Chapter 23

Feast and Famine in Food Webs: The Effects of Pulsed Productivity

Anna L. W. Sears, Robert D. Holt, and Gary A. Polis

Food webs are a useful way of describing and organizing relationships among species, but for the most part descriptions of food webs have been closed in space and static in time. This volume emphasizes that food webs are part of dynamic landscapes. Wind, water, and animals move materials far from their point of origin, across habitat boundaries. This flow between habitats is an intrinsic part of most food webs. In this chapter we add the dimension of time, focusing in particular on temporal variation in productivity. Environmental conditions are in constant flux. Below the pulse of shifting seasons there is a low rumble of climate change. It is still impossible to predict the weather accurately more than a week in advance. Temporal variation, like spatial variation, is not well integrated into food web dynamics. However, ecologists are beginning to assemble the theoretical tools, the empirical evidence, and the computer power needed to analyze the temporal dimension of food webs.

Temporal variation in productivity is in many ways analogous to spatial variation. In each case, a more productive compartment (in space or time) can provide a subsidy to a less productive one. Rather than being transported from one place to another, resources move through time from one period to another. A temporal subsidy may consist of alternative prey species, available when primary prey are in low abundance, or fat stores and food caches preserving resources from a more productive season. Passive dispersal in spatially heterogeneous environments typically leads to diffusion from higher to lower densities, which in ecological systems usually means from more to less productive habitats. Spatial effects tend to be asymmetric, with flows having more pronounced effects in less productive habitats. In a similar way, seasons, years, or life stages experiencing resource abundance can lead to bottlenecks in other seasons, years, or life stages if, for example, high densities overexploit resource pools or there are strong time-lagged responses by predators or infectious disease agents.

The analogy between flows in space and time is not perfect, however. Time moves in a single direction, and there is no reciprocal flow between temporal compartments. However, if the temporal subsidy is a living resource, such as an emergence of seventeen-year cicadas, predation in a pulse year may limit the magnitude of the next pulse. In contrast, spatial subsidies are often donor-controlled. Donor control implies that recipients do not affect the abundance or renewal rate of the subsidy. Marine wrack washing onto beaches is an example of a donor-controlled spatial subsidy (Polis, Anderson, and Holt 1997). A temporal subsidy is donor-controlled if it involves a pulse of detritus or abiotic inputs such as rainfall.

There is also a fundamental difference in how variation in space and variation in time affect population dynamics. Consider a species with discrete populations: in spatial population models of well-mixed systems, the finite rate of increase (λ) is dependent on the arithmetic mean of conditions across habitats. By contrast, with temporal heterogeneity (in which all individuals in a population experience the same conditions in a given year), λ is dependent on the geometric mean of conditions across years. The effects of bad years tend to dominate geometric means. However, the effects of favorable patches—pulses of growth in space—have much stronger effects on λ than the effects of good years—pulses of growth in time (Chesson 1985, 2000a). In short, the effects of bad years are stronger, and the effects of good years weaker, than the equivalent variation in space. Thus, in space and in time, the quality of the variation determines how it quantitatively affects the magnitude of λ.

In many situations, spatial and temporal subsidies are closely bound together. Transport through space is often seasonal, and at the very least includes a time lag between production and utilization of resources. For example, there is a time lag in the spatial subsidies of riparian systems. Materials that enter small tributaries from leaf litter and runoff are slow to work their way into the food webs of larger rivers. Fish (Winemiller and Jepsen, chap. 8, and Willson et al., chap. 19 in this volume) and birds (Jefferies, chap. 18 in this volume) transport nutrients between habitats, and their migratory patterns lead to pulses of productivity for their predators. Terrestrial-marine interchanges (Polis, Anderson, and Holt 1997) show tremendous temporal variation. On the Peruvian coast, El Niño leads to massive starvation of seabirds and marine mammals, whose carcasses litter the beaches. Ontogenetic shifts can also lead to time-lagged spatial subsidies, as when metamorphosing mayflies leave the aquatic environment for the terrestrial habitat. Terrestrial predators are thus subsidized in pulses by pond and stream communities (Nakano and Murakami 2001).

The purpose of this chapter is to review and synthesize current knowledge about the ways in which temporal heterogeneity in productivity may influence food web dynamics. There are three primary reasons for including this material in a book on spatial subsidies to food webs. First, as mentioned above, there are strong analogies between spatial and temporal variation in resources, and they can have similar dynamic effects. Second, because of these similarities, the theoretical work on temporal fluctuations is relevant to our development of spatial subsidy theory. Third, because of the pulsed nature of many spatial subsidies, researchers studying allochthonous inputs in food webs need to consider the possible influence of this temporal variation. At this time, there is little synthetic theory incorporating both temporal and spatial subsidies (but see Chesson 1985; Holt 2002; Holt and Barfield 2003; Holt et al., in press; Gonzalez and Holt 2002). Note that our focus on variation in production is only one slice through the broad topic of temporal variation in food web ecology, which includes disturbance regimes, fluctuations in interaction strengths, and colonization-extinction dynamics. Our empirical examples are biased toward terrestrial studies, but the theoretical insights are general to all systems.

As a prelude, we highlight the ubiquity of pulsed productivity in natural systems. We also note the importance of nonlinearities and how they affect population responses to environmental variation. As temporal fluctuations are rarely explicitly incorporated into formal food web theory, we start with what is known about the influence of environmental fluctuations on single-species population dynamics. We then examine predator-prey dynamics, first for specialist predators and then for generalist predators. A substantial amount of theory and empirical work has examined the effect of temporal variation on competition and diversity maintenance, especially in plant communities, and this work has suggestive messages for food web ecology. We end the chapter with a consideration of relevant empirical studies of food webs in fluctuating environments and draw some broad conclusions from our review.

