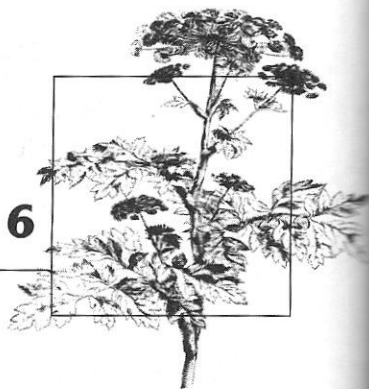


CHAPTER 6



Food Webs

OVERVIEW

This chapter introduces the basic attributes of food webs and reviews general patterns that arise from the examination of large collections of food webs. Simple predator-prey models introduced in the previous chapter are extended to make predictions about the dynamics of species in simple food webs with different structures. These models predict that some features of simple food chains, such as chain length and feeding on multiple trophic levels, may be associated with reduced stability. There are relatively few experimental tests of the predictions that food web theory makes about population dynamics. The available evidence suggests that food chain length may depend in a complex way on both productivity and constraints imposed by population dynamics, since increases or decreases in productivity both lead to decreases in food chain length. Other topics related to food chains and food webs, such as trophic cascades, are discussed in the context of indirect effects in Chapter 8.

FOOD WEB ATTRIBUTES

A **food web** describes the feeding relations among organisms in all or part of a community. Usually those feeding relations are described by a diagram linking the consumers and consumed with lines or arrows, as shown in the examples in Figure 6.1. **Links**, the lines, indicate a predator-prey interaction

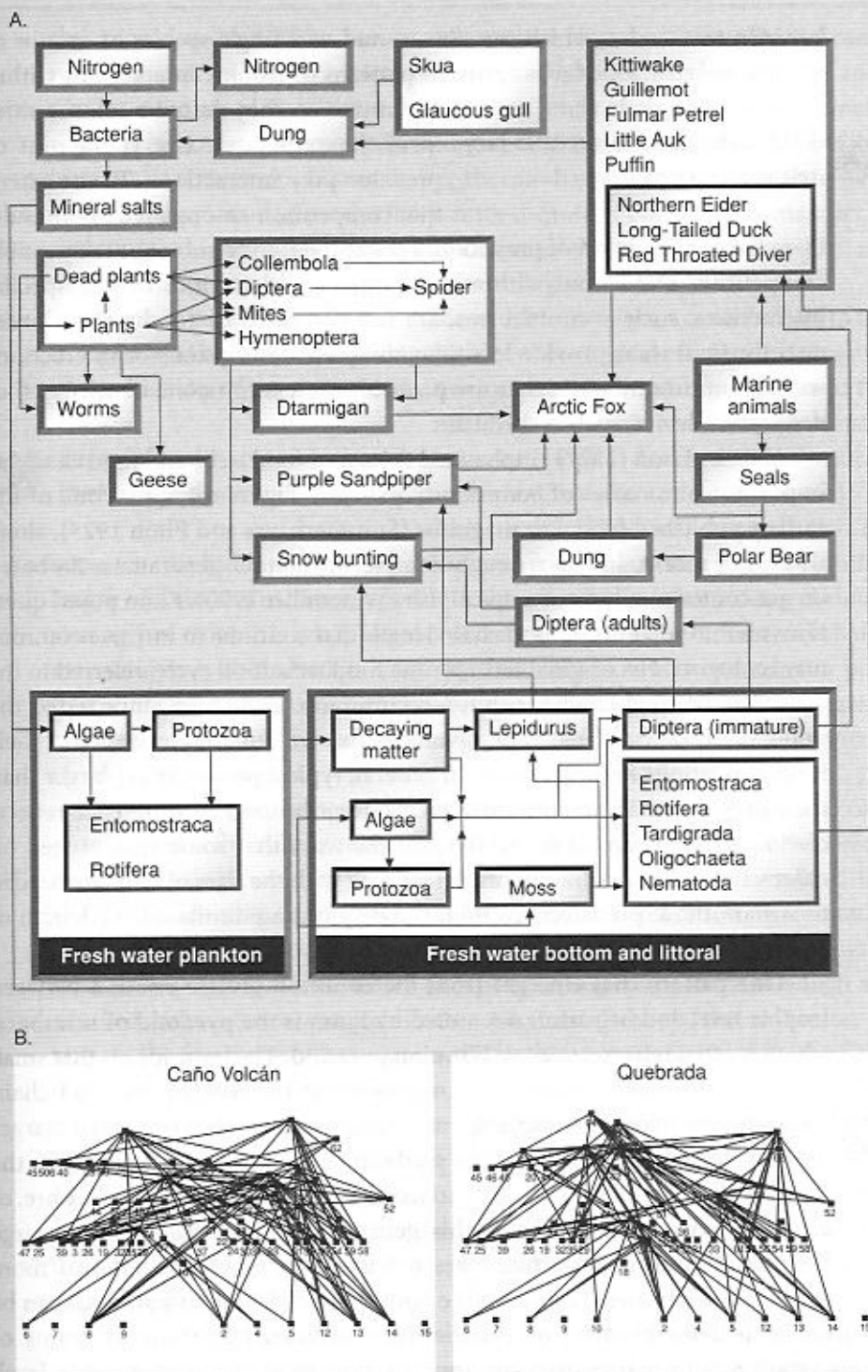


FIGURE 6.1. Examples of food webs. (A) An early food web, representing the major feeding relations on Bear Island. (Adapted from Summerhayes and Elton, 1923, with permission of Blackwell Science Ltd.) (B) Modern food webs, representing feeding relations within communities dominated by tropical freshwater fish in Venezuela. (Adapted from Winemiller, 1990, with permission of the Ecological Society of America.)

between two **nodes**, which can correspond to a single species or groups of species. Because food webs focus on patterns of trophic interactions within communities, they describe communities



Food webs describe predator-prey relations in community.

from the rather selective standpoint of predator-prey interactions. To the extent that competition among predators results

from the consumption of prey, food webs also outline a subset of the possible competitive interactions within communities. Other kinds of interspecific interactions, such as mutualisms, are not described by food webs. Consequently, food webs provide less than complete descriptions of interactions within communities, but they are probably no less complete than any other descriptive device, such as the niche.

Charles Elton (1927) emphasized the use of food webs and food chains as important summaries of community patterns. Figure 6.1 shows one of the earliest published food web diagrams (Summerhayes and Elton 1923), along with more recent, and disarmingly complex, computer-generated webs based on gut content analyses of tropical fish (Winemiller 1990). Elton posed questions about the limits of food chain length that continue to intrigue community ecologists. His original term for the food web, **food cycle**, referred to the collection of food chains within a community. Elton also emphasized the importance of basic patterns involving the sizes of organisms and their feeding relations in food chains. In general, typical predators are larger than their prey, and parasites are smaller than their hosts. This difference reflects obvious biomechanical constraints on the ways that some species feed on others, but these size differences, interacting with the sizes of habitats needed to sustain those predators, could ultimately impose limits on the length of food chains as well.

One pattern that emerges from the common inverse relation between trophic level and organism size noted by Elton is the **pyramid of numbers**, which is often referred to as an **Eltonian pyramid**. The basic idea is that small

organisms at the base of the food chain



Eltonian pyramids of numbers, are more numerous than their larger biomass, and energy.

predators, and so on up through the remainder of the food chain. There are, of

course, obvious exceptions to this generalization, especially where large primary producers (e.g., trees) are fed upon by much smaller and more numerous herbivores (e.g., aphids or other insects). Similar pyramids can be envisioned for biomass or productivity (measured in units of grams of carbon accumulating per unit area per unit time) for each trophic level. Inverted pyramids of numbers or biomass, where the abundance or biomass of a lower trophic level is less than in an adjacent higher trophic level, can also occur. This inversion can happen when primary producers are highly produc-

tive, reproduce rapidly, and are rapidly cropped by consumers. This is sometimes the case in relatively clear oligotrophic lakes, where herbivorous zooplankton reduce phytoplankton to very low levels of abundance or biomass, whereas high turnover rates of phytoplankton can support a large standing biomass of consumers. However, it is thermodynamically impossible to have an inverted pyramid of productivity, since the rate of energy or biomass accumulation in higher trophic levels cannot exceed that in lower levels, which are the sole source of energy for consumers on higher trophic levels.

Raymond Lindeman (1942) made another important contribution to the study of food webs by introducing the idea of **ecological efficiency**, a measure of the fraction of energy entering one trophic level that is passed on to the

next higher trophic level. Energy transfer

between trophic levels is often rather inefficient, on the order of 5% to 15%.

This inefficiency of energy transfer

between trophic levels provides one possible explanation for the limited length of food chains, since rather little energy remains after passing through four or five trophic levels. This idea is central to the notion that food chains may ultimately be limited in length by the interaction between primary productivity (the rate at which energy is fixed in primary producers as organic carbon) and the inefficiency of energy flow between trophic levels in food chains (Slobodkin 1960).

Despite the early recognition of the importance of food webs, most ecologists viewed webs as little more than descriptive devices. Then, in the 1970s, ecologists using two very different quantitative approaches revitalized the study of food web patterns. Joel Cohen (1978) focused interest on the statistical properties of food webs by showing that comparisons of many webs seemed to point to the existence of repeated properties, some of which are detailed below. Since the publication of Cohen's book, the collection of known food webs, which vary greatly in the taxonomic resolution of the feeding relations that they describe, has grown considerably. At about the same time, but using a very different approach based on Lotka-Volterra models of population dynamics in simple food chains, Robert May (1972, 1973) and Stuart Pimm and John Lawton (1977, 1978) raised interest in the consequences of food web structure for population dynamics. Their models explored whether differences in the structure of food chains and food webs affect the stability of populations.

Most descriptions of food webs are very incomplete, often lumping

or aggregating many species into single trophic categories, or nodes, which are sometimes called *tropho-species* to distinguish them from biological species.



