

Food Web Effects of Prey Size Refugia: Variable Interactions and Alternative Stable Equilibria

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ABSTRACT: Predators can have highly variable effects on the abundance and composition of food webs, ranging from strong to weak effects of top predators. Typical food web models assume that individual prey are identical in their susceptibility to predators throughout their lives, but many prey species become less vulnerable to predators through ontogeny. A simple set of models is explored where prey must pass through a vulnerable stage prior to achieving a predator-invulnerable size refuge. As productivity of the environment increases, the proportional impact of predators decreases because more individuals become and remain in the invulnerable adult stage. The addition of a competitor prey species that can not achieve size refuge results in contrasting outcomes. At low productivity, the small species wins in competition, and the system is strongly consumer controlled. At high productivity, the large species wins due to the presence of predators, and the system becomes less consumer controlled. At intermediate productivity, either the small or the large species can win depending on initial conditions, and the system can be either strongly or weakly consumer controlled. Such alternative stable equilibria derived from models with prey size refugia may help to explain many natural situations.

Keywords: size refugia, food webs, productivity, alternative stable equilibria.

It is becoming increasingly clear that food webs are structured by complex interactions between consumers from the top down and resources from the bottom up (e.g., Oksanen et al. 1981; Carpenter et al. 1985; Leibold 1989, 1996; Power 1992; Wootton and Power 1993; Polis 1994; Chase 1996; Persson et al. 1996b; Leibold et al. 1997). Nevertheless, there is considerable debate about the relative importance of each of these limiting forces and the

degree to which various complexities, such as heterogeneity within trophic levels, influence natural patterns of food web structure and abundance (Polis and Strong 1996; Hairston and Hairston 1997). There has been a recent surge of interest in measuring the relative strengths of these food web interactions (Paine 1988, 1992; Osenberg and Mittelbach 1996; Power et al. 1996; Wootton 1997; Laska and Wootton 1998), and recent meta-analyses have attempted to average the strengths of these forces by comparing and combining the results from multiple studies (Wooster 1994; Brett and Goldman 1996, 1997; Osenberg et al. 1997).

Despite attempts to quantify and average the strengths of resource and consumer limitation in food webs, the relative magnitudes of these interactions can vary considerably over space and time. In fact, there are many reasons to expect that both spatial and temporal variation among food web interactions should be quite common (e.g., Menge 1992; Chase 1996, 1998a; Menge et al. 1996; Travis 1996; Leibold et al. 1997; Osenberg et al. 1997; Chase et al., in press). One way that may lead to a considerable amount of variation in the relative strengths of interactions is when prey vary in their relative susceptibility to predation, such as the case considered in simple food web models (e.g., Vance 1978; Armstrong 1979; Holt et al. 1994; Leibold 1996; Grover and Holt 1998).

While food web models help to explain a significant amount of the variation observed in some natural systems (e.g., temperate lakes: Leibold et al. 1997; grasslands: Chase et al., in press), these models remain highly simplified and do not adequately explain much of the complexity often observed in natural systems. In particular, food web models, while they include variation among species within trophic levels, do not consider variation among individuals within a species throughout their lifetimes. Such ontogenetic changes of individuals within a species often have important ecological implications (e.g., Werner and Gilliam 1984; Wilbur 1988). One way in which nearly all multicellular (and even many unicellular) organisms change over time is that they grow larger. Body size is a fundamental feature of species that affects many aspects

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of their ecology and life history (e.g., Peters 1984). As organisms change in size, they change, among other things, in their abilities to acquire food, to reproduce, and to avoid being killed by predators.

Many ecological systems with strong consumer-limited food webs have predators that are much larger than their prey. For example, rough calculations from one of the most well studied consumer-controlled temperate lake ecosystems (Carpenter and Kitchell 1993) indicate a 10- to nearly 100-fold difference in the size of predator to prey (average algae, 0.05 mm; zooplankton, 1 mm; planktivorous fish, 25 mm; piscivorous bass, 200 mm). Other well-documented trophic cascades include predatory bass feeding on herbivorous minnows (Power et al. 1985), steelhead trout feeding on predatory fish and insects in streams (Power 1990), birds (Marquis and Whelan 1994) and lizards (Spiller and Schoener 1990, 1994; Dial and Roughgarden 1995; Chase 1998a) feeding on insects in terrestrial systems, and sea otters (Estes and Palmisano 1974) and birds (Wootton 1995) feeding on sea urchins; all of these studies describe cases where predators are considerably larger than their prey.