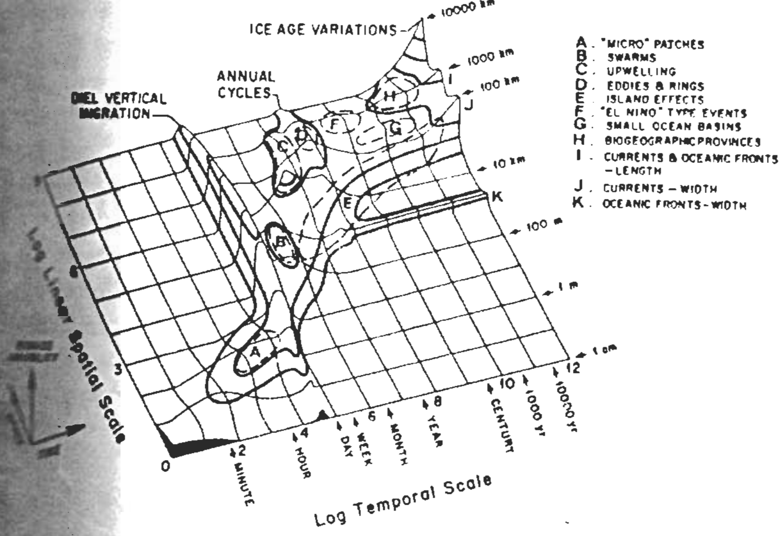
PRELUDE

The Ubiquity of Temporal Variation in Productivity

Resources fluctuate for all organisms along the trophic spectrum. [illegible] ductivity varies through time with rain, temperature, and sunlight. In [illegible] systems, nutrient levels may be shifted by seasonal upwelling, [illegible] pulses of terrestrial runoff and dust. Variation in plant productivity [illegible] into variable resource supplies for herbivores. Likewise, resources [illegible] tivores vary with plant productivity, the timing of release, and [illegible] ation in the microbial processes that break down plant material. [illegible] decomposition rates vary with temperature and moisture levels. [illegible] source availability for higher-level consumers is a function of [illegible] productivity and the accumulated biomass of herbivore and [illegible] populations.

Resource variation may arise from a variety of abiotic forces [illegible] different time scales (fig. 23.1). On a short-term local scale, daily [illegible] in light availability (De Madariaga 1995) and water mixing by [illegible] (Moline and Prezelin 1996) can cause high variation in [illegible] phytoplankton biomass. On longer time scales, but with regular [illegible] strong seasonal fluctuations in productivity reflect changes [illegible] precipitation, and temperature. Grasslands respond to annual [illegible] and Singh 1978; Sala et al. 1988; Pandey and Singh 1992), litterfall [illegible] ical forests occurs mainly in the dry season (Tanner 1980), and [illegible] ties of fruit flies rely on winter frosts to create feasts of necrotic [illegible] columnar cacti (Breitmeyer and Markow 1998). The arrhythmic [illegible] El Niño Southern Oscillation (ENSO) events causes global-scale [illegible] precipitation patterns every 2 to 7 years (Enfield 1989). El Niño [illegible] heavy rains to the eastern Pacific and drought to India, [illegible] Australia, and southern Africa, strongly affecting the productivity [illegible] regions (Wright et al. 1999). For example, Cane et al. (1994) [illegible] temporal variation in sea surface temperatures in the eastern [illegible] Pacific could explain over 60% of variance in maize yield in [illegible] Several longer-period oscillations in Pacific Ocean temperatures [illegible] modulate the intensity of El Niño events (Kerr 1999). On [illegible] scales, warm and productive interglacial periods have [illegible] Siberian conditions at temperate latitudes and aridity in [illegible] (Pons et al. 1995; Roy et al. 1996).

Environmental factors determine the basic characteristics of a [illegible] tivity pulse: intensity, periodicity, the pattern of productivity [illegible]



[illegible] 23.1 Stommel diagram of spatial and temporal scales of zooplankton biomass variability. [illegible] et al. 1978.)

[illegible] frequency. The intensity, or amplitude, of a pulse can be a function [illegible] combined effects of temperature, rainfall, and organismal traits. [illegible] is also strongly influenced by environmental factors. Seasonal [illegible] are relatively regular. Other environmental factors, such as precip- [illegible] may be highly erratic, increasing the overall unpredictability of a [illegible] The periodicity of a pulse affects the amount of reserves that are [illegible] Many bird species experience a trade-off between fat storage and [illegible] ability to migrate and avoid predators. Where winters are milder and [illegible] more predictable, birds tend to be leaner (Rogers and Smith [illegible] Gosler 1996; Katti and Price 1999). Similarly, some rodents hoard [illegible] food when resources are more constant (Livoreil and Baudoin 1996). [illegible] shape of the productivity decay curve influences the ability of dif- [illegible] ecosystem components to store productivity between good times [illegible] Important factors here are the rate of nutrient decomposition, [illegible] of change in temperature, and water availability. The frequency of [illegible] is felt differently by different organisms, depending on their life [illegible] and intrinsic temporal scales. Short-term temporal cycles in [illegible] productivity will be most important for organisms with short life [illegible] Larger, long-lived organisms may experience these oscillations as [illegible] noise.

It is crucial to examine the various temporal scales at which key organisms in the community respond to variation (Southwood 1977), particularly dominants, engineers (Jones et al. 1994), and keystone species (Paine 1966). Temporal rhythms in the lives of these species—including daily feeding patterns, behavioral responses to lunar cycles, and annual migrations, as well as generation times—may be particularly important in governing the overall response of the community to temporal variation in productivity. As Wiens et al. (1986) argued, it is important to remember that the dynamics of a long-lived species may be strongly affected by the dynamics of short-lived species with which it interacts (i.e., competitors or prey). In this way, environmental fluctuations may affect an organism both directly and indirectly through other members of the community. This is an essential reason for studying temporal heterogeneity in a food web context.

Note on Nonlinearity: How the World Really Works

Although linear relationships are easier to work with mathematically and statistically, the vast majority of biological and ecological processes involve nonlinearity. For example, a population's response to changes in resource availability is mediated by resource uptake, which is typically a nonlinear function of supply (i.e., a type II or III functional response, with saturation at high resource levels). The logistic model illustrates how density dependence implies a nonlinear relationship between population size and growth rate. Nonlinearities are also pervasive in the physiology of individual organisms. For instance, photosynthetic rate is a saturating function of light levels because reactions are limited by available enzymes.

Jensen's inequality provides a useful rule for predicting the qualitative effect of variation in resources (see Ruel and Ayres 1999). The basic principle here is that if the population size N_t, or some other variable, is a nonlinear function of resource levels, $N_t = f(R_t)$, then the average size of the population experiencing variable resource levels is not equal to the function evaluated at an average value of the resource levels: $\overline{f(R_t)} \neq f(\overline{R_t})$. Saturating or concave downward functions will have a lower value than expected in the absence of variation. Conversely, accelerating or convex functions will have a higher value than expected (fig. 23.2). The higher the variability of resource levels, the greater the deviation in the average population size from that expected in a constant environment.