Energy transfer between trophic levels is inefficient.



Three categories of food webs.

Before discussing the major patterns, it is important to first understand the terms and ideas used to describe aspects of the webs. Food webs are sometimes separated into three categories: **source webs**, **sink webs**, and **community webs** (Figure 6.2). Source webs describe the feeding relations among species that arise from a single initial food source, say a single plant species. Sink webs describe all of the feeding relations that lead to sets of species consumed by a single top predator, the sink. Community webs, at least in theory, describe the entire set of feeding relations in a particular community, although this ideal goal is never realized in practice because of the extraordinary complexity of most communities.

The following terms and concepts describe some rather abstract features

of food webs that form the basis for most comparative studies. It is worth keeping in mind that these abstractions are simply a way of quantifying some

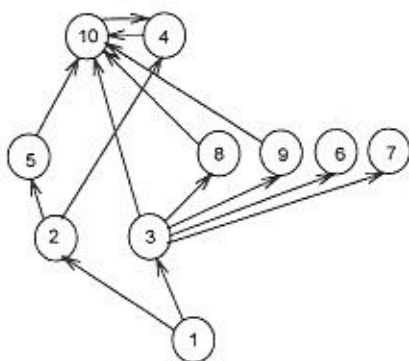
of the fascinatingly complex interactions within large collections of predators and prey.

■ **Trophic position.** The nodes or species in the webs are distinguished by whether they are **basal species**, **intermediate species**, or **top predators**. Basal species feed on no other species, but are fed upon by others. Intermediate species feed on other species and are themselves the prey of other species. Top predators have no predators themselves, but prey on intermediate or basal species. These notions refer to the feeding relations drawn in the webs, rather than to strict biological reality. For instance, it is arguable whether true top predators really exist, since the species depicted as top predators in food web diagrams are in fact attacked by various parasites and pathogens that usually are not included in food web diagrams.

■ **Links** are simply the lines that link consumers and the consumed. **Undirected links** represent a binary (all or none) property of interactions between a pair of species. If a species occurs in the diet of a predator, they are joined by an undirected link in a food web diagram. **Directed links**

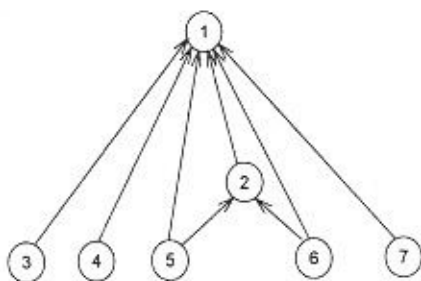
FIGURE 6.2. Source, sink, and community food webs. (A) Source web, based on the species known to feed on pine, from Richards (1926). (B) A sink food web, based on Paine's (1966) survey of feeding by *Pisaster*. (C) A community food web for Morgan's Creek, Kentucky, from Minshall (1967).

A.



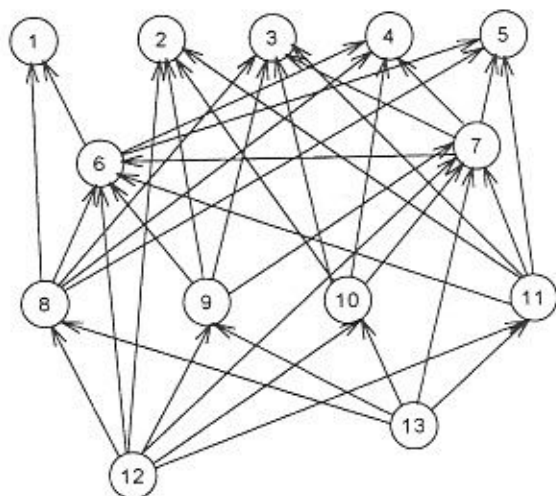
1. Pine, 2. Lepidoptera, 3. Aphids, 4. digger wasps, 5. ichneumon wasps
6. Hemiptera, 7. ants, 8. syrphid flies, 9. coccinellid beetles, 10. spiders

B.



1. *Pisaster*, 2. *Thais*, 3. Chitons, 4. Limpets, 5. bivalves, 6. acorn barnacles
7. *Mitella*

C.



1. *Phagocata*, 2. Decapoda - *Orconectes*, *Cambarus*, 3. Plecoptera - *Isoperla*, *Isogenus*
4. Megaloptera - *Nigronia*, *Sialis*, 5. Pisces - *Rhinichthys*, *Semotilus*, 6. *Gammarus*,
7. Trichoptera - *Diplectrona*, *Rhyacophila*, 8. *Asellus*, 9. Ephemeroptera - 5 species,
10. Trichoptera - *Neophylax*, *Glossosoma*, 11. Tendipedidae, *Simulium*, 12. Detritus, 13. Diatoms

are usually represented by arrows, which describe the net effect of each species on the other. Ignoring intraspecific effects, each pair of species can be joined by up to two directed links. When quantitative data on diet composition are available, as in Winemiller (1990), it is possible to use different thresholds to establish linkage; for example, species are linked only if one constitutes greater than some fixed percentage of the diet of another.

- **Connectance** is a way of describing how many of the possible links in a food web are present. One formula for connectance, based on undirected links, is

$$c = L/[S(S-1)/2] \quad (6.1)$$

where L is the number of undirected links and S is the number of species (nodes). This formula is based on the notion that in a web consisting of S species there are $S(S-1)/2$ possible undirected links, excluding any cannibalistic links. Highly connected systems contain many links for a given number of species. Another notion of directed connectance is the probability for any pair of species selected at random that a species will have a positive or negative effect on the other (May 1973).

- **Linkage density**, L/S , refers to the average number of feeding links per species. It is a function of connectance and the number of species in the web.
- **Compartmentation** refers to the extent to which a food web contains relatively isolated subwebs that are richly connected within subwebs but which have few connections between subwebs. One formula used as an index of compartmentation is

$$C_i = \frac{1}{s(s-1)} \sum_{j=1}^s \sum_{i=1}^s p_{ij} \quad (6.2)$$

for i not equal to j , where p_{ij} is the number of species that interact with both species i and species j divided by the number of species that interact with either species i or species j , and s is the number of species in the web (see Pimm and Lawton 1980; Winemiller 1990).

- **Trophic level** refers to the number of links + 1 between a basal species and the species of interest. For all but basal species, or species in linear food chains, the notion of a trophic level becomes rather uncertain because the number of links traced from a basal species to a species higher in the food web may vary with the path taken. One way of dealing with this problem is to represent the trophic level of a species as the

average of the number of links + 1 counted to arrive at that species from different basal starting points in the web (Winemiller 1990).

- **Omnivory** occurs when species feed on prey located on more than one trophic level. It is easiest to identify when considering simple food chains or pairs of food chains (Figure 6.3). **Same-chain omnivory** occurs when a species in a particular food chain feeds on trophic levels in addition to the one immediately below its own trophic level (see Figure 6.3). One example is the protist *Blepharisma*, which can feed on bacteria (the basal level) as well as on other protist species (the intermediate level) that consume bacteria. **Different-chain omnivory** occurs when a species feeds at different levels in multiple food chains. **Life history omnivory** occurs when different life history stages or size classes of an organism feed on two different trophic levels. An example would be the herbivorous larvae of frogs, which transform into insectivorous adult frogs after metamorphosis.

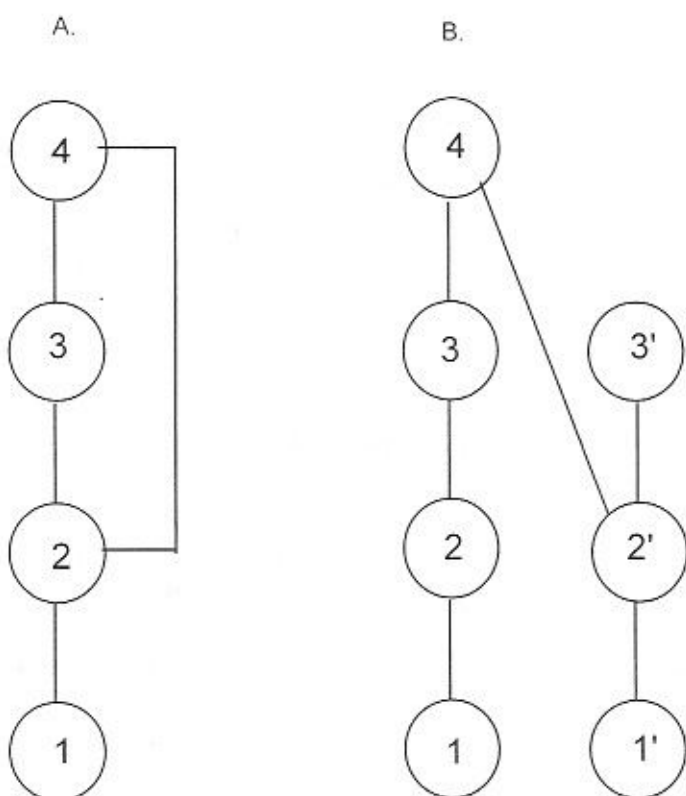


FIGURE 6.3. Examples of omnivorous linkages in food chains. (A) Same-chain omnivory, in which one species (4) feeds on two levels (2, 3) in the same food chain. (B) Different-chain omnivory, in which a species (4) feeds on different levels (3, 2') in two connected food chains.