Due to a number of constraints, the ratio of predator : prey size in many systems is often much smaller than that in the strong trophic cascades discussed earlier. When this is the case, the ability of predators to capture prey often varies with prey size (and/or age). I term the case where adults are able to grow too large to be eaten by predators "prey size refugia." Size refugia, or at least large differences in vulnerability to predators from birth to adulthood, are common in widely diverse types of systems and taxa of prey, including marine intertidal invertebrates (Connell 1971; Dayton 1971; Paine 1976), freshwater fish (Werner 1977; Werner et al. 1983; Tonn and Paszkowski 1986; Hambright et al. 1991; Hambright 1994; Persson et al. 1996a), trees (Connell 1971; Dublin et al. 1990), vertebrate herbivores (Errington 1956; Sinclair 1975; Messier 1994), grasshoppers (Schmitz 1993; Chase 1996), anuran tadpoles (Wilbur 1988; Werner and McPeck 1994), freshwater snails (Osenberg and Mittelbach 1989; Chase 1998b), and even microscopic ciliates (Balciunas and Lawler 1995).

In addition to prey size refugia being a deterrent to strong consumer-driven trophic cascades, they have also been implicated as a potential cause for alternative stable equilibria in natural communities. In a system where prey can achieve size refugia, alternative stable equilibria have been suggested to occur under certain conditions; one equilibrium is dominated by predators that control small prey individuals, and another equilibrium is dominated by large prey individuals that are less influenced by predation pressure (Paine 1976; Paine et al. 1985; Bazely and Jeffries 1986; Dublin et al. 1990; Chase 1998b).

In the following sections, I apply a modeling approach for examining food web dynamics on the basis of Holt et al. (1994; see also Grover 1997; Grover and Holt 1998). Specifically, I modify this approach to include variability in prey susceptibility through ontogeny. I show that the ability of prey to achieve size refugia leads to decreasing levels of consumer control with increasing productivity. Finally, I explore the dynamics of two species of prey competing for common resources and consumed by a common predator. One prey species can achieve size refugia, and one cannot. In this scenario, the final outcome can vary from strong to weak consumer control depending on the initial and environmental conditions of the system. Such alternative stable equilibria, however, are only possible under intermediate productivity, not low or high productivity.

Models

A Simple Food Chain Model

To contrast the predictions of simple models with those that consider prey size refugia, I first consider as a building block a simple food chain model with resources, predators, and one prey species that does not change with ontogeny. I use a modeling framework on the basis of Holt et al. (1994; see also Leibold 1996), who used a series of assumptions to collapse a three-dimensional system (three trophic levels) into two-dimensional graphs for ease of presentation and clarity. Similar modeling frameworks (e.g., Oksanen et al. 1981) give identical predictions under similar assumptions. Throughout, I make several simplifying assumptions in accordance with the previous modeling of this system. These assumptions include the following: food is a limiting resource for both predators and prey; consumers do not directly interfere with one another; consumers remove prey at a constant, time-limited rate, that is, a Type I (linear) functional response; different types of resources are substitutable in the consumer's diet (i.e., each resource contains all of the essential factors the consumer needs); and the system is closed so that the amount of nutrients is fixed and is apportioned either in free form or sequestered in consumer biomass. These assumptions appear reasonable as a first approximation, and this modeling framework has been used to develop a number of predictions about community structure (Grover 1994, 1995, 1997; Holt et al. 1994; Leibold 1996; McPeck 1996; Grover and Holt 1998).

Given the above assumptions, the population dynamics of basal resources (R), prey (N), and predators (P) can be described by the following set of differential equations:

$$\begin{aligned}
 dR/dt &= \frac{c'N}{b'} + \frac{cP}{b_p} + aNP\left(\frac{1}{b'} - \frac{b}{b_p}\right) - a'RN, \\
 dN/dt &= N(a'b'R - c' - aP), \\
 dP/dt &= P(abN - c).
 \end{aligned}
 \tag{1}$$

In these equations, parameters with primes refer to components of the prey (N) population, while parameters without primes refer to components of the predator (P). The variable c represents the density-independent loss rate of a species, and thus c is the density-independent loss rate for P , and c' is the density-independent loss rate for N . The variable a is the attack rate of P on its resource (N), while a' is the attack rate of N on its resource (R); b is the conversion of resources (N) consumed by P into new individuals of P , while b' is the conversion of resources (R) consumed by N into new individuals of N . To comply with the assumption of a closed system, the resource dynamics (dR/dt) are given by the amount of nutrients recycled by dead N and P plus the incomplete assimilation (i.e., waste products) of consumed prey minus those resources consumed by N (see, e.g., Holt et al. 1994; Grover 1997 for more detail).

As is typically done, I examine the system along axes of predators (P) and resources (R). To determine how N responds to the P - and R -axes, I set the dynamics of N (dN/dt) in equation (1) equal to 0, and solving for P , yielding

$$P = \frac{a'b'}{a}R - \frac{c'}{a}.
 \tag{2}$$

This equation depicts the zero net growth isocline (ZNGI) of N in relation to P and R . The x -intercept of this line is the abundance of R that N maintains in the absence of P and is solved by setting $P = 0$ in equation (2) and solving for R . In this case,

$$R^* = \frac{c'}{a'b'}
 \tag{3}$$

(R^* is the equilibrium level of resource R that consumer N maintains in the absence of predators, sensu Tilman 1982). With $P > 0$, the slope of the line, given by $a'b'/a$, denotes the effect of adding predators on the ability of N to have zero net growth with R (fig. 1). The shallower the slope of its ZNGI, the more affected N is by P (see Holt et al. 1994; Leibold 1996).