Saturating responses arise for very basic biological reasons. Any organism, viewed as a machine, has a limited capacity to process material resources. Predators need time to capture, subdue, and digest prey; herbivores need

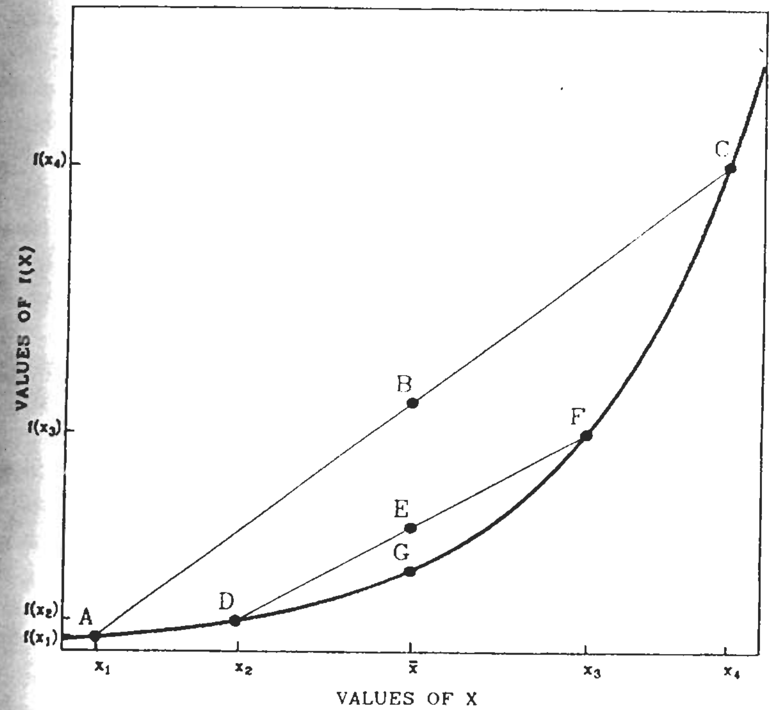


Figure 23.2 Illustration of Jensen's inequality, which is a consequence of nonlinear averaging. The variable X on the horizontal axis fluctuates between values x_1 and x_4 or the values x_2 and x_3. In both cases, the average value of X is $\bar{x}$. The function f, whose graph is given by the thick line, represents some property of a biological system dependent on the fluctuating variable X. Because the graph of f is nonlinear (not a straight line), the average value of $f(X)$ is not given by the point G (at $f(\bar{x})$), but by the point B or the point E, the midpoint of the straight line joining the points A and C or the points D and F. Note that the difference between $f(\bar{x})$ and the average of $f(X)$ increases with the variance of the flunctuations. (From Chesson and Huntly 1993.)

time to digest their cellulose-rich diet. Moreover, most animals are metabolically constrained in their ability to convert resources into fecundity. Even if intake rates are linear functions of resource availability, the net population response may reflect a saturating nonlinearity. Saturating responses in predator attack rates can lead to threshold effects in interspecific interactions, with systems pushed to high or low levels depending upon accidents of initial conditions (e.g., Ruesink 1998). A pulse in production can permit a species to "escape" a low equilibrium; this is a classic theoretical mechanism for insect outbreaks (Belovsky and Joern 1995). For these reasons, temporal variability tends to depress the average rate of resource consumption and realized population growth rates. However, accelerating responses can also arise in systems—for instance, because organisms adaptively shift between alternative activities (Abrams 2001). Nonlinearities also have profound implications for competitive coexistence. Species that would be competitively excluded under constant conditions can persist in a variable environment (see Chesson 2000b). To accelerate our understanding of the role of environmental variation in ecology and evolution, Ruel and Ayres (1999) recommend that ecologists become as familiar with Jensen's inequality as they are with the central limit theorem.

ENVIRONMENTAL FLUCTUATIONS IN SINGLE-SPECIES POPULATION MODELS

In complex communities in which consumers vary in their ability to respond to resource dynamics, it is difficult to separate out the relative importance of those processes that form the patterns we observe. Variation in productivity is one force that is likely to have strong effects on consumer dynamics. Rather than trying to average over exogenous variation in the environment in order to determine the "underlying" dynamics, we need to focus explicitly on the effect of variation on dynamics (Palmer et al. 1997). Ecological modeling is a good first step. We would like models to help us separate this complexity into comprehensible parts and to answer questions about both general processes and particular systems. Ideally, we would like to determine how the effects of temporal variation on populations translate through the food web to affect the dynamics of whole communities.

Population Dynamics as a "Transformation" of Environmental Fluctuations

Most theoretical models in ecology assume that populations have "autonomous" dynamics, in which the equation parameters are constant in time. In reality, the parameters of any model describing population or community dynamics can be expected to vary on different time scales (Holt and Barfield 2003). According to the jargon of systems theory, such systems are "driven" by external variation. Nisbet and Gurney (1982) describe a number of generalized examples of driven dynamics in their textbook on modeling fluctuating populations. If temporal variation is modest in scale, then nonlinear models of population and community dynamics reduce to well-understood linear approximations. For example, consider a population described by the usual logistic equation, but tracking temporal variation in productivity expressed as fluctuations in carrying capacity (K). If the

intrinsic rate of increase (r) is very small, the population oscillates with a much lower amplitude than the oscillation of K, and out of phase with it by about one-fourth period. By contrast, if r is very large, the population closely tracks the carrying capacity, oscillating in phase with K.

Practically speaking, this model conforms to our expectations about what "should" happen to the density of a population in nature, given fluctuations over various relative time scales. We expect that organisms with long relative generation times and slow population growth (small r) will average over high-frequency, short-time-scale environmental variations. Large-scale, low-frequency variations (the waxing and waning of ice ages is an extreme case) are much more likely to be tracked by populations (Chesson and Huntly 1993).

Integrating over a cycle in this linearized model, the time-averaged abundance of the population is $\bar{N} = K$. So temporal variation in productivity (as measured by K) does not alter the average population size. In general, however, this is not true, because with larger-scale fluctuations, nonlinearities (e.g., due to density dependence) become important. Moreover, additional dynamic phenomena may occur. In particular, an intrinsically stable but underdamped population (i.e., with an oscillatory approach to equilibrium) may oscillate at frequencies that are integer fractions (1/2, 1/3, etc.) of the frequency of the driving parameter. For instance, the environment may fluctuate annually, but the population may show multiannual cycles. This also implies that populations with intrinsic limit cycles in constant environments can become synchronized with the cycle of the driving parameter in variable environments.

We gain more insight by considering another population model with variable carrying capacity. Roughgarden (1975) analyzed a discrete-generation version of the Nisbet-Gurney model,

$$(N_{t+1} = r + 1 - \frac{r}{K_t} N_t) N_t.$$

He assumed that population fluctuations were relatively small and driven by changes in carrying capacity, with a low r so that, in a constant environment, the population was stable (i.e., $0 < r < 2$). Let $k_t = K_t - K'$ measure the deviation of current carrying capacity from the long-term mean, and let $n_t = N_t - K'$ measure the deviation of current population size from that same mean. The full model can be approximated by a linear model,

$$n_{t+1} = (1 - r)_n + rk_t.$$

Assume that the deviation in the current carrying capacity from a long-term average fits $k_t = qk_{t-1} + z_t$. This is a first-order autoregressive process where z_t is a random normal deviate with mean zero and variance V_e (environmental variation in carrying capacity) and q measures environmental predictability. The variance in the population is then

$$V_N = V_e \frac{r}{2-r} \times \frac{1+(1-r)q}{1-(1-r)q}.$$

The population dynamics thus transform variation in productivity into variation in abundance.

