease, consumptions of all five prey increase because intraspecific competition is lessening. At $N_{13} = 3.25$ the cod become satiated in benthos first, because benthos offer the least energy nutrition. Consumption of benthos declines as cod substitute to the other four prey.

To further appreciate the strict convexity of the growth curves, consider again arrowtooth in Fig. 5. As arrowtooth density increases, abrupt changes occur in the growth rates around
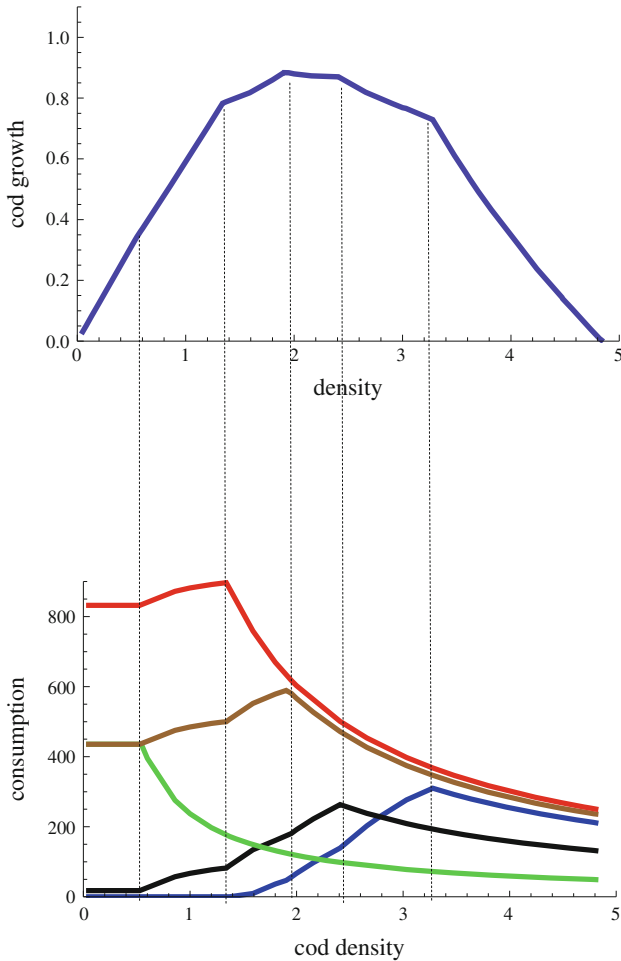
Fig. 7 Cod growth and cod consumption (kg) of its five prey (crab-*red*, adult pollock-*brown*, juvenile pollock-*green*, flatfish-*black*, benthos-*blue*) as functions of cod density. One unit of cod density is 100 individuals per km^2 of surface water. Consumption is kilograms of prey biomass per unit of cod per year

the connection points where an individual becomes non satiated in one of its prey species. These changes follow from the convex shapes of the segments that imply when growth is increasing in density it is at an increasing rate, but when it is decreasing in density, it is at a decreasing rate. Where the growth function is positively (negatively) sloped, to the left of a connection point the growth rate is increasing faster (decreasing slower) than to the right of the point. At a connection point, a prey species that was 'free' turns costly when the predator's marginal search cost for the species moves from zero to positive, and the predator substitutes to greater quantities of other prey that theretofore had been less desirable than the quantities of the free species. This has the effect of slowing down positive rates of growth and speeding up negative rates of growth around connection points. Also, as shown above, from (31), convexity can be linked to competition for prey increasing in predator density at a decreasing rate. Competition for a prey is measured by the cost of capturing the prey, so the search cost for prey is concave in predator density. Therefore, as competition increases

with density, each additional competitor places an ever decreasing drag on existing predator's success in gathering net energy. When species growth is increasing in density, the net energy earned by individuals is decreasing but at a decreasing rate so total growth is increasing at an increasing rate. The opposite effect occurs when species growth is decreasing.

Pollock growth curves can be derived as well although they are omitted here since space does not permit presenting the method used for age-structuring. Briefly, the curve for adult pollock exhibits a strong Allee effect like that shown in the bottom panels of Fig. 2. The interaction between the adult and juvenile populations is complicated, but basically at small adult densities there are too few hatches and, therefore, too few juveniles to provide recruits to compensate for adults lost to predation and old age. Positive growth for adults requires higher adult densities and more hatches, less predation including cannibalism on juveniles, and greater levels of recruitment.

6.2 Yield Curve Nonconvexities

For illustration, constant effort strategies are employed to harvest arrowtooth flounder using its growth curve from Fig. 5. Arrowtooth harvest is $H_{14} = \alpha E_{14} N_{14}$ where E is effort and $\alpha = 1$. The top panel of Fig. 8 shows the harvest, and assuming price of a unit of arrowtooth is one, the harvest is also total revenue. In the bottom panel average and marginal revenues are plotted along with one marginal cost curve.