Given the assumption that the system is closed so that

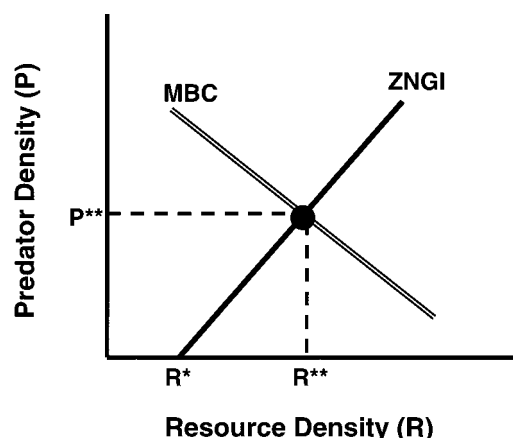


Figure 1: Zero net growth isoclines (ZNGI) of a prey species (N) consuming a resource (R), consumed by predator (P), plotted along predator and resource axes. Overlaid is the mass balance constraint (MBC) line denoting the possible values of P and R in a closed system. The intercept of the ZNGI with the resource represents the ability of prey to reduce resources in the absence of predators (i.e., R^*), and the slope of the ZNGI refers to the relative effect of adding predators on N 's ability to reduce R . The intersection of the ZNGI and the MBC is the equilibrium of the system (filled circle), and R^{**} and P^{**} denote the equilibrium densities of R and P , respectively (after Holt et al. 1994).

nutrient mass balance is maintained (i.e., the total amount of resources in the system is fixed), resource dynamics (dR/dt) are not strictly needed. Because the system is closed, resources are either in free form or tied up in prey or predator biomass. Because the parameters b' and b_p represent the conversion of resources (R) into N and P , respectively, the inverse of these N/b' and P/b_p represents the amount of resources tied up in the populations of N and P , respectively. Thus, for graphical simplicity, rather than presenting R as dR/dt , it can be instead be denoted as

$$R = S - \frac{N}{b'} - \frac{P}{b_p},
 \tag{4}$$

where S is the environmentally determined total amount of resources. Thus, this system contains a mass balance constraint function (MBC) when the predator is at equilibrium. When the predator is in equilibrium, the amount of nutrients in species N 's biomass is fixed, such that the total biomass along the predator and resource axes constrains the possible abundance of P and R along the MBC line. The MBC for this system is given by solving equation (4) for P after substituting the prey's equilibrium density (setting the prey's growth to 0 and solving for N ; $N^* = c/ab$) for N , which gives equation (5):

$$P = b_p \left(S - R - \frac{cb'}{ab} \right). \quad (5)$$

This MBC line has a slope of $-b_p$ and an intercept that is determined both by the species-specific parameters and the total resources in the system. The MBC line can be plotted on the same P - and R -axes as the ZNGI for N to determine the equilibrium point for P and R of the system (P^{**} and R^{**}) (fig. 1). As the MBC is partially determined by the supply of resources (S), increasing the environmentally determined productivity rate moves the MBC line to the right (i.e., increases the x - and y -intercepts linearly), which increases the equilibrium densities of P and R , but not N (this result is identical to that predicted from Lotka-Volterra-type food chain models; Oksanen et al. 1981; Holt et al. 1994).

This simple food chain has been made more complex in a variety of recent models by exploring how two prey species (N_1 and N_2) compete for a common resource (R) and are consumed by a common predator (P) (Holt et al. 1994). Briefly, the key features of this model predict that for the two species to coexist locally, two primary trade-offs must be upheld: first, the species must trade-off their efficiency to utilize resources (R^*) relative to their susceptibility to predators (slope of the ZNGI), and second, the species that is more susceptible to predators (and thus more efficient at consuming resources) must be able to maintain higher densities of predators than the other species (i.e., higher MBC); that is, the more susceptible species is better food for the predator's population. In addition to these two conditions, the supply rate of the resources must be such that the intersection of the ZNGIs falls between the two MBCs for the species to coexist. These conditions will be met at intermediate productivity. At low productivity, the more efficient species (i.e., more susceptible to predators) is predicted to win, whereas at high productivity, the less susceptible prey species (i.e., less efficient) is predicted to win. For much more detail and analytical analyses for this basic model, see Holt et al. (1994), Grover (1995, 1997), Leibold (1996), McPeck (1996), and Grover and Holt (1998).

