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FOOD WEB ARCHITECTURE AND POPULATION DYNAMICS: Theory and Empirical Evidence

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ABSTRACT

Food web theory makes quantitative and qualitative predictions about the patterns of population dynamics to be expected in food webs with particular structures. Some of these predictions can be tested by comparing population dynamics in simple food chains of different architecture. Few studies have been designed specifically to manipulate food chain properties as a test of food web theory, but relevant information can be gleaned from studies of predator-prey dynamics in which food chain structure is known to vary in important ways. For example, comparisons of prey population dynamics in the presence or absence of a predator can be used to infer the consequences of a small change in food chain length. Common consequences of increased food chain length include greater temporal variation in abundance and a greater frequency of local extinctions. Studies that compare the impact of omnivore and nonomnivore predators are so infrequent that few conclusions can be reached. Ex-

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perimental studies of links between productivity and food chain length or population dynamics are also scarce. However, an emerging theme is that both increased and decreased productivity sometimes result in shorter food chains, probably for different mechanistic reasons. Studies of trophic cascades indicate that differences in the length of linear food chains have important consequences for the standing stock of species in different trophic levels, regardless of any effects on dynamics. Finally, a few studies of relations between food web complexity and the dynamics suggest that more complex systems can be less stable than simple systems, although these effects probably depend on how complexity is distributed among trophic levels.

INTRODUCTION

Food Web Theory

Food web theory remains controversial, largely because it is difficult to test its chief predictions about population dynamics in natural systems (65). Although Elton (29) sensitized ecologists to the importance of basic food web concepts during the formative years of modern ecology, the quantitative study of food webs has only recently come into its own. The recent growth of interest in food webs has been stimulated largely by theoretical work on factors that might constrain patterns of trophic connections within webs (16, 83, 117, 172). Many generalizations about the structure and function of food webs are based on the dynamic properties of relatively simple models of food webs or food chains (65, 117, 123, 172). Other generalizations about the architecture of food webs arise from the comparative study of patterns in natural food webs (16, 80, 81, 161). Indeed, Lawton & Warren (67) noted that food web theory can be divided into studies providing a population dynamic explanation for the static patterns of food webs (8, 23, 36, 47, 49, 82, 83, 102, 113–115, 117, 120, 121, 124, 131, 137) and other approaches that provide descriptive statistical or graphical generalizations about web structure, without explicit reference to the effects of web structure on dynamics (16–19, 64, 80, 81, 101, 116, 122, 147, 165–172). We are primarily interested in examining the effects of food web architecture on population dynamics, because theory suggests some clearly testable hypotheses about the population dynamics of species embedded in webs of different structure.

We focus here on a restricted set of issues selected from within the broad realm of food web theory. Those issues include: 1. factors that limit the length of food chains, including constraints imposed by population dynamics and energetics, 2. relations between the length and complexity of food chains and the existence of trophic cascades, and 3. relations between food web complexity and population dynamics. All of these issues have a rich if not entirely realistic theoretical underpinning. Often, more than one theoretical framework has been proposed to account for a particular pattern.

In contrast to the wealth of theoretical work addressing food web patterns, the amount of experimental work that can be mustered to test food web theory is surprisingly limited. This limitation reflects two factors. First, the data needed to address the predictions made by food web theory about population dynamics are exceedingly difficult to measure for long-lived organisms in natural food webs. Predictions about the relative stability of populations require data on dynamics that span at least several generations (20). When those data exist, corresponding data on food web structure are usually lacking, or vice versa. Second, many empirically oriented ecologists retain a healthy skepticism about the applicability of food web theory to natural communities (125, 126, 161). That skepticism reflects, in part, concerns about the realism of the basic models used to analyze the properties of food webs.