As before, this model predicts that populations with small r will respond sluggishly to variation in production, and so will have low variance in abundance. Populations with high r will respond more quickly to environmental change, and so will have greater variance in abundance for a given amount of environmental variation. Moreover, the expression for V_N reveals that greater environmental predictability (q) increases population variability. An increased q means that there are runs of good and bad years, reflecting sustained pulses of productivity. The variation in productivity experienced by higher-level consumers will then depend on how prey react to variation in basal productivity. Particular species can either magnify or buffer environmental variation for the remainder of their community. Thus, species with high r are potent transducers of variation into a community.

Ripa and Heino (1999) generalized Roughgarden's results and showed that the ratio between the variance of population size and the variance of the environment also depends on the nature of density dependence for that population. Assuming that environmental states are positively correlated, where, for example, good years tend to follow other good years (Halley 1996; this corresponds to $q \to 0$ in Roughgarden's model), populations that tend to overshoot their carrying capacity ("overcompensating" to density) can actually have a lower variance than populations that undercompensate (and "track" environmental states better). This is interesting, because in models of constant environments, overcompensation leads to unstable dynamics. The same population feature that increases variation in constant environments can thus decrease variation in fluctuating environments.

Interactions between environmental fluctuations and density dependence have other important implications for population stability and species coexistence, depending on the relative time scales at which the nonlinearities act. Long-lived species can be strongly affected by short-time-scale environmental variation if that variation affects their recruitment. The intrinsic rate of increase (r) may be very low in long-lived species, but if most of their density dependence occurs during infrequent bouts of recruitment, environmental variation may be very important for species coexistence, regardless of whether the species are "tracking" variation (Chesson 2000b).

In natural systems, there are many ways for species to have nonlinear responses to pulsed productivity (Ruesink 1998). Dixon et al. (1999) argue that nonlinear responses by larval fish to forcing variables in the physical environment can account for frequently observed erratic or episodic recruitment in marine populations. They reason that the sequential action of processes acting on different life stages can have a multiplicative effect. Although the authors focus on physical factors such as transport processes, it is easy to generalize this idea. Consider a species with two distinct larval stages, in which survival at each stage varies linearly with food abundance, which we assume remains fixed within a generation. If the slopes of these linearities differ, survival from the egg to adult stages will then be a nonlinear (quadratic) function of food availability. Nonlinear population responses can thus emerge from a sequence of stages, each of which itself has a linear response. This process is similar conceptually to scale transition dynamics, whereby spatial variation in density dependence (via spatial subsidies, for example) produces nonlinearities in net population-level growth rates, even when local-scale survival and fecundity are linear functions of resource availability (Chesson 1997, 2000a).

Sometimes, erratic population behavior can be the result of long-term transient dynamics (Hastings 1998). Over ecological time scales, populations with strong density-dependent recruitment may never (for all practical purposes) approach their projected "long-term" dynamics, especially in systems subject to frequent disturbance. Neubert and Caswell (1997) demonstrate that even simple ecological models with linear dynamics and stable equilibria can display surprisingly large deviations, moving temporarily away from equilibrium following a perturbation. These deviations are magnified by nonlinearities. Transient dynamics can make it difficult to predict how a population will "translate" environmental fluctuations into population fluctuations.

Effects of Temporal Variation on Average Abundance

How do large-amplitude fluctuations in productivity affect average population size? The outcome may depend upon which demographic variable is influenced by variation in productivity. Consider the logistic model.

$$\frac{dN}{dt} = N(r_t - \delta_t N_t).$$

Here r_t is the intrinsic growth rate at time t, and δ_t measures the strength of density dependence at t. In a constant environment, where $r_t = r'$ and $\delta_t = \delta'$, the equilibrial abundance, or carrying capacity, is $r'/\delta = K$. If temporal variation enters only in r_t, with a mean r equal to r', and δ is constant, then using time averaging (Levins 1979), it can be shown that

$$\bar{N} = \frac{\bar{r}}{\delta} = K.$$

In other words, temporal variation in the intrinsic growth rate with constant density dependence does not affect average population size (although if variation is too severe, the deterministic assumption of time averaging breaks down; Renshaw 1991). However, if r is constant, but the strength of density dependence (δ) fluctuates, it can be shown (using Jensen's inequality) that

$$\bar{N} > \frac{r}{\bar{\delta}} = K.$$

Therefore, if productivity mainly affects the strength of direct density dependence (e.g., because aggression or cannibalism is more prevalent when food is limited), then temporal variation in production should increase average abundance (but see Chesson 1991 regarding the assumptions producing these varied results). The underlying mechanism is that when density dependence is weak (e.g., because cannibalism is rare when food is abundant), a population can grow explosively to high numbers.

Lima et al. (1999) studied sporadic density dependence in populations of the leaf-eared mouse (*Phyllotis darwini*) of coastal Chile. This rodent species has dramatic outbreaks that are correlated with high rainfall during El Niño years, which increases primary production. Using an age-structured population model, Lima and colleagues argued convincingly that the fluctuations in population density reflected both this extrinsic factor (reproduction is correlated with rainfall) and strong, delayed density dependence in adult survival. This density dependence was most likely due to delayed responses by specialist predators, but also may have resulted from the rodents overexploiting vegetation. In any case, this model showed that an increase in population size during good years can lead to severe "crunches" in subsequent years. This finding also suggests that density dependence can vary greatly through time, associated with variation in production.

This scenario seems to apply to ungulates as well (Sæther 1997; Gaillard et al. 1998). For example, in the greater kudu, variation in calf survival through the nonbreeding season is correlated with annual rainfall, which determines food availability. The relationship between calf survival and rainfall is strongly magnified in years with high population density, presumably reflecting more intense exploitative competition for food. Populations are particularly sensitive to years with unfavorable abiotic conditions following years with pulses of production because this is when density will be high relative to food supply.

MULTISPECIES MODULATION OF TEMPORAL VARIATION IN PRODUCTION

Single-species models demonstrate that environmental variation and intraspecific density dependence interact to influence the dynamics of populations and the average population size. However, interspecific interactions can also modify species' responses to temporal variation in production. If one species in a food web is directly affected (numerically or behaviorally) by temporal variation in production, such variation will be transmitted to all other species with which that species interacts.