- **Cycles and loops** occur if species have reciprocal feeding relations. A cycle occurs if each of a pair of species eats the other. The top predators in the food web shown in Figure 6.2A are an example of a cycle, where wasps eat spiders, and spiders eat wasps. A loop occurs if species 1 eats species 2, species 2 eats species 3, and species 3 then eats species 1. Cycles and loops generally occur where species have a range of size or age classes and where large individuals of each species are capable of eating smaller individuals of the other.
- **Rigid circuit** properties have to do with the way that overlaps in the prey consumed by predators can be described. For any food web, one can draw a predator overlap graph such that predator species that have at least one prey in common are linked by a line segment (Figure 6.4). If every series of three predators completes a triangle of line segments, the predator overlap graph is said to have the rigid circuit property.
- **Intervality** is a property that is related to the rigid circuit nature of predator overlap graphs. If a food web is interval, overlaps between predators can be represented by a series of overlapping line segments, as indicated in Figure 6.4. If line segments cannot be so placed, such that a segment must be broken to represent prey overlaps, the web is not interval. This admittedly esoteric property of food web graphs has a possible link to the dimensionality of the niche space required to represent feeding overlaps among species. Cohen (1978) has argued that if food webs are interval, then the niche space required to represent overlapping feeding relations is unidimensional, for example, a series of overlapping line segments arranged along a line.

PATTERNS IN COLLECTIONS OF FOOD WEBS

Cohen (1977, 1978) was the first to suggest that even coarsely drawn diagrams of food webs yielded some repeatable, and therefore interesting, patterns.

The ecological significance of these and other patterns remains controversial, since many ecologists have serious reservations about the accuracy and completeness of



Patterns emerge from comparisons of published food webs.

food web descriptions (Paine 1988). Many published descriptions of food webs are simply descriptive devices created to illustrate subsets of important interactions within communities and were never intended to serve as complete descriptions of trophic linkages. For example, Paine's (1966) *Pisaster* sink web only describes interactions between seven nodes, but the community contains at least 300 macroscopic species (Paine 1980)!

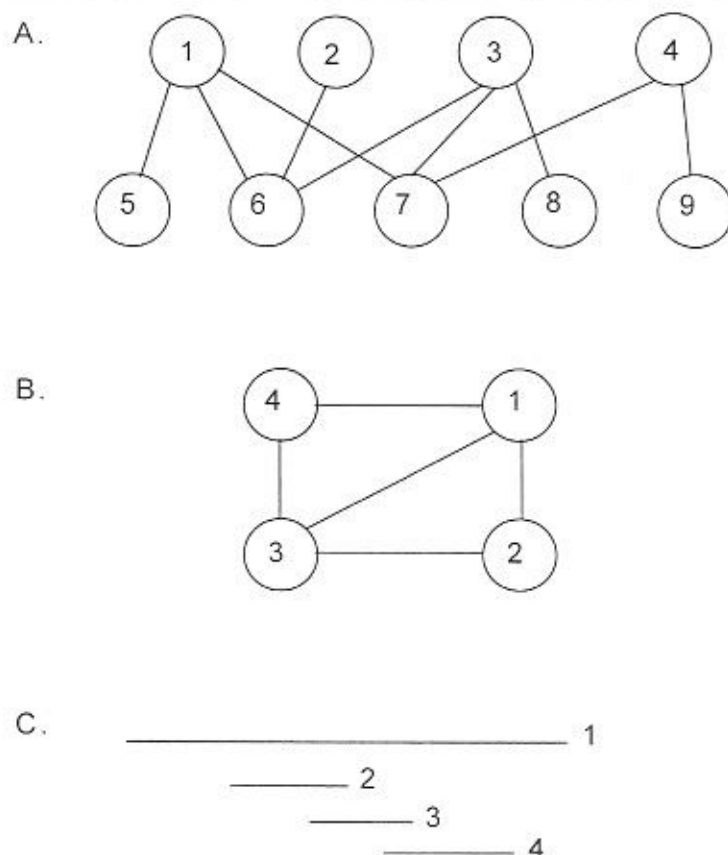


FIGURE 6.4. Examples of the rigid circuit property of a simple hypothetical food web. (A) The food web. (B) The predator overlap graph, in which line segments connect predators that share at least one prey species. Predators that share no prey species are not directly connected by line segments. (C) An interval graph, showing that overlaps in diet for predators can be represented by overlapping line segments arranged in a single dimension.

Lawton and Warren (1988), Lawton (1989), and Pimm et al. (1991) have summarized the broad patterns emerging from collections of food webs. The 10 important patterns summarized by Lawton and Warren (1988) are outlined below. Some of these patterns have become more equivocal with the advent of increasingly detailed food web descriptions. Despite the controversy surrounding the significance of these patterns, they are described here to illustrate the kinds of properties that studies of food webs address.

1. Many collections of food webs have constant ratios of predator to prey species, or ratios of basal to intermediate to top predator species. Cohen (1978) found that his collections of community webs yielded ratios of numbers of predators to prey of about 4:3 (Figure 6.5). At first glance

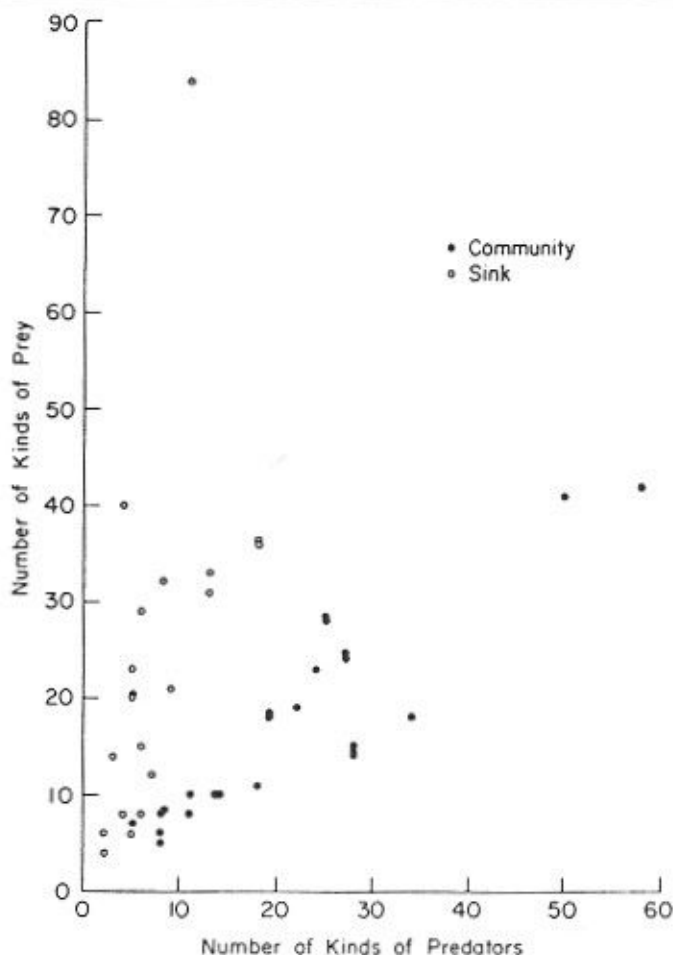


FIGURE 6.5. Relations between the numbers of predator nodes and prey nodes in collections of community food webs. The linear relation suggests a ratio of approximately four predator nodes to three prey nodes in the community webs shown by the filled circles. (From Cohen, 1978, © 1978 by Princeton University Press. Reprinted by permission of Princeton University Press.)

this seems odd, since it suggests that a larger number of predator species are being supported by a fewer number of prey species. It is less disconcerting when you consider that most prey “species” in this analysis are in fact highly aggregated collections of taxa—things like “insects” or “plants.” Later analyses extended the constancy of proportions to basal, intermediate, and top predators (Briand and Cohen 1984; Cohen and Briand 1984). Subsequent analyses of more detailed food webs have examined the effect that aggregating species into tropho-species has on food web patterns (Sugihara et al. 1989; Martinez 1991). Sugihara et al. found that additional aggregation of already aggregated webs did little to

change these patterns. Martinez (1991) found that aggregating a very finely resolved food web had little effect on ratios of predator to prey nodes, but did influence the ratio of top predators to total species, effectively overestimating the ratio of top predators to total species in highly aggregated webs.

2. Cohen's second major conclusion was that, more often than not, food webs tended to be interval in nature. There is no neat linkage between this property of food webs and any single biological process. As noted above, intervality is consistent with the notion that overlaps among predators in the prey that they consume can be represented by a series of line segments arranged in a single dimension. This may be the same thing as saying that a single niche dimension is sufficient to describe the feeding relations within a collection of predators. A descriptive model, called the **cascade model** (Cohen and Newman 1985; Cohen et al. 1985; Cohen et al. 1986), can produce webs that are interval, although the biological mechanism involved in generating these patterns remains uncertain. The cascade model assumes that a constant linkage density exists, and also assumes that species can be ordered into a hierarchy such that species low in the hierarchy can be consumed by ones higher in the ordering of species. This kind of ordering might result if predators must be larger than their prey, or if parasites must be smaller than their hosts.
3. Three-species loops are infrequent (Lawlor 1978). Close inspection of very detailed webs has shown that two-species cycles and three-species loops can arise in systems with size-dependent or stage-dependent predator-prey interactions (Polis 1991). In such systems, the roles of predators and prey can reverse with reversals in the relative sizes of interacting species, as larger organisms generally eat smaller ones.
4. Early analyses suggested that the number of links per species, **linkage density**, was constant across collections of food webs in which the nodes consisted of highly aggregated sets of species (Cohen and Newman 1985; Cohen et al. 1986). If this is the case, then connectance should decline hyperbolically with increasing species richness, according to the relationship given in Equation 6.1. Analysis of other, more detailed, food webs in which nodes correspond to less aggregated groups shows instead that connectance is constant over a fairly broad range of species richness (Figure 6.6; see Martinez 1992).
5. The average proportions of links between basal, intermediate, and top species also seem relatively constant (Briand and Cohen 1984). This pattern may be no more than a simple consequence of constant linkage

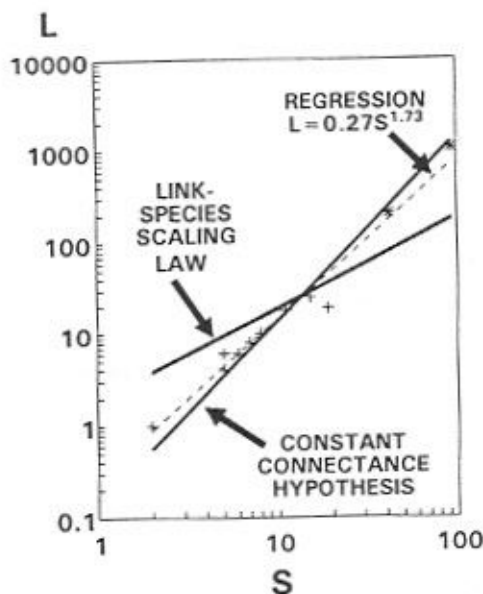


FIGURE 6.6. Alternate patterns suggested by the constant connectance hypothesis and constant links per species hypothesis. L and S refer to numbers of links and species per web. For highly resolved webs based on less-aggregated trophic nodes, the constant connectance hypothesis provides a better description. (Reprinted from Martinez, 1992, with permission of the University of Chicago Press.)

density and the constant proportions of species in basal, intermediate, and top positions.