Renewed interest in the dynamics and architecture of food webs draws heavily on the contributions made by theoretical analyses and the comparative method, while experimental tests of food web theory have lagged far behind theoretical advances (65, 123). Our goal is to emphasize that some predictions of food web theory are empirically testable, although the tests are often more tractable in somewhat contrived or artificial systems than in nature. We present a selected overview of the kinds of experimental studies that can be used to test selected aspects of food web theory. Along the way, we emphasize the special features of experimental design needed to make inferences about food webs. Because so few experiments have been designed specifically to test food web theory, our conclusions must remain very tentative. Nonetheless, some tantalizing patterns have begun to emerge. Below we briefly review some predictions of food web theory that relate population dynamics to food chain length, omnivory, complexity, and other aspects of trophic architecture that are open to experimental tests.

Food Chain Length, Population Dynamics, and Energetics

Elton (29) observed that food chains are short. Energy often passes through only about four or five species in a chain before being passed along to decomposers. Particularly detailed descriptions of trophic interactions suggest that longer chains can be found (38, 44, 80, 125, 158). Several hypotheses have been proposed to account for the length of food chains.

Ideas about the factors that limit the length of food chains fall into two groups. One group emphasizes the constraints imposed by ecological energetics. The other group focuses on the possibility that certain food chain configurations, long chains in particular, are unlikely to persist because they are dynamically unstable, regardless of energetic constraints. Both groups of ideas present testable hypotheses. If the length of food chains is constrained by available energy, then experimental increases or decreases in productivity should cause commensurate changes in food chain length. If food chain length is constrained by population dynamics, species in longer food chains should exhibit the hallmarks of less stable dynamics when compared to the same species in shorter chains. The problem in putting these tests into action involves logistic constraints associated with the range of productivity that can be realistically manipulated in most systems, and the need to observe population dynamics over a time frame long enough to assess stability.

Population dynamic explanations for the limits to food chain length rely on the notion that long chains are locally unstable, or recover from perturbations more slowly than do shorter chains; they are therefore less likely to persist. Pimm & Lawton (120) used model food chains to argue that the complex population dynamics of trophically linked species could constrain food chain length. Their results suggest that over a short range of food chain length (2–4 levels) and a small constant number of species (4 total), populations in longer model food chains will recover from perturbations more slowly than those in shorter chains, and they are therefore less likely to persist. These conclusions have generated some debate (e.g. 137, 145), but there have been very few empirical tests of possible effects of food chain structure on population dynamics (e.g. 63).

Omnivores feed on more than one trophic level (120, 121). Lotka-Volterra models of food webs that include omnivory tend to be less stable than webs without omnivory (120). Early surveys of natural food webs suggested that omnivory was infrequent (114). However, population dynamic explanations for the relative lack of omnivory have been questioned (169), and subsequent surveys suggest that omnivory may be more common in nature than was previously thought (125, 144, 154, 158, 161).

Other models of linear food chains predict a variety of dynamic behaviors that depends on the details of the interactions. For instance, Hastings & Powell (48) showed that simple linear food chains consisting of three species can exhibit chaotic dynamics. The distinction between this finding and the local stability seen in Pimm & Lawton's analysis probably reflects differences in the ways that predators and prey are assumed to interact. A key difference is that Hastings & Powell's model incorporates nonlinear (saturating) functional responses and numerical responses, while these are linear functions in the models of Pimm & Lawton. Other similar models of three-level food chains are extensions of Monod models for population dynamics in continuous culture, and they also include nonlinear functional and numerical responses (21, 152). These models display a rich array of dynamics, ranging from stable limit cycles and stable point equilibria through unstable dynamics that result in the loss of species, depending on the values of parameters used.

Some energetic explanations for the limits to food chain length rely on the notion that energy transfer between trophic levels is inefficient, and therefore food chain length is assumed to be limited by the inefficient transfer of energy up through the chain. Lindeman (71) attributed the short length of food chains to the inefficiency of energy transfer between trophic levels. This hypothesis implies that food chains can be longer in more productive habitats (32). For similar reasons, Oksanen et al (103) predicted an increase in food chain length as productivity increased.