Specialist Predator-Prey Models

Nisbet and Gurney (1982) describe a Lotka-Volterra model with a time-dependent prey intrinsic growth rate,

$$r = r_0(1 + \phi_t).$$

They analyzed both the case in which ϕ_t is strictly "noise" and the case in which ϕ_t is periodic. If the Lotka-Volterra system approaches equilibrium monotonically, aperiodic fluctuations will produce noncyclic population fluctuations, while quasi-periodic oscillations in r will produce phase-remembering quasi-cycles. (The term "quasi-periodic" refers to complex patterns of fluctuations that are the sum of simpler periodic fluctuations or cycles.) If the Lotka-Volterra system has an oscillatory approach to equilibrium, aperiodic fluctuations produce quasi-cycles that eventually dampen out, and quasi-periodic fluctuations give complex quasi-cycles. Environmental noise alters the deterministic signal in either case, but intrinsic fluctuations have complex interactions with either random noise or periodic variation. The effects are particularly strong if the prey population has a large carrying capacity or the predator has a high attack rate and a low death rate.

Quasi-cycles may lead to the extinction of either predators or prey if their amplitudes become too great. With this same model, using time averaging (Levins 1979), it can be shown that variance in prey numbers is always less than variance in prey intrinsic growth rate. The predator responses absorb fluctuations in prey numbers. This finding illustrates that the transformation of environmental fluctuations into population fluctuations is influenced by feedbacks through other species in communities.

The above theoretical results focus on relatively rapid environmental change. If the change in production is sufficiently slow, the community may be viewed as being at a "moving equilibrium" (Holt and Barfield 2003). Simple food chain models (e.g., Oksanen et al. 1981; Oksanen and Oksanen 2000) predict that an increase in basal productivity should increase the abundance of the top trophic level, although the effect may be small if intermediate levels have saturating functional responses. However, this qualitative prediction may not hold if there are multiple species present at different levels (Abrams 1993) or if the system is unstable (but persistent) due to strong nonlinearities (Abrams and Roth 1994; Abrams et al. 1998). Increased production may indirectly depress the abundance of top consumers in communities with unstable dynamics (e.g., cycles), even to the point of extinction (Abrams and Roth 1994). The reason for this effect is that increasing production can increase the temporal variance of abundance in the system. If the top predator has a strongly saturating functional response, then (by way of Jensen's inequality), fluctuations will lower its overall feeding rate, and thus lower its average abundance. Short-term responses to a pulse of productivity can differ greatly from long-term responses (Ives 1995) because the latter include all the indirect effects acting within and among species.

In another theoretical study, Monger et al. (1997) explored how periodic fluctuations in carrying capacity influenced the dynamics of a three-link food chain with time-lagged recruitment in the intermediate trophic level. As in Nisbet and Gurney's results for intrinsically stable systems, high-frequency fluctuations had little effect on system dynamics (see also Holt and Barfield 2003). With low-frequency fluctuations and intrinsically stable population dynamics, abundances tracked the moving equilibrium. Intermediate frequencies could generate large-amplitude, erratic population fluctuations, or subharmonic oscillations. In systems that are marginally stable, top predators, which tolerate rapid fluctuations in production, could suffer extinctions in the presence of lower-frequency variation.

Another approach to analyzing environmental fluctuations is to perform spectral analysis on time series data. Using an analogy to the color of light, a power spectrum describes how total variability in a time series is partitioned among different wavelengths. White dynamics imply stochastic, unpredictable variation; red dynamics are slow, long-term fluctuations; and blue dynamics are high-frequency, short-term variations (Lawton 1988). Most population dynamics are white or red (Pimm and Redfearn 1988). Ripa et al. (1998) recently carried out a general analysis of the spectral character of noise in two-species food webs. They assumed that the species are interacting, and that in the absence of fluctuations, the community would exhibit stable dynamics. These assumptions permitted them to linearize the system. They also assumed that only one species directly experiences the environmental variation; for instance, it may be a prey species whose birth rate is correlated with stochastically varying rainfall. Their question was how, in general, the spectrum of fluctuations in the prey compares with that in the predator.

The results are somewhat different for species with continuous reproduction than for those with discrete, synchronized generations. In the former case, the species that experiences environmental variation will have a power spectrum that is dominated by higher frequencies (i.e., is "bluer") than that of the second species. Interestingly, this result does not depend upon the nature of the interaction (e.g., predation vs. competition), but is a general claim. In other words, the second species will show fluctuations over longer time scales than the directly affected species. The analytical results of Ripa et al. depend upon linearized analysis, but numerical studies suggest that this result is rather robust, even far from equilibrium. With discrete generations and undercompensation, the second species always has a redder spectrum than the directly affected species. In effect, time lags reduce the ability of populations to respond to rapid density changes in the species they interact with, buffering the effects of rapid environmental fluctuations.

A reddened spectrum has numerous implications for population and community dynamics. If birth rates closely track resource abundance and resources have a red spectrum, there will be "runs" of resource-poor years. In a closed population, this increases the risk of extinction, particularly for species with simple life cycles (e.g., annual insects). By contrast, in open populations maintained by immigration, a reddened spectrum tends to increase local population size (Holt et al., in press; Gonzalez and Holt 2002). Consider a population maintained by immigration in a habitat where, on average, it has a negative growth rate (i.e., a "sink" population). If there is a reddened spectrum in the local habitat, the local population may experience runs of good years with positive growth rates, even if, on average, it has a negative growth rate. Because it has persisted by virtue of immigration during poor years, it remains present and poised to exploit runs of good years and explode to high numbers. Averaging over the entire time series, one finds that the average abundance has been greatly increased by reddened variation, compared with a constant environment with the same average rate of decline in the local habitat.

This unexpected "inflationary" effect of temporal variation in open populations has many consequences. In general, reddened temporal variation magnifies the effect of system openness, making local processes even more sensitive to spatial fluxes of all sorts (Polis, Anderson, and Holt 1997; Holt and Barfield 2003). The results of Ripa et al. (1998) suggest that as variation percolates through a food web, its spectrum may redden. If so, the inflationary effect of temporal variation in spatially open communities may be important even in parts of the food web well removed from the direct effect of variation in production.

Generalist Predators and Temporal Subsidies

The most natural way to consider temporal subsidies in food webs is in the context of generalist consumers that use multiple resources. Generalist predators can respond both numerically and behaviorally to a resource pulse. Examples of this scenario were reviewed by Ostfeld and Keesing (2000). Such consumers exploit pulses of resources, such as masting fruit or insect outbreaks, and as the pulse declines, shift to another prey species or resource. In the short term, during the course of the pulse event, some species may experience a release from predation as predators become satiated by the pulsed resource. However, if predation limits total prey abundance overall, alternative prey should experience apparent competition (Holt 1977, 1984, and chapter 7 in this volume). These effects can destabilize predator-prey dynamics and may lead to the exclusion of one of the prey species.