A Food Chain with Prey Size Refugia

As discussed earlier, while most models assume that individuals do not change through time, individuals often vary considerably in a number of attributes with age. For mathematical tractability, I consider a relatively simple two-stage model to capture the main dynamics of a system in which small individuals (juveniles; N_j) are susceptible to predators, while large individuals (adults; N_A) are com-

pletely invulnerable. Only adults can reproduce. Both life stages consume the same resources (R). Juveniles (N_j) convert their resource acquisition into growth to the adult stage at rate g_j' , and have density independent mortality at rate c_j' . Adults (N_A) convert their resources into reproduction to the juvenile stage at rate b_A' and have their own density-independent mortality rate (c_A'). The dynamic equations for such a system, by using a formulation similar to that used in equation (1), are

$$\begin{aligned} dR/dt &= \frac{c_A'N_A}{b_A'} + \frac{c_j'N_j}{g_j'} + \frac{cP}{b_p} + aN_jP \left(\frac{1}{g_j'} - \frac{b}{b_p} \right) \\ &\quad - a_j'RN_j - a_A'RN_A, \\ dN_j/dt &= a_A'b_A'RN_A - g_j'a_j'RN_j \\ &\quad - c_j'N_j - aN_jP, \\ dN_A/dt &= g_j'a_j'RN_j - c_A'N_A, \\ dP/dt &= P(abN_j - c), \end{aligned} \quad (6)$$

where the remaining parameters (a 's, b 's and c 's) are as in equation (1).

To view this more complicated system, with a two-stage life history (i.e., juvenile and adult), in the same manner as the simpler one-stage system considered above, I solve for the equilibrium densities of juveniles (N_j^*) and adults (N_A^*). As with any typical consumer-resource interaction, the equilibrium density of susceptible juveniles is given by setting the dynamics of predators (dP/dt) equal to 0 and solving for N_j , which gives

$$N_j^* = c/ab. \quad (7)$$

Next, the equilibrium density of adults is determined by setting $dN_A/dt = 0$, substituting N_j^* (eq. [7]) for N_j and solving for N_A , which gives

$$N_A^* = \frac{g_j'a_j'bcR}{ac_A'}. \quad (8)$$

Combining the dynamics of prey into a single equation ($dN_j + dN_A$), setting them both equal to 0, substituting N_j^* (eq. [7]) and N_A^* (eq. [8]) for N_j and N_A , respectively, and solving for P thus yields the ZNGI for the entire prey population on P - and R -axes:

$$P = g'_j a'_j \frac{R(a'_A b'_A R - c'_A - c'_j)}{a} \quad (9)$$

Thus, the ZNGI of a species with predator-susceptible, nonreproductive juveniles and predator-invulnerable, reproductive adults has an x -intercept (R^*) given by setting $P = 0$ in equation (9) and solving for R , which gives

$$R^* = a'_j c'_A g'_j + \sqrt{a'_j c'_A g'_j \left(\frac{-4a'_A b'_A c'_j + a'_j c'_A g'_j}{2a'_A a'_j b'_A g'_j} \right)} \quad (10)$$

and a nonlinear, exponentially increasing function with $P > 0$, indicating that prey is less dynamically affected by predation with increasing resource productivity (R ; fig. 2).

As above, the resource dynamics (dR/dt) are assumed to be in a closed system, where resources are either in free form (S), in juvenile (N_j/b'_j) or adult (N_A/g'_j) prey, or in predators (P/b_p). Thus the equation for resources can be given by a mass-balance term:

$$R = S - \frac{N_j}{b'_j} - \frac{N_A}{g'_j} - \frac{P}{b_p} \quad (11)$$

As above, N_j^* (eq. [7]) and N_A^* (eq. [8]) can be substituted for N_j and N_A in equation (11), which upon solving for P gives the MBC line for this system:

$$P = b_p \left(\frac{-bcc'_A - a_j b b'_j c R - a'_j c'_A R + a'_j c'_A S}{a b'_j c'_A} \right) \quad (12)$$

(fig. 2). Note that this MBC has a steeper slope than the MBC for the species without a size refuge adult stage. This is because the adult size refuge allows prey to be less dynamically affected by predators but still supply food for predators through susceptible juveniles. Here, as the environmental resource supply (S) increases, the position of the MBC moves to the right. The equilibrium where the MBC and ZNGI intersect becomes proportionally less distant from the origin with increasing total resources (R), and thus the relative impact of P on N becomes increasingly smaller with increasing resources. This is because, with increasing resources, the number of juveniles growing to size refuge adulthood increases. However, increasing resources also increases the number of juveniles being born to adults, which allows food for predator consumption. Here, in opposition to the pattern predicted without age structure, both P and N ($= N_A + N_j$) increase, while R

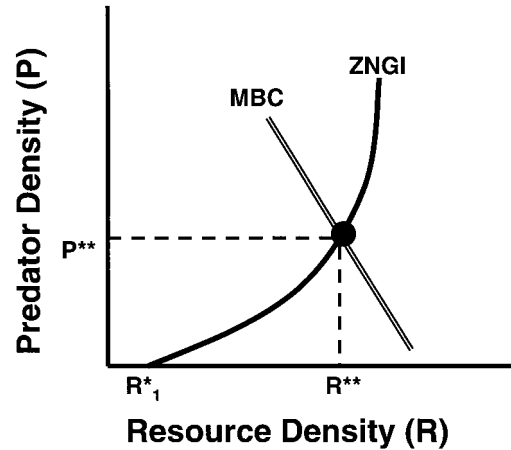


Figure 2: ZNGIs and MBCs for a species that has a two-stage life history: one stage, predator-vulnerable, nonreproductive juveniles, and the other stage, predator-invulnerable adults. The intersection of the ZNGI and the MBC is a stable equilibrium, and R^{**} and P^{**} are as in figure 1.

increases to an asymptote, with increasing productivity or resource supply (S). In addition, the relative strength of the effect of predators on the food chain, and the consequent trophic cascade, declines with productivity due to the nonlinear ZNGI (for an empirical example of this effect, see Balciunas and Lawler 1995).