In contrast to the foregoing argument, many simple food chain models predict that stable predator-prey interactions will be destabilized if resource augmentation increases the prey's carrying capacity or intrinsic growth rate. This phenomenon has been termed "the paradox of enrichment" (133, reviews: 3, 24, 86). Abrams & Roth (3) point out that this prediction must somehow be reconciled with the ideas of Oksanen et al (103) that predict an increase in food chain length along a nutrient gradient. Abrams & Roth (2, 3) analyzed the responses of unstable two- and three-level model food chains to enrichment. They found that enrichment could either increase or decrease the abundance of the top predator, depending on the form of the functional responses, the level of immigration into the system, and the presence or absence of refuges. It seems likely that two opposing effects of increased energy availability interact to determine food chain length. Increased productivity creates a greater potential food chain length, but that potential is accompanied by reduced dynamic stability caused by energy input into a chain of a given length. These opposing factors may contribute to the apparent lack of correlation between productivity and food chain length noted by some authors (117).

Other hypotheses combine energetic and dynamic explanations for the limited length of food chains. Hutchinson (55) and Hastings & Conrad (49) suggested that predators feeding low in the food chain can attain large population sizes because there is more energy available at lower levels. In turn, predators with large population sizes may be less prone to extinction than species with smaller population sizes that feed higher in the web. This advantage could be offset by other factors, especially if species lower in the food chain experience a greater risk of predation than do those near the top of the chain (90, 117). Size constraints on predators may also limit food chain length. Predators are usually larger than their prey (29), and correlations between body size, home range, growth rate, and resource availability place an upper limit on feasible predator body sizes, which in turn may limit the number of trophic levels that can be assembled in a food chain (142). This hypothesis is reasonable but difficult to test. The relative sizes of predators and prey may also account for other aspects of food web architecture (67).

Relations Between the Length and Complexity of Food Chains and the Existence of Trophic Cascades

Trophic cascades occur when the addition or deletion of a higher trophic level affects the standing stock of species in lower levels. Paine (105) apparently coined the term *trophic cascade,* although the basic idea was well developed in the writings of Hairston et al (43) and Fretwell (32). Cascades reflect shifts in levels of abundance or biomass at equilibrium, rather than a change in dynamics per se. The theory of how cascades should work in simple, short, linear food chains is well developed (1, 32, 103). The problem is that natural chains are seldom linear, and even modest departures from linear food chains can prevent cascades (1). Despite this, there are many examples of trophic cascades, particularly in aquatic systems (e.g. 129).

Trophic cascade theory predicts that the biomass and population dynamics of species are determined in part by the number of trophic levels in the food chain to which that species belongs (e.g. 12, 43, 103, 134). The theory is an outgrowth of the classic paper by Hairston, Smith, & Slobodkin (43), which predicted that the particular trophic level that a species occupies will determine whether it is most likely to be regulated by competition or predation. They argued that in three-level terrestrial food chains, to the extent that carnivores decrease the abundance of herbivores, carnivores will alleviate competition among herbivores for their food, the primary producers. In turn, herbivores limited to low population densities by their predators will not be sufficiently abundant to graze producers down to levels where interplant competition is unimportant. Consequently, the abundance of trophic level two (herbivores) is controlled by predation, but the abundance of levels one (plants) and three (carnivores) should be resource limited.