Apparent competition via temporal subsidies is probably a frequent scenario in nature, with predators switching between food sources as they increase in response to abiotic environmental cues. At the onset of good periods, temporally subsidized consumers may have stronger top-down effects on their resources than would be expected in the absence of a subsidy, and can suppress resource eruptions. In apparent competition models, shared predation favors habitat partitioning among prey, similar to

that resulting from resource competition (Holt 1984). In contrast, theory and empirical evidence suggest that shared predation can select for temporal clustering of prey species. This effect is particularly likely if predators have weak, short-term responses to upsurges in prey numbers and can become satiated, or if prey experience strong direct density dependence (Brown and Venable 1991; Holt 1997a). This effect has been suggested as the force responsible for synchronous, episodic masting of seed plants (see Janzen 1976; Ostfeld and Keesing 2000) and the concordant emergence of multiple species of the periodic cicada, *Magicicada* sp. (Williams and Simon 1995). Temporal clustering will decrease the predation risk to any particular prey population in the cluster, but can increase the intensity of predation on prey outside the cluster. Temporal "refugia" may also be important for reducing the impact of generalist predators. Seed banks, dormancy mechanisms, and long-lived, inedible adult or juvenile stages allow prey species to escape during pulses of intense predation (although these stages often have their own suite of predators).

Persistence in the community is facilitated by any factor that reduces the overall rate of population decline during "lean" periods. Often, predators have dormancy mechanisms, fat stores, or food caches that permit them to persist when prey are few and far between. In many cases, generalist predators would not be able to survive without some form of temporal subsidy to carry them through periods of low resources. Low levels of temporal subsidy may stabilize the community by permitting predator persistence. Predator populations will not die out during times of low resources, and thus prey populations will be less likely to overexploit their own resources.

In the case of spatial subsidies, Huxel and McCann (1998) found that simple food chains are stabilized by a low level of donor-controlled subsidy trickling in from another habitat. Low levels of allochthonous inputs stabilized food webs when species fed on autochthonous sources preferentially. Increasing the input level sufficiently or changing feeding preferences decoupled the food chain by permitting overexploitation of local prey, resulting in species losses (see also Holt 1984 and chap. 7 in this volume). Translating this finding to its temporal analog, low levels of alternative prey (particularly carrion or other donor-controlled food sources) may stabilize food webs. Predator populations that could otherwise fall to dangerously low levels when prey are dormant can subsist during lean periods on alternative prey and respond more rapidly to prey pulses during good periods (see also Ives and Settle 1997). McCann and Hastings (1997) examined models in which omnivorous predators could eat both intermediate consumers and basal resources. This type of omnivory stabilized the

Chesson and Huntly (1997) recently reviewed the long-term implications of temporal variation for competitive coexistence. While temporal fluctuations have little effect on coexistence in linear additive models of competition, they are an important factor promoting coexistence in models containing biologically reasonable nonlinearities. The primary role of temporal fluctuations in competition (or other sources of density dependence) is to provide opportunities for temporal niche partitioning, so that different species are better able to survive or acquire resources in different years. Niche partitioning means that intraspecific competition will always be more intense than interspecific competition because the greatest amount of resource overlap occurs between individuals of the same species. Temporal niche partitioning is an important component of the storage effect, which, along with nonlinear responses to fluctuating resources, can explain the puzzling coexistence of large numbers of similar species in plant communities.

The storage effect is easily observed in desert communities of winter annual plants. In the desert, rain falls sporadically among years, from the early fall through midwinter, at a range of temperatures. At each rain, a mixture of plant species germinate from the resting seed bank and compete for water and soil nutrients. These plants are short-lived as adults, often completing their entire aboveground life cycle in just a few weeks. Some species germinate disproportionately better following warm rains, others following cold rains. The seeds of each species enter the seed bank and germinate gradually through the coming years—a timed-release capsule of past recruitment. The "storage" of good recruitment years in a long-lived seed bank can facilitate competitor coexistence.

It is not variation alone that allows coexistence. Coexistence requires (1) niche partitioning, in which species are differentiated in their responses to the varying environment; (2) positive covariance between the environment and competition, such that individuals have a greater competitive effect when the environment is favorable and a lower competitive effect when the environment is unfavorable; and (3) buffered population growth, in which a seed bank or long-lived adult stage allows species to make low investments in reproduction during years when the environment is unfavorable. Storage at any trophic level allows a consumer (whether autotroph or heterotroph) to integrate pulses of resources metabolically over time. Organisms can persist through lean periods by using stored energy and exploiting resources as they become available. Chesson has recently shown that spatial variation can produce a closely analogous "spatial storage effect" (Chesson 2000a). Rather than good and bad periods being linked through time by seed dormancy, good and bad patches are linked through

space by dispersal. This theory is very general, and is likely to be useful for the theoretical exploration of spatial subsidies in food webs.

Relative nonlinearity in competitive response also allows coexistence in temporally variable conditions, even in the absence of the storage effect. Assume that two consumer species exploit a single limiting resource and have saturating, nonlinear relationships between feeding rates and resource availability. Species A has a higher feeding rate at low resource levels, whereas species B has a higher feeding rate at high resource levels. In a constant environment the resources will equilibrate at a constant level, and the species with the lower R^* will win. However, if there is large-scale seasonal variation in resource supply rates, resources may fluctuate between high and low levels. Such variation can permit the coexistence of the two competitors on a single resource. This mechanism hinges on species-specific nonlinear responses to the shared limiting resource. If the feeding rate were to increase linearly with resource availability in both species, then even in the presence of high variation in resource availability, we would observe competitive exclusion.

Understanding the controls on competitive interactions and the maintenance of diversity within trophic levels is important for food web ecology because the existence of heterogeneities within levels influences how temporal variation in production is translated to higher trophic levels.

FEAST AND FAMINE IN FOOD WEBS

It is complicated to model temporal variation in multispecies communities. Early verbal models focused on the effects of temporal variation on life history patterns or considered temporal heterogeneity primarily in terms of disturbance. Recently, a growing number of empirical studies have forged ahead (see Ostfeld and Keesing 2000), looking for consistent patterns of response to pulsed productivity. These studies all emphasize the importance of some form of storage, as well as the importance of generalist predator species, which link the dynamics of their various resources.