Two Prey Species: One Can Achieve Size Refugia, One Cannot

Next, I consider the case where two prey species compete for common resources but are consumed by common predators. This scenario is qualitatively similar to the one modeled previously by Holt et al. (1994) and Leibold (1996), except that in this case defense against predation is conferred through ontogenetic variation and size refugia. For maximal contrast, I consider the case where one prey species is equally susceptible to predators at all ages (as in eq. [1])—hereafter referred to as species 1, while the other prey species has an ontogenetic shift such that it grows through a susceptible juvenile stage to an invulnerable adult stage (as in eq. [6])—hereafter referred to as species 2. In this article, I only consider the case where the competitive ability of the species without the size refuge is greater than that of the species with a size refuge in the absence of predators ($R_1^* < R_2^*$; eq. [3] < eq. [9]). This type of scenario is expected if there is some fitness cost (in physiological maintenance and growth) associated with delaying reproduction in deference to somatic growth, creating a trade-off between resource competition and size-related defense against predation. Other possibilities of the

relative positions of the two species' ZNGIs (e.g., the ZNGIs do not intersect) are plausible, but not interesting for the dynamics discussed here.

Given the assumed tradeoff between size-related defense and resource competition, the ZNGIs of these two species cross only once in the positive state space (fig. 3), satisfying the first criterion for stable local coexistence. Thus, the nonlinearity of the ZNGI for species 2 does not, in and of itself, lead to dynamics fundamentally different from a linear ZNGI. Recall from above, however, that for two species to have stable local coexistence, two other conditions must be met. First, their ZNGIs must intersect at a point between the MBCs for each species. This condition will depend on the environmental resource supply to the system. Second, the MBC for the better resource competitor (lower R^*) must be above and to the right of the MBC for the worse resource competitor. This condition is due to the nature of the species interactions and should often be true in simple, unstructured food web models (e.g., McPeck 1996). Specifically, under simple conditions, it is expected that a species that is a better resource competitor, but more susceptible to predators, should be relatively better food for that predator (i.e., have a higher MBC).

However, when prey change in their vulnerability to predators with age, a very different outcome is possible. Because juveniles are highly susceptible to predators, but invulnerable adults continue to supply juvenile prey in a donor-controlled fashion, it is possible that species 2 (the defended species) can be better food for predators and thus maintain a higher MBC. If this statement is true, the relative positions of the MBCs would be reversed and not lead to a locally stable coexistence of the two species. Specifically, if the inequality

$$b_{p_2} [(-b_2 c_2 c'_{A_2} - a'_1 b_2 b'_{A_2} c_2 R - a_2 b'_{A_2} c_{A_2} R + a_2 b'_{A_2} c'_{A_2} S) / a_2 b'_{A_2} c'_{A_2}] > b_{p_1} \left(S - R - \frac{c_1 b'_1}{a_1 b_1} \right) \quad (13)$$

is satisfied (where parameters with "2" subscripts [e.g., a_2, b_2] refer to species 2's parameters, whereas parameters with "1" subscripts [e.g., a_1, b_1] refer to species 1's parameters), the MBC of species 2 lies above and to the right of the MBC for species 1.

If inequality (13) is satisfied, the species that maintains the lowest density of resources (R^*) in the absence of predators also maintains the lowest density of predators (P^{**}) and there is no trade-off between resource competition and apparent competition (sensu Holt et al. 1994). Resulting from this reversal of the position of the MBCs in this size-structured food web, when the ZNGIs cross

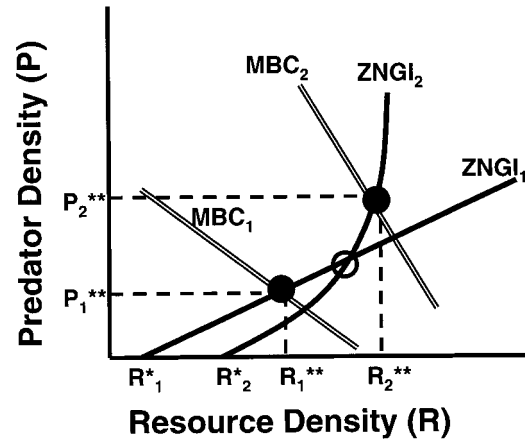


Figure 3: ZNGIs and MBCs for two species, one with a simple life history, as in figure 1 (species 1), and one with a two-stage life history, where juveniles are susceptible to predators, but adults are invulnerable, as in figure 2 (species 2). When the ZNGIs cross within the two MBC lines, the intersection of the ZNGIs is an unstable equilibrium (open circle). Intersections of each species' ZNGI with its MBC are also feasible equilibria, both of which are locally stable (closed circles). Equilibria in which the system will rest will depend on initial conditions.