6. Food chains are relatively short, usually containing no more than five or six species (Elton 1927; Hutchinson 1959; Pimm and Lawton 1977; Pimm 1982). This pattern is partly due to the low taxonomic resolution of many webs, as food chains tend to increase in length in more detailed webs (Martinez 1991). Both energetic (Lindeman 1942; Slobodkin 1960) and population dynamic (Pimm and Lawton 1977) hypotheses have been proposed to account for this pattern. These ideas are described in greater detail below.
7. Omnivory appears to be relatively infrequent in some systems (Pimm and Lawton 1978), but this may be a consequence of inadequate description rather than biological reality. In more recent detailed descriptions of some food webs (Sprules and Bowerman 1988; Polis 1991; Martinez 1992), omnivory is common. Omnivory also seems common in webs rich in insects and parasitoids, or in decomposers.
8. Connectance and estimated interaction strength appear to vary between webs in relatively constant and variable environments (Briand 1983).

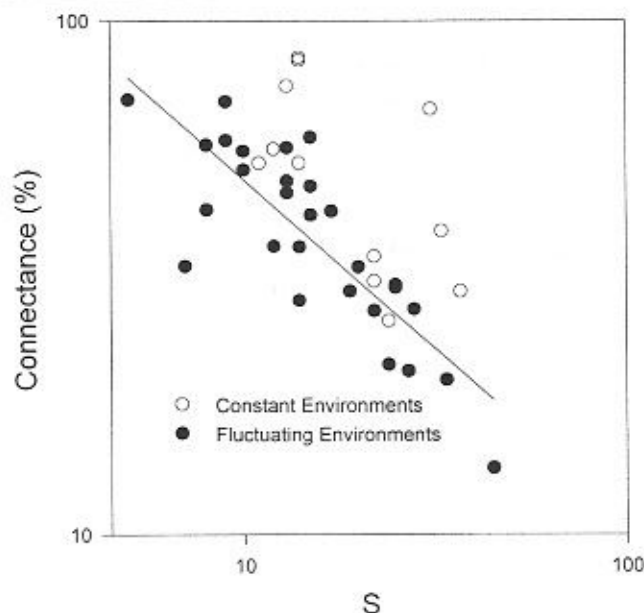


FIGURE 6.7. For a given level of species richness, s , food webs in constant environments (open circles) have higher levels of connectance than webs in fluctuating environments (filled circles). (Redrawn from Briand, 1983, with permission of the Ecological Society of America.)

Webs in variable environments appear to be less connected than ones in more constant environments (Figure 6.7). If one assumes that an inverse relation between connectance and per capita interaction strength exists (from May 1973; see the discussion of stability and complexity below), then species in more variable environments also interact more strongly.

9. Webs do not seem to be strongly compartmented or subdivided (Pimm and Lawton 1980). Some exceptions occur in situations in which webs describe communities that span discrete habitat boundaries, but even then, subwebs tend to be interconnected.
10. Food chains in two-dimensional habitats, such as grasslands, seem to be shorter than those in three-dimensional habitats, such as lakes, open oceans, or forests with a well-developed canopy structure (Briand and Cohen 1987).

EXPLANATIONS FOR FOOD WEB PATTERNS

Explanations for food web patterns draw heavily on two kinds of models: dynamic models based on extensions of the Lotka-Volterra predator-prey



Possible causes of some food web patterns.

models, and static models, such as the cascade model of Cohen et al. (1985), that make no specific reference between population dynamics and food web patterns.

Dynamic models attempt to explain food web patterns on the basis of food web configurations that promote stable equilibrium population dynamics, which presumably allow populations to persist for long periods of time, as opposed to configurations that are unstable and that presumably fail to persist for very long. The models used to predict these patterns are based on relatively simple Lotka-Volterra models that have been extended to include more than two species (May 1973; Pimm and Lawton 1977, 1978).

For a system of n species, the differential equation for the dynamics of species i looks like

$$dX_i/dt = X_i(b_i + \sum a_{ij}X_j) = F_i \quad (6.3)$$

where b_i is the per capita population growth rate of species i , a_{ij} is the per capita effect of species j on species i , including intraspecific effects when $i = j$, and X_i is the abundance of the species i , in a system of n species. The stability of these systems depends on the properties of the Jacobian matrix (see the appendix), which consists of the matrix of partial derivatives $\partial F_i / \partial X_j$ evaluated at the equilibrium densities of the n species, the X_j^* . Models of simple food chains can be constructed by choosing the elements of the Jacobian matrix from an appropriate range of values. Different food chain configurations can be modeled by setting entries to zero, positive, or negative values, as shown in Figure 6.8. The return time of the system, which is approximately the time required for the system to return to equilibrium following a perturbation, is roughly $1/\lambda_{\max}$, the reciprocal of the largest negative eigenvalue of the Jacobian matrix. This approach allows comparisons of the stability and return times for simple-model food webs of different configurations.

Stuart Pimm and John Lawton (1977) used this approach to assess the dynamics of systems of four "species" arranged in food chains of different



Models suggest that long food chains may be unstable.

length. The assumptions included were that basal species were self-limiting (negative a_{ii} 's for basal species), whereas other

species were limited only by their food supply and their predators. For each food chain configuration, numerical entries in the appropriate Jacobian matrix were selected at random from a uniform distribution of values of the appropriate sign and magnitude. This process was repeated 2000 times, a process called Monte Carlo simulation, to produce frequency distributions of return times and to estimate the frequency of stable and unstable webs. One result, shown in Figure 6.9, is that all of the food chains consisting of four

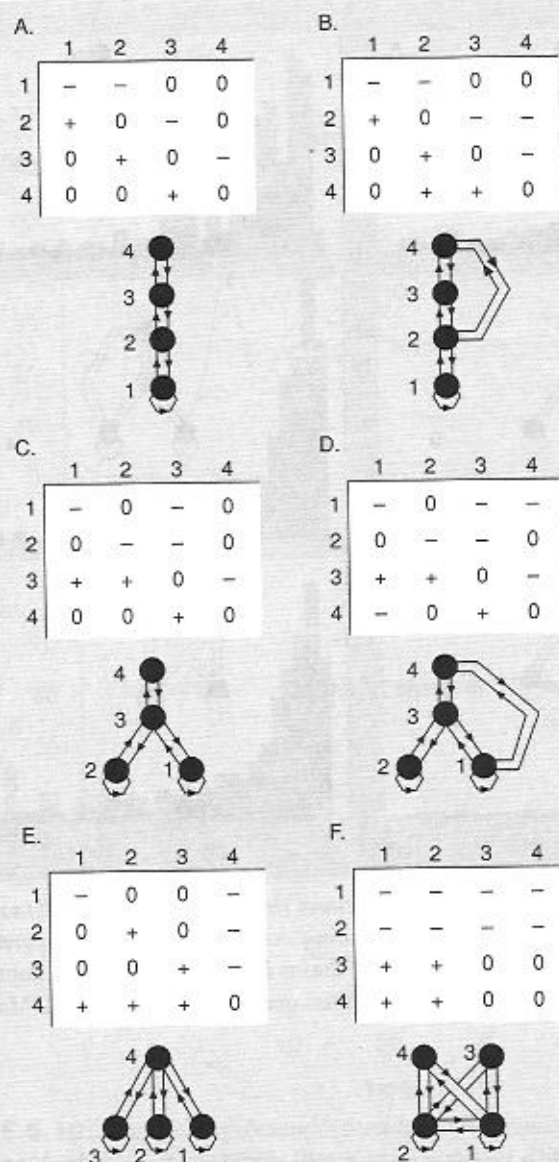


FIGURE 6.8. Schematic Jacobian matrices and corresponding food chains, showing systems simulated by Pimm and Lawton in their studies of the dynamics of model food chains. Numbers identify species located in particular trophic positions. Positive and negative signs in the interaction matrices correspond to directed links in the food chains. Negative signs on the diagonal correspond to intraspecific density dependence. (Adapted with permission from *Nature* 268: 329–331, S. L. Pimm and J. H. Lawton. © 1977 Macmillan Magazines Limited.)