Fretwell (32) and Oksanen et al (103) extended this idea, observing that predators that restrict prey biomass to low levels also reduce their own resource base. Such predators should themselves remain scarce and be unable to support a higher secondary predator. Under conditions where predators overexploit prey, additional trophic levels could be added only if increases in energy or nutrients boost per capita prey productivity (32, 103). Predator populations supplied with faster growing prey could produce sufficient biomass to support another trophic level. Upon addition of another trophic level, prey biomass in the second trophic level could increase again if additional resources became available, because predators in the third trophic level would be limited by consumers in the fourth trophic level (33, 42, 103). This scenario leads to a stepwise addition of trophic levels with increasing productivity, as might occur along a gradient of light or limiting nutrients. There is intriguing correlational evidence for a stepwise addition of trophic levels along a gradient running from oligotrophic to eutrophic lakes in Northern Europe (107). This process implies a limit to food chain length set by physiological limits to the productivity of organisms along a gradient of increasing resource availability. In cases where prey have reached the maximum productivity set by physiological constraints, additional resources will not lengthen the food chain (2, 42, 103).

Predator-prey dynamics are very important in most trophic cascade scenarios, and thus cascade theory may not be very distinct from Pimm & Lawton's (120) population dynamic explanation for why food chains are short (139). A predator that becomes scarce by overexploiting its prey would become more vulnerable to stochastic extinction (139). Examples of extreme overexploitation are uncommon in nature (146), but of course, if overexploiting predators tend to become rare, examples should be difficult to find! Hence, the nature of this process makes its prevalence impossible to ascertain by the simple inspection of natural food chains.

Food Web Complexity and Dynamics

Community ecology has a long tradition of conjectures about relations between complexity and stability (30, 40, 76, 83). Increasing complexity generally implies increasing species richness, connectance, or numbers of trophic levels in a community. Stability is well defined for systems of differential equations (10, 27, 83, 117), but the operational measures of stability applied to natural or experimental populations are less precise (20, 85, 117). Measures such as the standard deviation over time of the log of population density may only represent loose allegories for mathematical stability (138). However, these statistics are intrinsically interesting because of what they imply about the predictability of community composition. Measures of the temporal variability of population size have their own special problems related to the temporal and spatial scales of measurement (85). Despite these potential problems, they are often the only measures available for comparing the dynamics of populations.

Expectations about the stability of populations in food webs of differing complexity come from two rather different ecological traditions. The two traditions are not entirely at odds, since they focus on different things. The first tradition assumes a positive relation between stability and complexity. Some early theoretical work by MacArthur (76), and Elton's (30) comparisons of natural and artificial systems, reinforced the widely held belief that simple communities were in some way less stable than complex ones. Elton's observations (30) of organisms in natural and modified communities suggested that communities with few species tend to be unstable. In retrospect, Elton's anecdotal examples of unstable simple food webs could be explained by factors other than low complexity (40, 88, 117). MacArthur (76) suggested that increased prey species richness would enhance the stability of a predator population, because there would be more alternate pathways for energy to reach the predator population in the event that one or more of its prey populations crashed. The extent of trophic linkage between a given number of species was later formalized as the concept of connectance (34, 82), the number of realized links between species divided by the total number of possible pairwise links.

The second tradition assumes a negative association between stability and complexity. May (82) used mathematical models of food webs to argue that more complex communities should be less stable than simple communities. May's analysis did not address the situation considered by MacArthur (76), specifically whether feeding on different numbers of prey species would affect the stability of the predator population. May's conclusions about relations between complexity and the stability of the entire system depended critically on some biologically unrealistic assumptions used to generate randomly connected model webs (23, 64).

Connectance in some natural food webs apparently declines with increasing species richness, as May predicted (e.g. 8, 17). However, descriptions of natural food webs tend to omit connections, and lump species into categories at lower trophic levels, casting doubt on the robustness of some of these patterns (106, but see 131). More recent work with finely resolved food webs suggests that connectance may in fact be constant across webs of varying species richness (81).

Empirical studies of the connectance-stability relation have identified potentially interesting patterns in natural communities (8, 130), but the correlational nature of these studies makes it difficult to infer clear causal relations between stability and connectance. In an array of field studies, Pimm (117) found no consistent empirical relation between species diversity and food web stability. Few of the field studies reviewed by Pimm (117) were specifically designed to test the effects of species diversity on stability, and several studies were simply anecdotal reports of "simple" systems that seemed stable, or "diverse" systems that seemed variable. We are unaware of experiments that have demonstrated effects of connectance on population dynamics by varying connectance while holding species richness constant in webs of real organisms.