within the two MBCs, there are three possible equilibria, two of which are locally stable (fig. 3). Whereas each species increases towards its MBC to the right of its ZNGI, the equilibrium where the two species coexist is unstable. Instead, the two locally stable equilibria occur where each species exists alone (Holt et al. 1994; Grover and Holt 1998). Thus, the realized equilibrium of the system will depend on the initial conditions. That is, when a species that can achieve size refugia competes with a species that cannot achieve such a refuge in the presence of predators, alternative stable equilibria are possible. One stable equilibrium is characterized by dominance by the smaller species that cannot achieve a size refuge. Here, predator effects are relatively strong. The other stable equilibrium is characterized by dominance by the larger species that achieves size refuge after growing through a susceptible phase. In this case, predator effects become relatively weaker.

The plausibility of whether these alternative stable equilibria will be realized also depends on environmental conditions, in particular the total resource supply (S). Figure 4 shows the effect of varying S on the dynamics of the system. The first set of MBC lines represents a low-productivity system (low S). Here, the MBCs are to the left of the intersection of the ZNGIs, and species 1, which cannot achieve a size refuge, has a lower R^{**} and P^{**} and wins in competition but is strongly predator limited. The second set of MBC lines represents an intermediate-productivity system (intermediate S). Here, the ZNGIs inter-

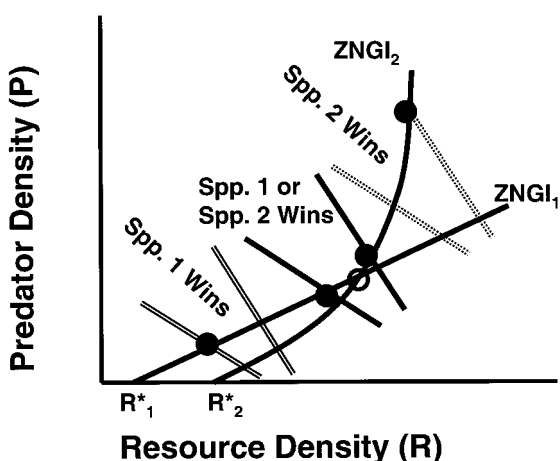


Figure 4: Effect of varying resource productivity in the system shown in figure 3. Productivity is indicated by the relative positions of the MBCs. At low productivity, denoted by double-lined MBCs, only the equilibrium where the small species (species 1) exists alone is feasible (and stable). At intermediate productivity, denoted by solid MBC lines, the dynamics are as in figure 3, with three possible equilibria, the outer two of which are stable, with the final outcome depending on initial conditions. At high productivity, denoted by dotted MBC lines, only the equilibria with the species that can achieve size refugia (species 2) is feasible.

sect within the MBCs, and the system will be dominated by either species 1 or species 2 (as described earlier), depending on initial conditions. In this scenario, predators have either a large or a small relative impact on prey populations for species 1 and species 2, respectively. The highest set of MBC lines represents a high productivity site (high S). Here, species 2, with a size refugia, dominates, and the relative impact of predators is smaller.

To summarize, this model predicts that at low productivity, small prey species should dominate but be limited by predation, showing relatively strong trophic cascades. At intermediate productivity, either small or large species can dominate, depending on initial conditions, and predators have either strong or weak effects. Thus, at intermediate productivity, alternative stable equilibria are expected. Finally, at high productivity, large prey are expected to dominate, and predators should have relatively weak effects, with consequently weaker trophic cascades (fig. 4).

Limitations and Extensions of the Simple Models

One of the most important simplifications of the above modeling scenario is that inorganic nutrients are considered to be the limiting factor for the prey species. This is so that the mass-balance assumption (the amount of nutrients in the system are fixed) can be used to constrain the system into the two-dimensional graphical approach

outlined by Holt et al. (1994). The MBC approach was developed, and is primarily used, with an empiric system of plants in mind. Plants are generally limited in some form by such nutrients, and thus the MBC assumptions are likely to be upheld. In the strictest sense, then, the model developed above would be most directly related to plant species that ontogenetically vary in susceptibility to consumers (herbivores in this case); indeed, several types of plants, from algae to woody species vary considerably in size and susceptibility to herbivory throughout their lives.

Nevertheless, the basic model presented above can be generalized to situations where some currency other than nutrients, such as energy, is the limiting factor. This might be more likely when considering cases where the prey species of consideration are animals. When energy is limiting, the strict assumptions of mass balance to model the dynamics of the resource population (eqq. [4], [11]) do not hold because energy is lost through entropy. However, Leibold's (1996) model makes predictions that are nearly identical to Holt et al.'s (1994) under similar conditions but is not similarly restricted by a mass-balance constraint.