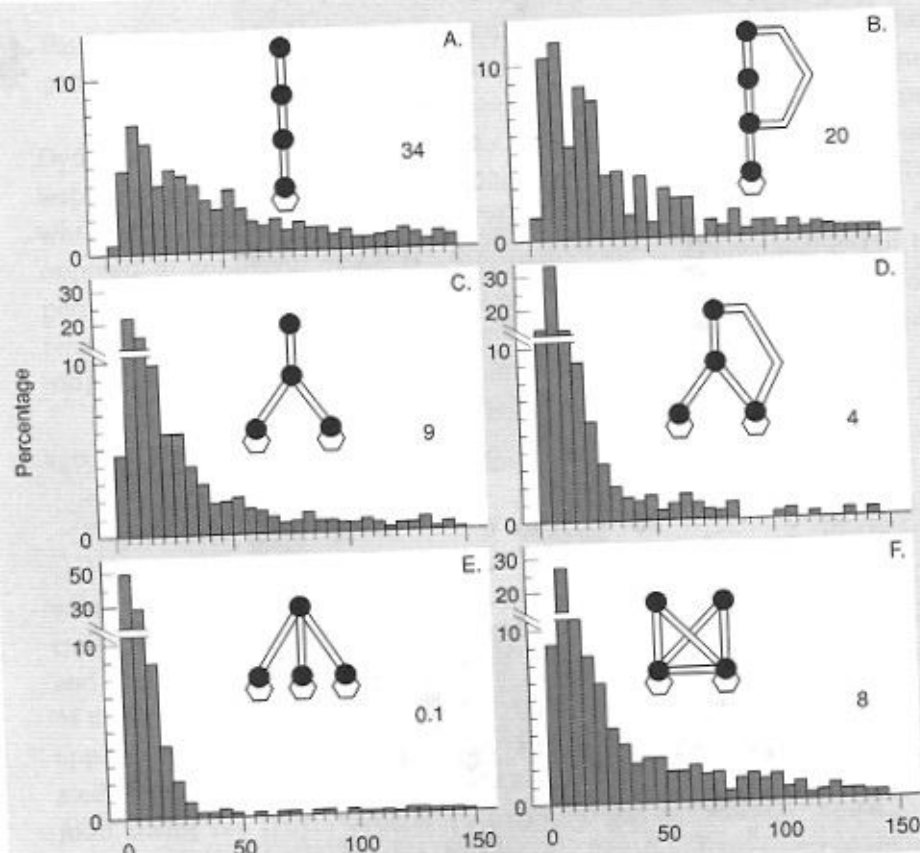


FIGURE 6.9. Frequency distributions of return times (horizontal axis) for the model food chains described in Figure 6.8. Longer food chains, shown in panel A, have a greater frequency of long return times than the shorter chains in panels C and E. (Adapted with permission from *Nature* 268: 329–331, S. L. Pimm and J. H. Lawton. © 1977 Macmillan Magazines Limited.)

species arranged without omnivorous feeding links were locally stable, but return times were substantially longer in longer chains. Longer return times suggest that populations in longer chains would require longer periods of time to return to equilibrium values following a perturbation. Pimm and Lawton equated these prolonged return times in longer chains with reduced stability, in the sense that they would recover more slowly after perturbation. An example of that property is shown for a pair of two-level food chains in Figure 6.10, which are contrived to differ in their return times. If perturbations are large or frequent, populations in systems with long return times might be more prone to extinction.

Recent work suggests that the greater stability of the shorter food chains

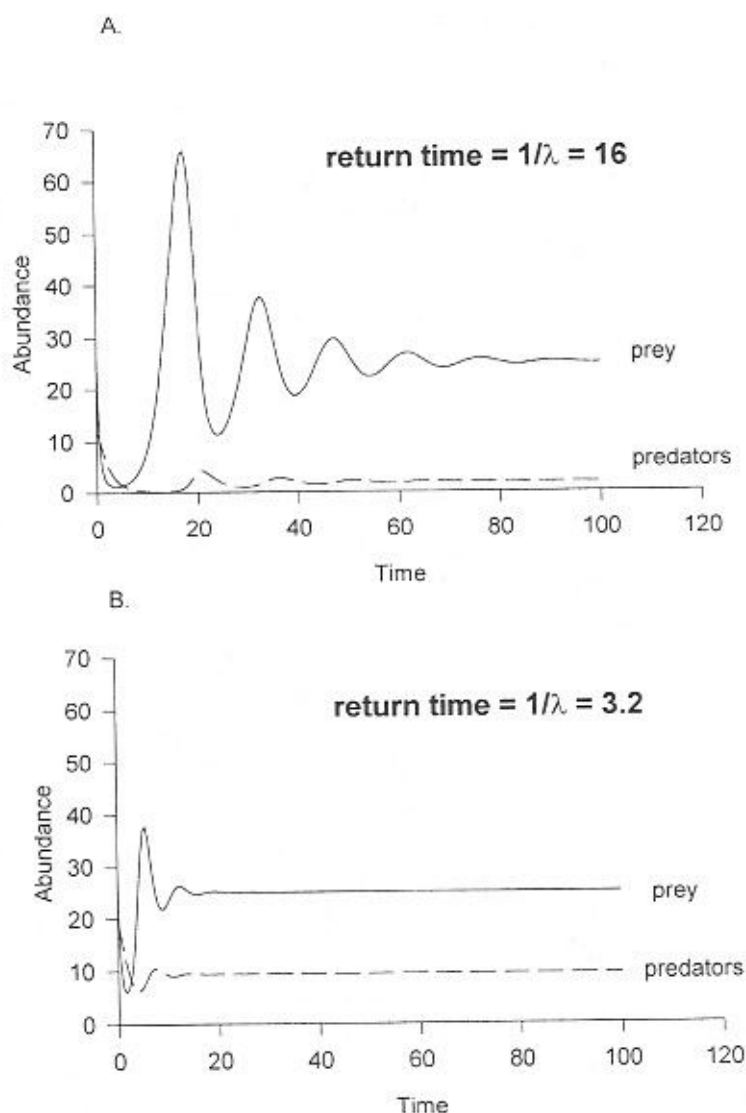


FIGURE 6.10. Examples of dynamics produced by differences in return times in simple two-level food chains described by Equations 5.3 and 5.4. Differences in return times are generated by giving the prey a higher rate of increase (2.5 versus 0.5) in the system with the shorter return time. Simulations of both systems begin at the same displacement from equilibrium.

modeled by Pimm and Lawton (1977) may be an artifact of the way that density-dependent population regulation was assumed to operate in model chains. Sterner et al. (1997) pointed out that the shorter food chains modeled by Pimm and Lawton had greater numbers of species on the basal trophic level with density-dependent self-regulation. Consequently, the greater stabil-

ity may have been a consequence of a greater frequency of density-dependent self-regulation and not of food chain length per se.

The second aspect of food chain architecture considered by Pimm and Lawton (1978) was the effect of same-chain omnivory on population dynamics within these relatively simple four-species food chains. As before,



Omnivory may also destabilize food chains.

omnivory could be modeled by including appropriate entries in the Jacobian matrix and then evaluating the eigenvalues of the Jacobian. Omnivory had an even more

striking effect on dynamics than did food chain length. Fully 78% of the longer chains with an omnivorous link were unstable. Of the remaining 22% that were stable, return times were on average shorter than in comparable food chains without omnivores. The conclusion was that omnivorous systems should be rare, given the unstable behavior of their dynamics. However, those relatively few stable systems that contained omnivores should be more stable (in the sense of having shorter return times) than comparable food chains without omnivores.

Robert May (1972, 1973) used a similar approach to compare the stability of webs differing in species richness, connectance, and the intensity of interactions between species. Rather than using webs of a particular predetermined structure, May constructed randomly connected food webs consisting of s model species. Each of the species was assumed to display intraspecific density-dependent regulation, which is modeled by placing -1 's down the diagonal of the Jacobian matrix from upper left to lower right. Interactions between species are modeled by selecting off-diagonal elements of the Jacobian matrix at random and then filling the entries with positive or negative values from a normal distribution with a mean of zero and variance i . The larger the value of i , the larger a nonzero value describing the strength of an interaction is likely to be. In this model, connectance, c , is the probability that an off-diagonal element will be nonzero. May explored the relative contribu-



Random food webs may be less stable as complexity increases . . .

tions of s , species richness, c , connectance, and i , which he termed interaction strength, to the stability of these model systems. His main result was that as s

becomes arbitrarily large, to a reasonable approximation, the system will be stable if $i(sc)^{1/2} < 1$. This means that increases in i , s , or c will tend to be destabilizing in randomly connected model food webs. Counter to the conventional wisdom of most field ecologists, (e.g., Elton 1958), increases in the complexity of a system involving increases in either the number of species (n) or the richness of trophic connections (c) should create greater instability in that system. One reason for this is that in increas-

ingly complex systems, there are more ways for things to go badly wrong, in the sense that there are more opportunities for unstable interactions to arise.

Other theoretical ecologists have suggested that May's conclusions depend critically on the way in which he constructed his models and that different models lead to rather different conclusions. Donald DeAngelis (1975) found that stability increased with increasing values of connectance, c , under conditions where 1) predators consumed only a small fraction of prey biomass, that is, predators had only modest effects on prey abundance, 2) predators in higher trophic levels were strongly self-regulated, and 3) there was a bias toward what DeAngelis called donor dependence in interactions. Donor dependence implies that for a situation in which species j is eaten by species i , $\partial F_i / \partial X_j > \partial F_i / \partial X_b$, or in other words, the predator's dynamics are more strongly affected by changes in prey abundance than by predator abundance.

Lawrence Lawlor (1978) also questioned whether May's model food webs were biologically realistic, since randomly connected food webs are likely



... but random webs differ from real ones in many ways.

to contain problematic features such as three-species feeding loops. The probability that a randomly constructed web will contain no three-species loops, given that

it contains n species and has a connectance of c , is $[1 - 2(c/2)6]^{(s!(s-3)!)}.$ This probability becomes vanishingly small as s and c increase to the levels used in May's original study. The upshot is that for many values of n and c , May's approach produces webs that have a high probability of containing three-species feeding loops. Although Lawlor argued that this was an unrealistic feature of May's approach, recent detailed studies of complex natural food webs show that three-species feeding loops do in fact occur (Polis 1991).

There is one other idea relating stability to complexity, but it differs from the ideas discussed above in focusing on the stability of a top predator rather than on the stability of the entire food web that contains the predator. Robert MacArthur (1955) argued that predators feeding on multiple prey species are more likely to weather crashes in the abundance of a single prey species than are specialized predators that depend entirely on a single prey species for their food (Figure 6.11). The idea is fairly simple and involves the notion that the existence of more than one pathway of energy flow to a predator should buffer the predator against fluctuations in prey abundance, as long as fluctuations in prey abundance are not positively correlated over time (i.e., fluctuations are not simultaneous and in the same direction).