Yield increases steadily over the range of effort levels from $E_{14} = 0.0$ to $E_{14} \approx 0.169$ where the latter corresponds to the peak of the arrowtooth growth curve in Fig. 5 where $N_{14} \approx 145$. Over this range as arrowtooth density decreases from carrying capacity, arrowtooth transition from being non satiated in all prey to non satiated in zooplankton only at $N_{14} \approx 183$. The transition creates a kink in the yield curve at $E_{14} \approx 0.115$ that in turn creates a kink in the average revenue curve and a discontinuity in the marginal revenue curve. Below $N_{14} \approx 145$ arrowtooth become satiated in juvenile pollock as well as zooplankton, and yield begins to fall rapidly with further effort. For effort levels above $E_{14} \approx 0.23$ the arrowtooth population crashes; $E_{14} \approx 0.23$ is slightly above the arrowtooth growth rate along the linear segment of the growth curve where arrowtooth is satiated in all three prey. Because a species that is satiated in all prey exhibits density independent growth ($\partial \Delta N / N \partial t = $ constant), there is no effort level that will produce a harvesting steady state. Essentially, if individuals in the harvested species are satiated in all their prey, further reductions in the species population will not give individuals any further competitive advantage in hunting prey. The individuals are earning their maximum net energy and the species is at its maximum growth rate; sustained harvest effort levels that exceed this growth rate will drive the population to extinction.

The non convexity of the yield production function has important implications for harvesting strategies. Five of them are:

(1)   With the logistic or most other single species growth functions, the yield function is strictly concave and marginal revenue over effort falls to zero at maximum sustained yield (MSY). Static efficiency requires MR = MC and for MC > 0, the optimum effort must fall left of MSY effort. The optimum MR can be very small, and optimum MR → 0 as MC → 0. For the yield curve generated above, optimum MR > 0 and may be large at MSY. Thus, using a decreasing MR as a signal for approaching MSY may not be useful.

(2)   The discontinuities in the MR curves imply 'sticky' optimum efforts. That is, MC may change significantly, say within the gaps below points b′or c′ in Fig. 8, without changing the optimum effort. (See Bulte 2003) for kinked harvest curves in an LV Holling Type III model.)
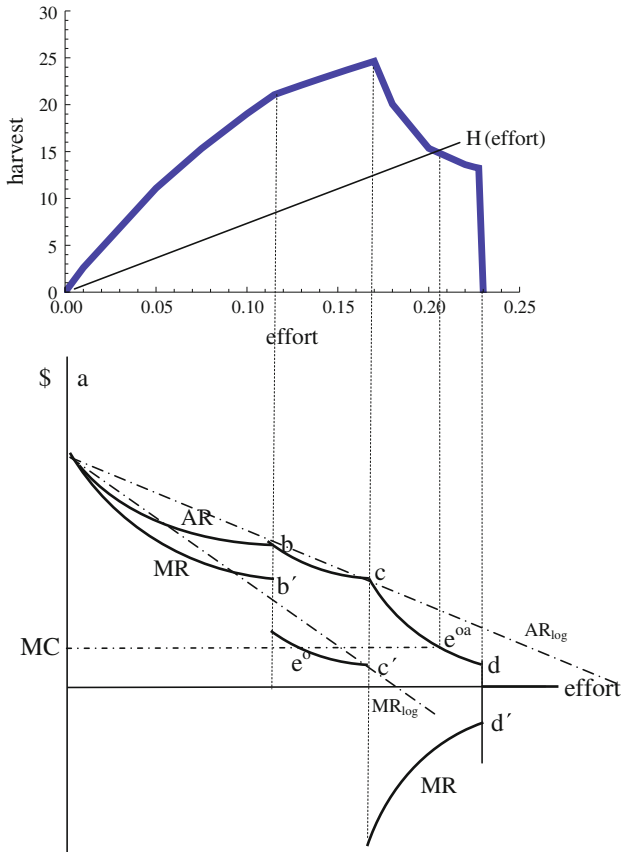
Fig. 8 The yield function for the arrowtooth predator in the top panel where yield is in units of 1 individual arrowtooth per km^2 of surface water. The *bottom panel* shows average revenue and marginal revenue and cost *curves*. The *bottom panel* uses the same horizontal axis as the *top panel*, and the *dot-dash lines* in *bottom panel* are average and marginal revenues from logistic growth in the *bottom left panel* of Fig. 5

(3) In Fig. 8, point e^{oa} represents an open access equilibrium and point e^o the optimum equilibrium for the same marginal cost. Rationalizing the fishery to move from the former to the latter equilibrium by lowering effort will produce efficiency gains as expected; but unexpectedly, the gains initially are increasing in effort reductions, because of the positively sloped, negative portion of MR in Fig. 8. Once point c$'$ is reached, gains from further effort reductions fall off abruptly. In other words, reducing effort yields rapidly increasing rents initially, but then the rent gains fall off sharply.