Leibold (1996) models basal resources by using rates of supply and rates of impact, as might be expected in an energy-limited system. In this case, the stability of the system is determined by examining the relative positions of the impact vectors and supply vectors (in a manner analogous to Tilman 1982). If each species has a greater impact on the factor that most limits it (predators or resources), the species will coexist provided their ZNGIs intersect and the supply of resources falls between the impact vectors (Leibold 1996); a result directly analogous to Holt et al.'s (1994) prediction that the species will coexist if the MBC for the better resource competitor (and more predator susceptible) is above and to the right of that of the other species. Alternatively, as I have shown above (see also Holt et al. 1994; Grover and Holt 1998), if the worse resource competitor (and less predator-vulnerable) species is better food for predators, the relative position of the MBCs is reversed such that stable coexistence between the species is not possible. Similarly, in Leibold's (1996) formulation, if each species has a greater impact on the factor that is least limiting to it (e.g., the less vulnerable prey species has a greater impact on predators [i.e., is better food] than the more vulnerable species), coexistence will not be possible, and one or the other species will exist alone, depending on initial conditions. This result is qualitatively identical to the one predicted with the mass-balance assumption presented above.

Another potential limitation of the model presented here is that I explicitly assumed that predators have a Type I (linear) functional response, whereas a Type II (saturating) functional response might be more appropriate under

many biological conditions. While Leibold (1996) has shown that saturating (Type II) functional responses can give similar predictions to the linear case under many cases, Abrams's (1999) more complete analyses show several situations where the parameter values leading to coexistence or exclusion can vary depending on the shape of the functional response. However, this result will not likely change the qualitative conclusions of the models presented here. In the case of a size-structured population, the Type II functional response will influence the number of individuals that grow from the juvenile stage to the adult stage but will not influence adult reproduction or death in any way. This decoupling of the juvenile stage eaten by predators from the reproductive stage will dampen the effects of any complexities in the functional response on the overall dynamics of the system (Abrams and Walters 1996). Thus, while including a Type II (or more complicated) functional response is beyond the scope of this article, such complexities will only change the relative positions of the ZNGIs and MBCs but will not, except under extreme conditions, change the qualitative predictions of the analyses presented here.

As a final consideration, the models I have presented above are highly simplified caricatures of how stage-structured interactions must really work in natural systems. I have assumed only two stages and that only resources (and not other physiological constraints) limit the number of juveniles growing to adulthood and the reproduction of adults. To do a proper stage-structured model of this sort of situation, a much more complicated (and less general) analysis would be needed. While such a complete analysis would be instructional, it is unlikely that the qualitative conclusions of this much simpler model would be dramatically changed. In addition, my assumption that adults and juveniles consume the same resource is central to the specific predictions presented above. However, it can often be the case that juveniles and adults do not consume the same types of food (e.g., Werner and Gilliam 1984). Such a situation will undoubtedly change the shapes and positions of the ZNGIs and MBCs, specifically, the nonlinearity of the ZNGI. However, the qualitative conclusions of alternative states will be robust provided that juveniles provide sufficient food for predators such that the positions of the MBCs are reversed relative to the case without size structure.

Discussion

Many species of prey are quite large relative to their predators. In fact, predators often can only effectively capture young individuals of a prey species, while healthy adults remain relatively safe. Such ontogenetic changes in susceptibility are frequently achieved through size-related de-

fenses, but other types of defenses such as structures or chemicals can also vary with age. Although size refugia were emphasized in the above models, any sort of ontogenetic changes where adults are less vulnerable to predation than are juveniles will have similar effects.

The stability of simple food webs with prey species that vary in their susceptibility to predation with age have been considered in models of slightly different form (Hastings 1983; McNair 1987; Abrams and Walters 1996). However, these models did not consider how such ontogenetic changes might influence the relative importance of consumer limitation or how environmental or initial conditions might influence the outcomes of the interactions.

Ecological systems that show strong consumer control tend to have prey much smaller than their predators, including birds and lizards consuming insects (Spiller and Schoener 1990, 1994; Marquis and Whelan 1994; Dial and Roughgarden 1995; Chase 1998a) and fish consuming smaller fish and invertebrates (Power et al. 1985; Leibold 1989; Power 1990; Carpenter and Kitchell 1993; Brett and Goldman 1996; Leibold et al. 1997). The types of dynamics discussed above, however, where prey can grow too large to be effectively killed and consumed by predators, seem to be an important way in which prey can reduce predator efficiency in some circumstances (Errington 1956; Paine 1976; Paine et al. 1985; Hambright et al. 1991; Hambright 1994; Balciunas and Lawler 1995; Persson et al. 1996a; Chase 1998b).