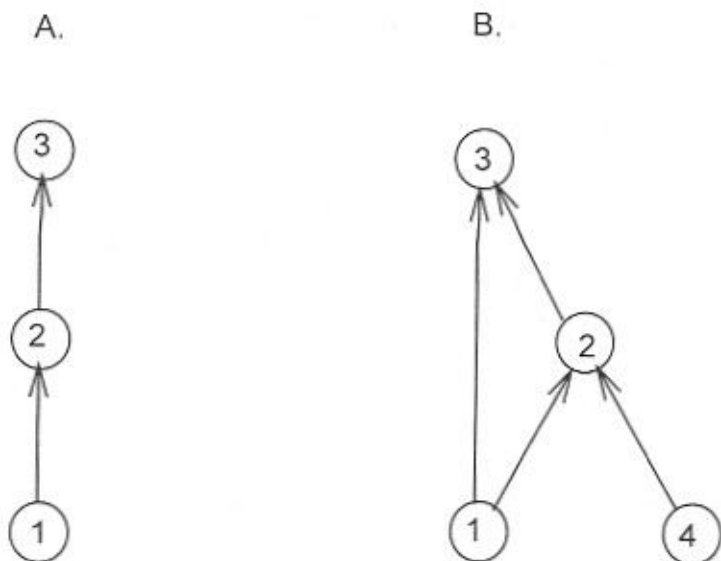


FIGURE 6.11. Examples of single and multiple trophic pathways in specialized and generalized predators. (A) In the simple food chain, extinction of either species 1 or 2 will lead to the extinction of species 3. (B) In the more complex chain, alternate pathways of energy flow exist, such that some energy will reach species 3 if species 1 is lost and 2 remains, or vice versa.

EXPERIMENTAL TESTS OF FOOD WEB THEORY

Causes of Food Chain Length

Most explorations of the possible causes of patterns in food webs rely heavily on models because the dynamics of species in natural food webs are difficult to study. Long-lived species require equally long-term studies to separate apparent dynamics from artifacts imposed by life history traits (Frank 1968; Connell and Sousa 1983). For example, very long-lived organisms, such as trees, might appear to be stable simply because their dynamics occur on a different timescale than do those of shorter-lived organisms, such as bacteria. To avoid such artifacts, temporal changes in population sizes must be scaled against the generation time of the organisms in question. It is also very *difficult to collect information about the dynamics of complex multispecies systems in which species operate on very different timescales*. Consequently, experimental studies of links between food web attributes and the population dynamics of their component species tend to focus on simple systems containing organisms with short generation times. There is also the nontrivial problem of *actually determining the feeding relations in a natural food web*. Determining the major feeding links in a single food web can consume years of dedicated effort (e.g., see Polis 1991; Winemiller 1990), even without

making an attempt to observe population dynamics! Despite all these problems, there have been some experimental tests of food chain hypotheses performed with organisms having short generation times.

If food chain length is determined primarily by the inefficiency of energy flow between trophic levels, experimental manipulations of productivity should affect the lengths of food chains. Pimm and Kitching (1987) and Jenkins et al. (1992) have tested the effects of variation in productivity on the relatively simple food webs that develop in water-filled tree holes in tropical Australia. The longest food chains in naturally occurring tree holes have been resolved to four trophic levels: 1) detritus, primarily leaf litter that falls into the tree holes and forms the basal trophic level and main source of energy that supports the food chain, 2) larval mosquitoes and chironomid midges, 3) larvae of a predatory midge, *Anatopynia*, and 4) predatory tadpoles of the frog *Lechriodus fletcheri*. Another nice feature of this system is that small



Experiments show that food chains are longer in more productive environments.

plastic containers that retain water can be used as artificial tree holes in experimental studies. Typical tree-hole food webs develop when these containers are placed near trees. Pimm and Kitching (1987)

manipulated productivity by adding different amounts of litter to a series of artificial tree holes, and observed the food chains that developed. Litter additions bracketed the normal amount observed (903 g/m²/yr) and included additions of one-half normal, normal, and two times normal amounts of litter. The additions produced slight, but nonsignificant, increases in the abundance of *Anatopynia*, and significant declines in the abundance of *Lechriodus*. Kitching and Pimm concluded that, if anything, increasing productivity decreased food chain length. Subsequent experiments by Jenkins et al. (1992) examined patterns of food web development over a greater range of experimentally manipulated levels of productivity. This time, productivity varied over two orders of magnitude, including levels of detritus input that were natural, 0.1 times natural, and 0.01 times natural. Community development was followed for up to 48 weeks by establishing a total of 15 replicates at each level of productivity and then destructively sampling 3 replicates in each series after 6, 12, 24, 36, and 48 weeks of community development. These results suggested that decreasing productivity resulted in decreases in the number of coexisting species, the number of trophic links, and maximum food chain length (Figure 6.12).

Other studies of protists in simple laboratory microcosms support the notion that dynamics become increasingly unstable with increases in productivity or food chain length. Luckinbill (1974) showed that an apparently unstable interaction between two ciliated protists, the prey *Paramecium* and its predator *Didinium*, became increasingly stable when the amount of food

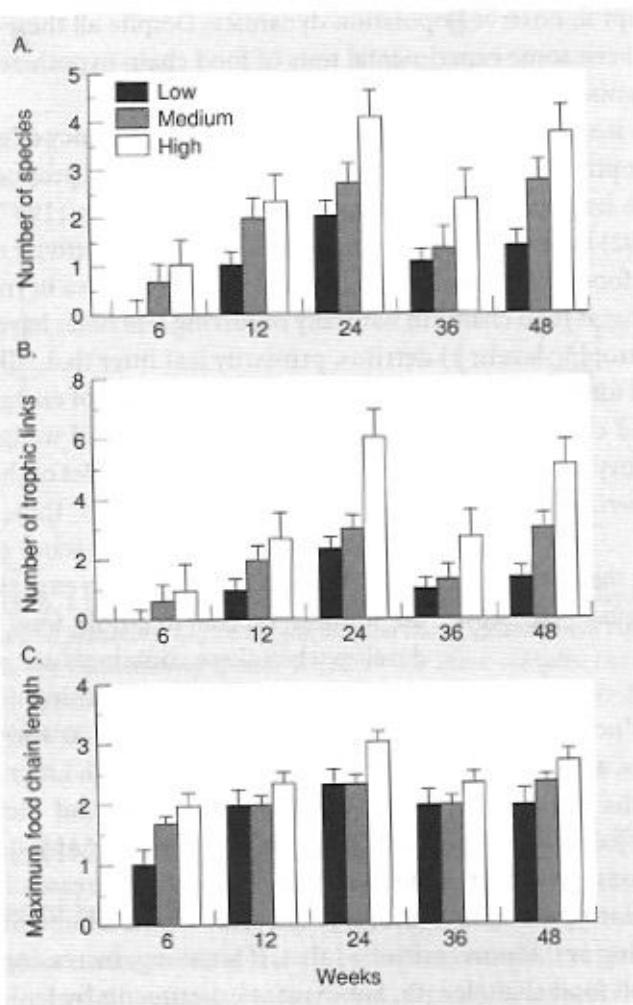


FIGURE 6.12. Number of species, number of links, and food chain length in tree-hole communities subjected to different levels of nutrient inputs for 48 weeks. Different levels of productivity, denoted high, medium, and low, correspond to 1 times, 0.1 times, and 0.01 times normal levels. (Adapted from Jenkins et al., 1992, with permission from *Oikos*).

entering the system was reduced. Luckinbill manipulated food input by adding increasingly dilute suspensions of bacteria, which served as food for *Paramecium*. At the highest food concentration used, 6 ml bacteria per 350 ml total, abundances of *Paramecium* and *Didinium* go through a single strong oscillation that results in extinction after about 6 days. Dilution to 2.0 ml bacteria per 350 ml total yields about five repeated oscillations and persistence for 34 days (Figure 6.13). The relation between persistence and food supply appears nonlinear, with a threshold of greatly enhanced persistence occurring between 4.5 ml bacteria per 350 ml total and 2.5 ml bacteria per 350 ml total.