(4) A logistic growth curve for arrowtooth is shown as the dashed curve in the bottom left panel of Fig. 5. The curve is constructed using the same carrying capacity and maximum growth rate as found for the GEEM-generated curve. In Fig. 8 the average and marginal revenues associated with the logistic growth are plotted as the dashed-dotted curves. Comparing the open access (AR = MC) and optimum (MR = MC) equilibriums, the logistic optimum calls for greater effort than the GEEM optimum, and the logistic open access indicates an effort that would crash the population. Basically, based on Fig. 5, the logistic growth curve shows more robust growth than its

GEEM counterpart; therefore, it rationalizes greater effort levels. Another important difference not shown is that a single-species logistic-growth analysis would rely on a stationery growth curve and an unchanging carrying capacity. But the GEEM growth curves and carrying capacities will change as human activities change. For example, we can show that if the zooplankton steady-state density were to decrease by 10%, perhaps owing to ocean acidification or climate shifts, the arrowtooth growth curve would shrink slightly with a 7% small carrying capacity.

(5) The growth curve for a predator with numerous prey would be constructed from many piecewise, non linear segments. (See for example the growth curve for cod with five prey in the model versus the growth curve for crab with one prey.) Consequently, in fishery management using the logistic or other familiar growth functions may be good approximations for species with many prey, but potentially ruinous for species with few prey.[9] For the one-prey crab from Fig. 5, the yield function would be increasing from the origin and strictly concave up to the MSY effort level, after which it falls off vertically. Thus, at MSY effort the fishery may be very productive with MR substantially exceeding MC, yet a small increase in effort could collapse the stock. Such rapid response of stock density to increasing effort was observed in the infamous 1992 collapse of the northern cod off Newfoundland, once the world's largest stock (Hutchings 1996).

7 Concluding Remarks

Bioeconomic fishery models focus on human behavior and incentive structures, but the simple descriptions of the biology can lead to incorrect conclusions as demonstrated here. This is true in the absence of uncertainty; including uncertainly may add to the errors in the simple ecology models, but adding uncertainty to GEEM would be difficult and beyond the present reach of this paper. Some ecological models of fisheries include considerably more biological detail, although they typically are weak in depicting human behavior (See Whipple et al. 2000) for a review of ecological models.) However, all of these ecological models ignore optimizing behavior by individual organisms so that explaining the shape of growth functions based on the mechanistic representation of predator-prey and competitive relationships is problematic. Accordingly, the techniques employed in GEEM may be useful to adapt to current ecological and bioeconomic models.

This paper shows how non convexities in harvest production functions and the economic implications can be tied to specific biological behavior by individuals in a food web. The harvested species all have been predators, although this is not limiting; all species, including small forage fish such as sardine or herring, are predators of something and would be harvested similarly. Predators are assumed to behave as if they are optimizers responding to price signals, which is consistent with optimum foraging theory in ecology. Satiation and predator substitution among prey are shown to be central in determining growth rates and yields. Basically, harvesting reduces stock density and thereby reduces competition, which means lower-cost predation by individuals in the escapement population. If the stock is depleted enough, costs are reduced to the point where the escapement individuals become satiated in

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[9] The number of prey per predator will vary by age, time of year, and abundances. In the model presented here only some of the major prey are included for each predator, and the consumption/reproduction relations are adjusted for this fact. Still, the number of prey can vary significantly across predators. For example, among the flatfish in our foodweb, yellowfin sole have a significantly more varied diet than flathead sole and Alaska plaice (Lang et al. 1995).

some or all their prey. Complete satiation implies predation is relatively easy, the individuals are earning the maximum possible energy, and the species is growing at its maximum rate. In this situation, a sustained fishing effort higher than the growth rate crashes the stock. In practice, the critical effort level would be difficult to predict because it can occur where marginal harvest revenue is high and well in excess of marginal effort cost.

Satiation and substitution are familiar concepts in economic consumer theory. Several decades ago a host of experiments examined whether these concepts carried over to non human subjects, mainly rats and pigeons (Kagel et al. 1995). The experimenters found that non humans largely behaved as predicable Hicks-Slutsky consumers, weighing the benefits and costs of alternative choices. A working hypothesis in this paper is that such laboratory behavior carries over to the field, a hypothesis that is supported by tests of optimal foraging theory (Stephens and Krebs 1986), and by the individual behavior in GEEM with real ecological data. The results provide insights into how non human behavior affects ecological production functions, and ultimately the delivery of ecosystem services.

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