Effects of Temporal Heterogeneity on Life History Patterns

In one of the first verbal models to explicitly connect temporal variation with community structure, Noy-Meir (1973, 1974) proposed the pulse-reserve hypothesis to explain population dynamics and life history strategies in deserts. He suggested that desert populations are buffered from their harsh and fluctuating environment because animals and plants store up reserves (fat, starch, etc.) during good (wet) periods, which they rely on to survive through bad (dry) periods. Similarly, detritus is "stored" by the ecosystem during good times and used by detritivore populations during bad times. These detritivore populations may later provide nutrients to plant populations and provide an alternative source of prey for consumers (Polis and Strong 1996). The gradual reinfusion of detrital material dampens the destabilizing effects of pulsed productivity. The community is stabilized because stored detritus provides a temporal subsidy for detritivores and allows this resource population to survive bad times. Consumer populations can be maintained through bad periods either by their own stored reserves or by reserves stored by other parts of the system: detritus, detritivores, roots, and so forth. These temporal subsidies, translocating organic matter and energy from good times to bad, are thought to be central to the dynamics of desert communities (Noy-Meir 1973, 1974; Polis 1991). Noy-Meir's pulse-reserve concept did not explore the importance of pulses for interspecific interactions (see Chesson 2000b), but brought attention to the importance of specialized life history characteristics (especially storage) in moderating the effects of harsh conditions.

Southwood (1977) also emphasized the importance of temporal and spatial variation in shaping life history characteristics. According to Southwood, organisms and their habitats are linked in a feedback system that determines when they will reproduce, migrate, or go dormant. His conceptual model involved a two-by-two "reproductive success" matrix specifying whether an organism would breed here or elsewhere, and now or later. These choices were dependent on a "time heterogeneity index" based upon the length of time any particular location was suitable for breeding and the variation (heterogeneity) in the length of this period. During times of low productivity, resources are depleted, and fecundity is often lower for both plants and animals. The degree to which population size decreases with adversity depends on the life history characteristics of storage, longevity, and mobility. Long-lived sedentary species will average over fluctuations. This model was an ambitious effort to categorize habitat types and match them to forces of selection in complex communities. Like Noy-Meir, Southwood particularly emphasized the importance of dormancy mechanisms in unpredictable environments.

Effects of Temporal Heterogeneity on Diversity Gradients in Food Webs

Menge and Sutherland (1976) included temporal heterogeneity as a factor in their conceptual food web model. Although primarily concerned with temporal variation in disturbance, they argued that trophic complexity depends in part on the rate and stability of primary and secondary productivity. Resource population densities may fluctuate, and bad weather may reduce consumer foraging periods. In the long run, specialist consumers may be excluded due to unpredictable resources. Menge and Sutherland predicted that temporal heterogeneity could lead to trophic simplicity and increased competitive exclusion (as the effect of predation decreased), which would further reduce species diversity. The theory outlined earlier in this chapter does not give clear support to Menge and Sutherland's predictions. Temporal heterogeneity in resources can either increase or decrease average population size, depending on the openness or insularity of the focal populations, and moreover, can provide axes for temporal niche differentiation (Gonzales and Holt 2002; Holt et al., in press). Also, while eliminating keystone predators (Paine 1966) may increase competitive exclusion, increased exclusion is not a necessary outcome of reduced predation (Chesson 2000b, Abrams 2001). The outcome of reduced predation depends on whether predation is density-dependent or density-independent, the selectivity of the predators, and whether trade-offs exist between competitive ability and tolerance of predation.

Pulsed Resources and Community Dynamics

Ostfeld and Keesing (2000) reviewed a number of empirical food web studies that explicitly examined the effect of variation in resources. These studies provided excellent examples of temporal subsidies in terrestrial communities. Many of them followed the effects of mast seeding events, tracking the productivity pulse through primary consumers to their predators (fig. 23.3). Corresponding to the apparent competition model, consumers and predators responded numerically to the pulse of production and had unusually strong top-down effects on their alternative prey species. For example, mast seeding of oak and hornbeam trees in Poland led to high winter survival rates and strong numerical responses by rodents. The following year, high densities of mast-fed rodents had strong top-down effects on insects and ground-nesting songbirds. Rodent predators (owls and martens) also responded numerically and peaked a few months to a year after the rodents did (up to 2 years after the mast crop). These predators also preyed heavily on songbird populations (Jedrzejewska and Jedrzejewska 1998). Overall, Ostfeld and Keesing's review exposed a number of generalities: (1) consumers of pulsed resources are often generalists, which display a time-lagged numerical response; (2) as the pulsed resource diminishes, consumers tend to switch to alternative prey; (3) the generalist consumers

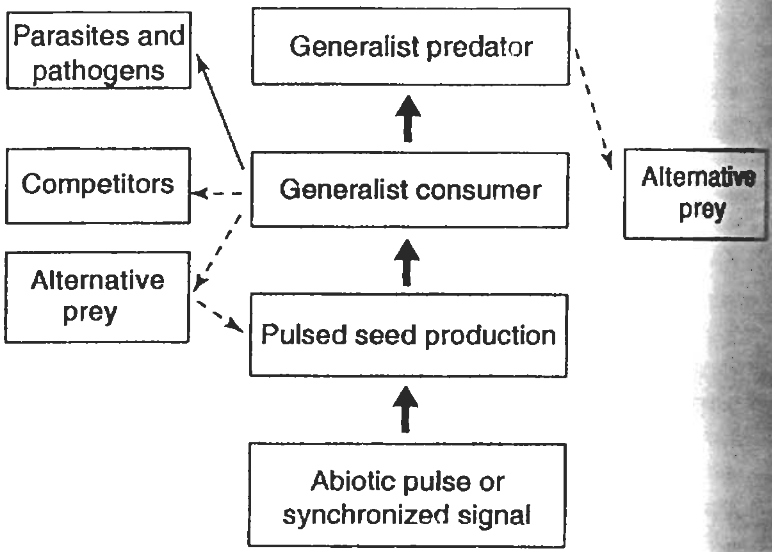


Figure 23.3 Conceptual model of the effects of pulsed resources permeating through a food web. The direction of the arrows represents the direction of causal change in abundance or biomass. Solid lines indicate a positive effect and dashed lines a negative effect of one trophic group on another. (Adapted from Ostfeld and Keesing 2000.)

act as a pulsed resource for their own predators; (4) the response of consumers varies as a function of their specialization, mobility, and rate of population response to the resource.

These findings fit well with our theoretical overview. Generalist predators are those most likely to exploit temporal subsidies because of their ability to switch between prey species. Mobility is an especially important trait for consumers of pulsed resources because it allows them to acquire spatial as well as temporal subsidies. The rate of numerical response to the pulsed resource depends on the intrinsic rate of increase (r) of consumer populations. Fast-reproducing (high r) rodents tracked resources fairly closely. As in the single-species models above, populations with low r tended to integrate across resource peaks, rather than tracking them. It is likely that resource pulses will slowly attenuate as they move through a food web. Through storage (seed banks and perennial tissue) and release (to herbivores or detritivores), producers buffer consumer populations from variation in resources (see also Levey and Stiles 1992). Similarly, storage by primary consumers buffers secondary consumers from fluctuations in primary productivity. Overall, storage mechanisms should dampen the effects of environmental stochasticity.