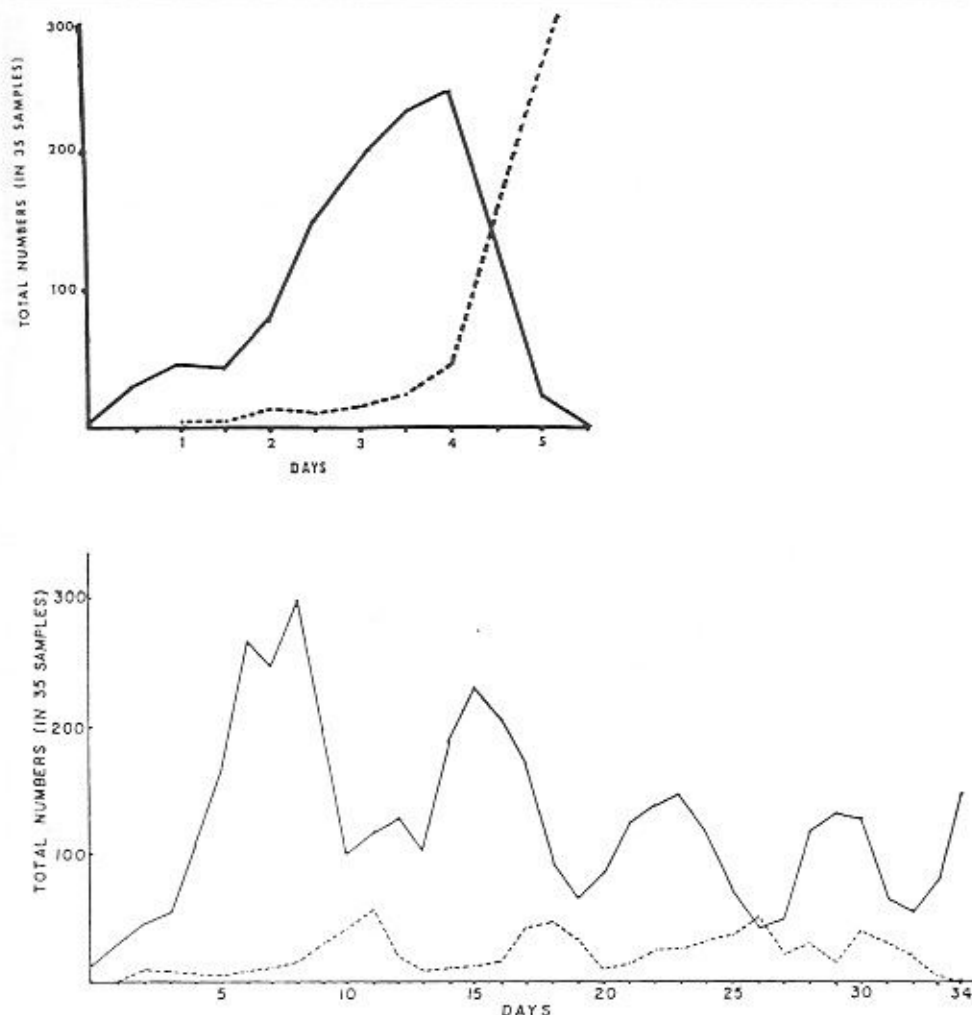


FIGURE 6.13. Examples of decreasing stability of simple food chains with increasing levels of energy input. Dashed lines show the abundance of the predator, *Didinium*. Solid lines show the abundance of the prey, *Paramecium*. (Top) A single oscillation ending in prey extinction after six days at high nutrient levels. (Bottom) Sustained oscillations for the same species interacting at lower nutrient levels. (Reprinted from Luckinbill, 1974, with permission of the Ecological Society of America.)

Thus, dynamics become increasingly unstable, and extinction becomes more likely, at higher nutrient levels.

If population dynamics are less stable in long food chains than in short ones, experimental manipulations of food chain length should produce

observable differences in population dynamics.



Long food chains display more variable dynamics than shorter chains.

Specifically, dynamics should be more variable in longer chains. Sharon Lawler and Peter Morin (1993b) found

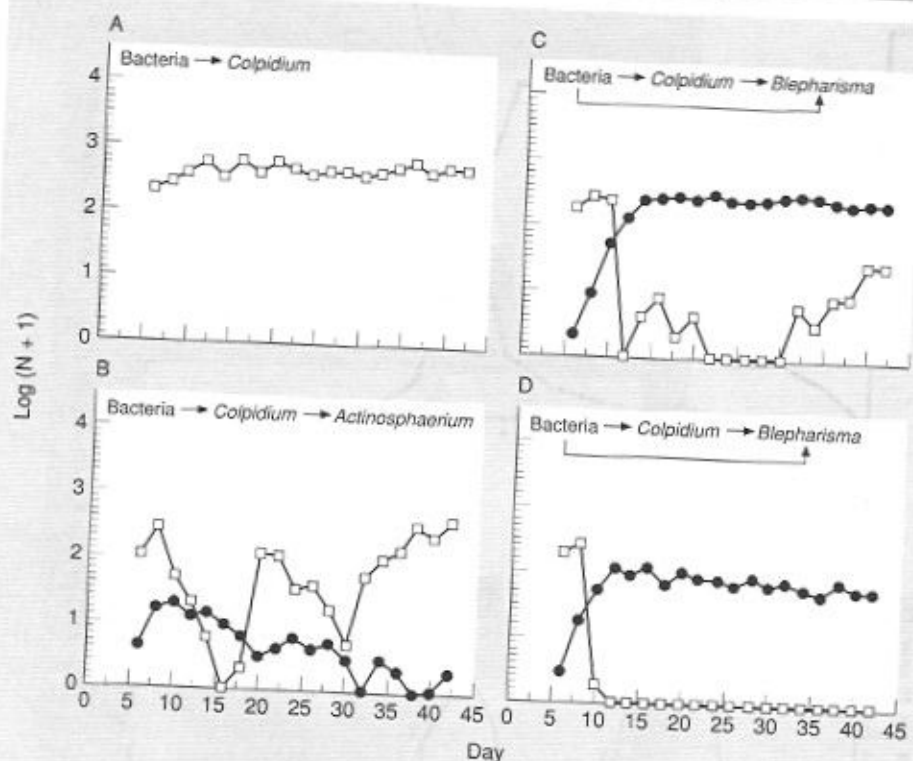


FIGURE 6.14. Increased temporal variation in population dynamics that accompanies an increase in food chain length by one trophic level. Populations of the same species, *Colpidium*, in long food chains (B, C, D; open squares) exhibit greater fluctuations in abundance over time compared with their dynamics in shorter food chains (A). (Adapted from Lawler and Morin, 1993b, with permission of the University of Chicago Press.)

that the population dynamics of protists in simple laboratory food chains become less stable with modest increases in food chain length. They compared the temporal variability of populations of the same bacterivorous protists in short food chains in which bacterivores were the top predators and in slightly longer food chains in which the bacterivores were intermediate species preyed on by another predatory protist. In the majority of cases, an increase in food chain length caused increased temporal variation in abundance (Figure 6.14). Increased temporal variation in abundance would be consistent with longer return times in longer food chains, as in Figure 6.10.

These somewhat conflicting results suggest that productivity influences the length of food chains, but in a curvilinear way (Figure 6.15). Below natural levels of productivity, there is insufficient energy to sustain higher trophic levels, and species may be lost. Above natural productivity levels,

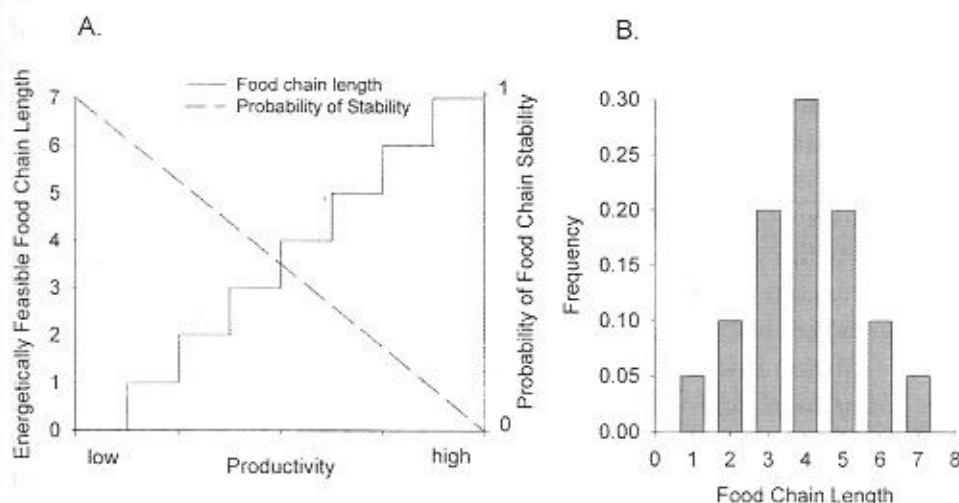


FIGURE 6.15. (A) Hypothetical relations between productivity and food chain stability or persistence. (B) Effects of productivity and stability on possible distributions of food chain length within or among habitats. At low productivity levels, food chain length is determined primarily by energy availability. Higher levels of productivity make longer food chains energetically possible, but may also decrease the probability that the longer chains will be dynamically stable. This scenario is consistent with observations of decreased food chain length in response to increases or decreases of productivity, if most food chains initially occur at intermediate levels of productivity.

species may be lost either through direct toxic effects of eutrophication or through the increasingly unstable dynamics that occur in some systems as productivity increases (Rosenzweig 1971; Luckinbill 1974). Some simple predator-prey models become unstable as productivity increases (Rosenzweig 1971). Some simple laboratory predator-prey systems also become increasingly unstable as productivity increases (Luckinbill 1974).

Omnivory, Increasing Trophic Complexity, and Stability

Morin and Lawler (1996) found that omnivorous protists had rather unpredictable effects on their prey and were unable to confirm the hypothesis that omnivores have particularly destabilizing effects on simple laboratory food chains consisting of bacteria and protists. However, they did find that omnivores had consistently larger population sizes than did other nonomnivorous predators under comparable conditions. This conclusion is tempered by the small number of omnivorous species that they examined. One fairly consistent feature of omnivore population dynamics was predicted by MacArthur (1955). Omnivorous protists that can feed on both bacteria and other bacterivorous protists tend to have more stable, less temporally variable dynamics than nonomnivorous, relatively specialized predators that track the fluctuations in a single prey species (Morin and Lawler 1996). Species with more

than one prey are less likely to fluctuate greatly in abundance when one of their prey fluctuates in abundance.

Andrew Redfearn and Stuart Pimm (1988) used the comparative method to test MacArthur's hypothesis. They surveyed published accounts of the population dynamics of herbivorous insects that were known to feed on many versus few species of plants. Their results provide some qualified support for MacArthur's hypothesis, in that less-specialized species tend to show reduced fluctuations in population dynamics over time when compared with more-specialized insects that feed on relatively few species.

Sharon Lawler (1993b) also used studies of protists in laboratory microcosms to explore whether more complex food webs were less stable than simple ones. Her simplest systems consisted of four different three-level food chains containing different species of bacterivores and top predators but



Increasing complexity can decrease food web stability. similar bacteria. Each of these four food chains was known to be stable. These chains were then paired and combined to form eight different communities con-

taining four protist species, or one community containing all eight protist species (Figure 6.16). The main result was that webs containing increasing numbers of species, and increasing possibilities for kinds of predator-prey interactions, exhibited significant increases in the frequency of extinctions of component species. This finding is in general agreement with May's (1972, 1973) original suggestion that increasing complexity in food webs may decrease rather than increase the stability of the system as a whole.