The well-studied trophic cascade in temperate lakes is often considered to be one of the few success stories showing strong food web interactions in a natural ecosystem (Polis and Strong 1996) and has even been suggested to be one of the few successful generalities of community ecology (Lawton 1999). However, a recent review shows that the trophic cascade in lakes can be highly variable (Leibold et al. 1997). Indeed, it is interesting to note that in the most often cited example of these lake trophic cascades by Carpenter and Kitchell (1993), the common planktivorous fish were small minnows of the family Cyprinidae, narrow-bodied and soft-finned fish that are highly susceptible to piscivores throughout their lives (see also Vanni et al. 1990; Mittelbach et al. 1996). However, the dominant planktivorous fish in many eastern North American temperate lakes are bluegill, *Lepomis macrochirus*, and other members of the rotund, spiny-finned Centrarchidae fish family. These planktivores can frequently grow too large to be effectively captured and eaten by piscivores, and the trophic cascade can be weakened or averted (e.g., Werner et al. 1983; Hambright et al. 1991; Hambright 1994; Mittelbach et al. 1996; Persson et al. 1996a).

An interesting and important feature of the models described above is that alternative stable equilibria are pos-

sible, depending on initial conditions. Alternative stable equilibria have been suggested under a number of theoretical conditions. If alternative stable equilibria are common in nature, this can have profound impacts on the way we view and manage the natural world (e.g., May 1977). However definitive evidence for alternative stable equilibria in natural communities, particularly experimental evidence, has been lacking (e.g., Connell and Sousa 1983; Sutherland 1990; Knowlton 1992). In addition, there are often many potentially confounding and complicated factors that make it difficult to understand or predict whether true alternative states equilibria exist and what the mechanisms might be that lead to them.

Grover and Holt (1998) present a model of similar form to the one presented here, where another mechanism, that of adaptive predator behavior, can also lead to the existence of alternative stable equilibria in a food web. In fact, there are probably a number of mechanisms that can lead to alternative stable equilibria in models of similar form. Any mechanism that causes a prey species that is less dynamically affected by predators to also be better food for predators will cause the relative position of the MBC lines to reverse and will lead to potential alternative stable equilibria. Furthermore, Van der Koppel et al. (1996) present a model that predicts alternative stable equilibria under intermediate productivity conditions due to decreasing consumer abilities with increasing resource standing crops (i.e., a hump-shaped functional response). These models use different mechanisms but make very similar predictions to the ones presented above. Nevertheless, the mechanism of size refugia (or other changes in defense through ontogeny) provides a potentially important mechanism that may lead to alternative stable states in a variety of natural communities. Indeed, some of the best documented cases of alternative stable states in natural systems may be interpreted in the light of such size-structured models.

Paine (1966) removed a common starfish from the intertidal zone off the coast of Washington State, and found a dramatic increase in abundance of mussels. However, starfish were unable to revert the site back to its original state after starfish were allowed to recolonize the experimental area because of the large, invulnerable size achieved by the mussels (Paine 1976). Paine et al. (1985) found a similar result of alternative states after a starfish removal and reinvasion experiment in New Zealand but found no such evidence from an identical experiment in Chile. In light of the model presented earlier, I would predict that both the Washington and New Zealand sites would be relatively productive because alternative states appeared to be maintained. However, the mussels at the Chile site were unable to achieve size refugia, suggesting that it might be less productive. Unfortunately, the productivity rates of

these intertidal communities are not readily known, and thus an explicit test of the above models with these results is impossible.

Vertebrate herbivores often play a large role in influencing plant abundance and diversity and have also been implicated in potentially maintaining alternative stable states due to size refugia (e.g., Connell 1971; Bazely and Jeffries 1986; Dublin et al. 1990; Dobson and Crawley 1994). For example, in the Serengeti of Africa, herbivores (particularly elephants) have been suggested to maintain alternative stable states between grasslands and woodlands (Dublin et al. 1990). Similarly, in an experimental study, Bazely and Jeffries (1986) excluded herbivorous geese from a salt marsh community, showing a major change in plant abundance and species composition. After herbivores were allowed to reenter the plots, they were unable to revert the system, then dominated by large shrubs, back to its original state.

Finally, a system I have studied also appears to conform to the types of dynamics discussed here (Chase 1998*b*). Results from surveys and experiments showed that at low productivity, predators strongly limited herbivore biomass, dominated by small species, and had cascading indirect effects extended to plants. At intermediate productivity, initial conditions influenced the final outcomes, one outcome with strong predator effects on small herbivore species, and the other with weaker predator effects on larger herbivore species. At high productivity, large herbivores dominated regardless of initial conditions, and predators had relatively weak overall food web effects.

To conclude, body size is an important feature of species, influencing a number of aspects of their ecology and life history. The dynamics modeled in this paper can also have important implications for a species' life-history decisions. Optimal life histories are determined by balancing the costs and benefits that are associated with investment into somatic growth and reproduction. If body size influences mortality associated with predators, prey species should adjust their life histories to maximize their expected fitness (e.g., Crowl and Covich 1990; Resnick et al. 1990; Abrams and Rowe 1996). Such life-history decisions may have important influences on food web dynamics, including the potential for alternative stable states depending on initial conditions and plastic life histories. These types of prey life-history decisions in relation to food and predation pressure, and consequent food web effects are considered in a companion article (Chase 1999).

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