Time-lagged numerical and behavioral responses make it difficult to interpret ecological patterns. Wiens (1986) found that the dynamics of shrub-steppe bird populations in the Great Basin did not match the dynamics of their habitats. Variation in rainfall altered vegetation height and community composition, and plant species differed in their rate of response to these environmental changes. The plants were slow to respond to the changes in precipitation, the insect community (which the birds feed on) had a slow numerical response to the vegetation changes, and the birds were slow to make a behavioral adjustment to the changes in plant cover and insect densities. If this study had been conducted in a single season, it would have been impossible to determine the population dynamics from the observed patterns.

Productivity fluctuations may have complicated effects on species interactions. Hogstad (1995) found that fieldfare (*Turdus pilaris*) nesting behavior fluctuated in response to pulses of weasel predation. In years when there were few rodents, weasels attacked the fieldfares in a density-dependent manner, leading to a preponderance of solitary nesting. In high-rodent years, the weasels switched to rodents and ignored fieldfares; colonial nesting then became the norm, apparently to reduce predation by birds (the colonies protect themselves by mobbing the predator). In this case, the nesting behavior of birds was affected by fluctuations in the density of rodents, their apparent competitors.

Additional Complications

In open systems, and at the level of whole assemblages, it may be difficult to relate patterns of variation in resource availability to patterns of variation in consumer abundance. Herrera (1998) describes a 12-year study of frugivorous birds and fleshy fruits in a Mediterranean montane community that revealed decoupling at two levels. Total fruit abundance fluctuated temporally from 5 to 80 fruits m^{-2}. However, variation in each of the six most abundant fruit species was not related to annual variation in rainfall. It seems likely that primary production varies in response to rainfall, but this did not translate into predictable patterns of variation in fruit. This is another way in which temporal variation in one component of an ecological system is "filtered" through the dynamic responses of species (here, resource allocation by individual plants). Moreover, though there was substantial annual variation in frugivorous bird abundance, it was not correlated with variation in fruit availability. Herrera suggests that this decoupling of resources and consumers reflects the importance of abiotic factors (such as temperature) and, in particular, the wide range of the consumer populations. The abundance of migratory frugivorous birds at a particular site may be governed by processes operating over much of the Palearctic, obscuring any effect of local variation in resource availability.

If variation in productivity is driven by nutrients, then plant nutrient contents are likely to change. Huxel (1999) has argued that integrating food quality into standard consumer-resource models can be stabilizing. Turning his argument around, temporal variation in food quality driven by fluctuations in primary production could be an unsuspected source of variation in consumer numbers. Carpenter and Pace (1997) propose that nutrient fluctuations may be responsible for maintaining alternate stable states of dystrophy or eutrophy in whole-lake ecosystems. If so, then nutrient fluctuations could have huge ecosystem-level effects that determine which species can tolerate a particular habitat.

FOOD FOR THOUGHT

This chapter grew from an inspiration to extend the concept of spatial subsidies and landscape-level food web influences to the temporal scale. Time has always been included in population models, either implicitly or explicitly, but we have been slow to focus on temporal heterogeneity itself. The temporal subsidy concept reinforces our instinctive understanding that the natural world is constantly changing and that these changes happen over a variety of time scales and patterns. Jensen's inequality demonstrates that this variation may have large effects on the outcome of population dynamics and species interactions. Because of this, we cannot use population models to predict the trajectories of natural communities without taking into account the effects of temporal variation.

In the models and natural systems we have reviewed here, certain commonalities arise. General models demonstrate that the rate of population growth (r or λ) relative to the time scale of a productivity fluctuation will determine whether that population will track or average over the fluctuations. Storage is also extremely important, as it modifies how species respond to fluctuations in productivity. A population may have a rapid numerical response to favorable conditions, but through storage in long-lived adults or persistent stages, that population may not decline at the onset of unfavorable conditions. How well a population tracks environmental change will determine how productivity pulses are translated to the rest of the food web. It is difficult to predict how community dynamics will be altered by temporally varying productivity, and the outcome is contingent on

the characteristics of the species making up the community (e.g., life history traits, the nature of density dependence) as well as on the web of species interactions. However, initial empirical work demonstrates that common patterns arise in diverse systems.

Because species and community characteristics strongly modify population dynamics, food web studies call for intensive natural history observations. Ecologists need long-term demographic data to quantify how communities react to variation in the environment. This requirement can be an obstacle to experimental testing because operational time scales may be very long, especially when predator populations have a time-lagged response to their prey. A traditional way to surmount this problem is to use organisms with very short life spans and fast reproductive rates. Mesocosms and microcosms have been useful for testing a wide variety of theoretical predictions, from Lotka-Volterra models (Gause 1934) to apparent competition (Lawler 1993; Bonsall and Hassell 1997). Although these systems may lack verisimilitude, they allow researchers (within a single lifetime) to follow a numerical response to system perturbations.

In light of recent successes in documenting the effects of pulsed productivity in field experiments, it may be reasonable to undertake some larger-scale experiments in agricultural systems. The rice planting scheme described by Ives and Settle (1997) is an excellent example. On a regional scale, fields are either planted synchronously, or planting is staggered throughout the year. Rice cultivation occurs year-round in many areas, and herbivorous insects and their predators have relatively rapid dynamics, so dynamics unfold swiftly. This type of study provides a wealth of information on both spatial and temporal food web subsidies and the factors that modify their effects (such as migration rates).

We are in a period of rapid global change—ironically, as a result of past productivity stored as petrochemicals that are now subsidizing human population growth. Global weather changes are altering local surface temperatures and precipitation patterns. Many resources are being depressed to low levels, while human waste products and toxins increase. One outcome may be an increase in environmental variability, both in resources such as water and nutrients and in disturbance forces such as storms and forest fires. Invasive species can provide sustained temporal pulses of novel resources, shifting resident predator-prey dynamics (Holt and Hochberg 2001). These global-scale changes are a critical reason for studying food webs in an explicit temporal context. Some outcomes may be predictable; others are likely to be complete surprises (Schneider and Root 1996). The experiment is on, but we may wish to modify some of the treatments.

ACKNOWLEDGMENTS

We would like to thank P. T. Stapp, F. Sánchez-Piñero, M. Rose, A. Boulton, and J. Vander Zanden for their intellectual insight and encouragement. We also thank P. Chesson, G. Huxel, E. Preisser, and L. Yang as well as an anonymous reviewer, for their helpful comments on the manuscript. We are grateful to the National Science Foundation for support including grants DEB9527888 and DEB9806657 to GAP and an NSF graduate research fellowship to ALWS, and to the University of Florida Foundation.