Interaction Strength

Paine (1992) has suggested another empirical approach to studies of interactions in natural food webs. His approach focuses on the experimental measurement of interaction strengths for an assortment of predators and their prey. The approach is labor intensive, since it involves measuring how prey respond to replicated removals of various predator species. Paine's operational measure of interaction strength is an index, I , that is calculated using the following expression:

$$I = (D_p - D_0)/(D_p)P \quad (6.4)$$

where D_p is the density of the prey with a known density of predators, P is the known density of predators, and D_0 is the prey density when predators are removed. Negative values indicate negative per capita effects of predators on prey, but positive effects are possible if predators facilitate certain prey by removing others, as in Paine (1966).

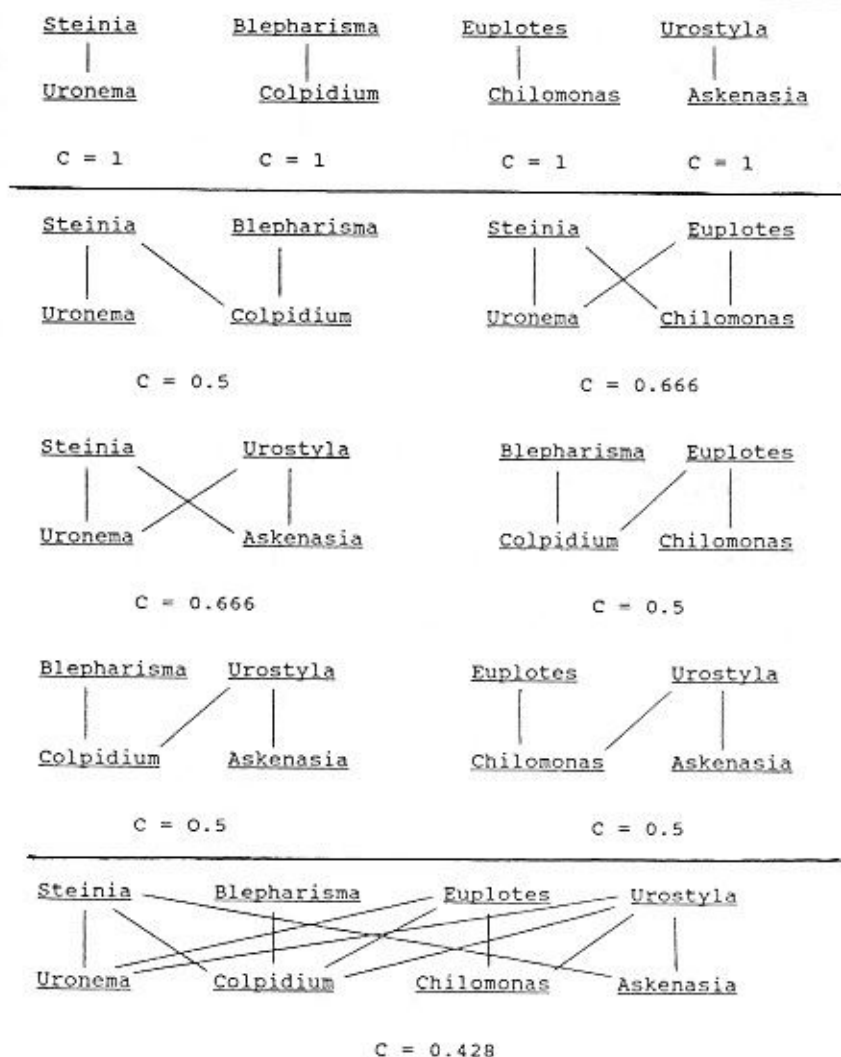


FIGURE 6.16. More complex food webs produce more frequent extinctions in simple laboratory microcosms. Protist food webs consisted of two, four, or eight protist species, with each web replicated five times and having the values of connectance, c , listed below the web. Only 1 of 40 populations (2.5%) went extinct in the two-species webs, whereas 26 of 120 populations (21.7%) went extinct in the four-species webs, and 11 of 40 populations (27.5%) went extinct in the eight-species webs. (Data from Lawler, 1993b.)

Application of this approach to an array of seven species of herbivores (predators) known to feed on sporelings (prey), the recently settled juveniles of intertidal brown algae, showed that



Many interactions in natural food chains are weak.

only two of the seven species had strong significantly negative effects on the prey.

The remaining five of the seven interacted either weakly or even positively with the prey. Paine's results suggest that the

use of known trophic links, rather than interaction strengths, may badly overestimate the frequency of important trophic connections in real food webs. It is also important to point out that Paine's measure of interaction strength is very different from the one used by May (1973). Paine's measure potentially includes both direct and indirect effects (see Bender et al. 1984; Yodzis 1988). May's interaction strength involves only direct effects, since it is the value of a partial derivative evaluated at equilibrium for a particular pair of species. The various measures of interaction strength that have been used by ecologists are described and compared in an important paper by Laska and Wootton (1998).

SOME FINAL QUALIFICATIONS CONCERNING EMPIRICAL PATTERNS

Food web research is an active, dynamic, and rapidly changing field. As more and better descriptions of food webs accumulate, some of the original generalizations about food web patterns have become problematic (see Lawton 1989; Pimm et al. 1991). Examples of two current concerns are whether some of the original major patterns seen in collections of food webs are independent of the scale of taxonomic resolution used in depicting the web (termed **scale independence**) and whether the patterns within webs vary significantly within communities over relatively short—seasonal or annual—timescales.

Scale independence refers to whether basic patterns, such as connectance, linkage density, food chain length, or ratios of numbers of taxa in different trophic categories, depend critically on the level of taxonomic resolution employed. The first studies that compared differences involving relatively coarse levels of taxonomic resolution suggested scale invariance (e.g., Briand and Cohen 1984; Sugihara et al. 1989). More recent studies of the effects of aggregating highly resolved webs, in which most nodes in the web correspond to real species or genera, suggest that aggregation may distort some patterns (Martinez 1991, 1992; Polis 1991). Webs with greater taxonomic resolution tend to have greater numbers of omnivores, longer food chains, and roughly constant connectance when compared with webs in which nodes are highly aggregated collections of many biological species.

A second question concerns the degree of temporal variation in food web patterns. Most published food web diagrams depict interactions that are possible, but may include interactions that are



Food web patterns vary over time.

infrequent or interactions among seasonally fluctuating species that are seldom simultaneously active in the same community. They are collages, rather than single snapshots, of the interactions

within a community. A few studies have explicitly explored patterns of temporal variation in food web patterns. Kitching (1987) found substantial temporal variation in the composition of his tropical tree-hole communities. Warren (1989) also found substantial temporal variation in the patterns that he observed in an exceptionally well-described pond food web (Figure 6.17). Schoenly and Cohen (1991) also explored patterns of temporal variation in a small collection of webs in which at least some data on temporal variation could be found. The general pattern is that temporal aggregation of food web patterns probably overestimates the actual number of taxa that are interacting at any particular time. By lumping nonsimultaneous interactions, say, interactions between a long-lived predator and short-lived phenologically separated prey, temporal aggregation also overestimates the actual level of connectance in the community at any particular time.

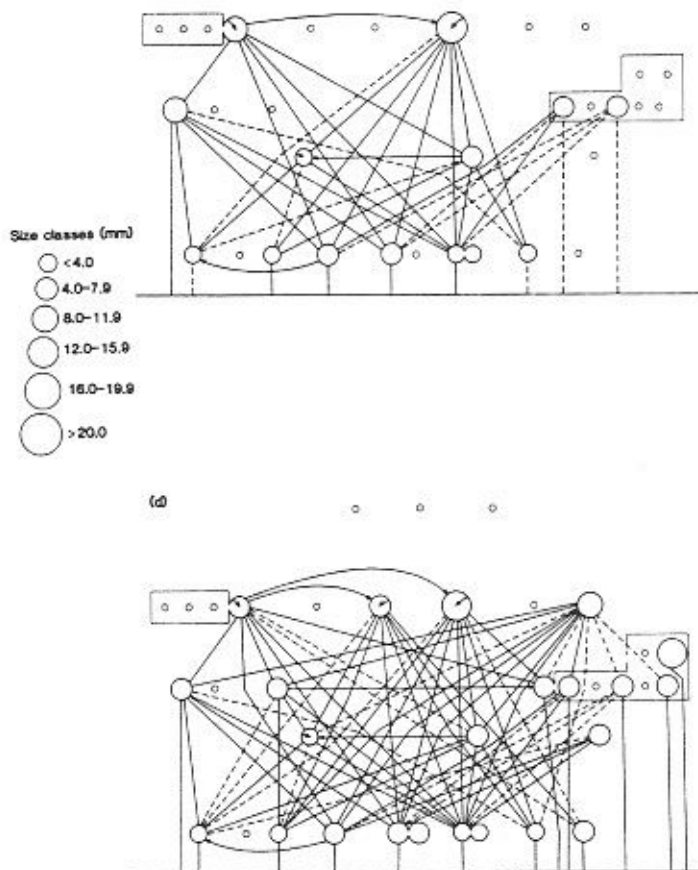


FIGURE 6.17. The structure of real food webs varies considerably over time. This figure shows temporal variation in the patterns within a food web in a small pond. (Top) Food web in March. (Bottom) Food web in October. (Reprinted from Warren, 1989, with permission from Oikos.)

CONCLUSIONS

Even if many of the early generalizations about food web patterns eventually fail to survive the careful scrutiny of increasingly detailed data sets, food webs will retain an important role in community ecology. Food webs can identify pathways of potentially important interactions, including indirect effects (Wootton 1994b), and they emphasize that communities are far more complex entities than arbitrary collections of pairwise interactions among species. Experimental tests of food web theory are rare (see Morin and Lawler 1995), and much important work remains to be done in this area.