WAYS TO TEST FOOD WEB THEORY

Linking the Dynamics of Model Food Webs and Real Species

Tests of theory can be qualitative or quantitative. A qualitative test assesses the general agreement between broad dynamic patterns predicted by models and those observed in experimental systems. For instance, if a model predicts that a given shift in food chain structure will produce a shift from stable to oscillating population dynamics, and an analogous change occurs when the structure of a food chain is experimentally manipulated, then some qualitative agreement between theory and experimental evidence would seem to exist. If the predicted pattern fails to materialize, then the theory is found wanting. Of course, it is always possible that populations in model and real settings will display similar dynamics for entirely different and fortuitous reasons. For this reason, quantitative tests are needed to rule out spurious agreement between the dynamics of real food chains and their model representations. In our view, a quantitative test would involve first estimating the parameters of the model used to predict food chain dynamics. Then, the parameterized model can be used to predict the dynamics that might be observed in an experimental system. A decision about whether any model provides a reasonable fit to experimentally observed dynamics is a question ultimately settled by the statistical approach used to assess the goodness of fit between predicted and observed dynamics. For systems like food chains that are prone to chaotic behavior (48), which means that their temporal dynamics will be exquisitely sensitive to initial conditions, quantitative tests may not be a realistic goal. Clearly, quantitative tests will be much more difficult to accomplish than are qualitative tests.

Dynamic Implications of Long Return Times or Locally Unstable Equilibria

Qualitative tests of food web theory require some way of comparing the dynamics of species in different food webs with the general predictions of food web theory. One key attribute of the model food chains studied by Pimm & Lawton (120, 121) was the tendency for longer food chains to exhibit longer return times. Strictly speaking, all of the chains without omnivores were locally stable and would return to an equilibrium following a perturbation. The existence of longer return times means that when displaced from an equilibrium, populations in model chains with longer return times would display damped oscillations for a longer period of time before returning to stable equilibrium levels. One consequence of the longer return times of longer food chains should be the existence of prolonged oscillations following a perturbation. Such oscillations should translate into a statistical signature that should be measurable as an increase in temporal variation in abundance (see 150).

Models with an unstable local equilibrium can yield a diversity of dynamic behaviors, including stable limit cycles, chaos, or the extinction of one or more species (10, 27). Systems with an unstable local equilibrium point may persist indefinitely (60), but they probably exhibit higher levels of temporal variability than do systems with stable equilibria and rapid returns to those equilibria. A key point is that an unstable system need not generate the extinction of a species, but it should display greater temporal variation than would a locally stable system with a short return time. The other difference, of course, will be the shorter persistence time of species in systems where extinctions occur.

There has been much debate about whether local stability in model systems is analogous to the persistence of species in nature. Some authors have argued that only systems with stable equilibria are likely to persist in nature (117). Others have shown that systems without a locally stable equilibrium may nonetheless persist indefinitely (14, 60). Indeed, nonequilibrium metapopulation systems may persist for long periods of time, despite the presence of regular local extinctions (14). Rather than cavil over what measure of dynamic behavior is the best predictor of persistence in natural systems, we prefer to focus on whether the qualitative behaviors predicted by particular models are consistent with the observed dynamics of populations.

EMPIRICAL EVIDENCE

Food Chain Length and Dynamics

Evidence for the effects of food chain length on population dynamics mostly comes from three sources: 1. microbial food chains assembled under continuous culture or batch culture conditions, 2. arthropod predator-prey or parasitoid-host systems in laboratory microcosms, and 3. a small assortment of field systems where population dynamics can be compared among situations where food chains differ in some known way, usually because of the presence or absence of an important predator. Of these sources of information, laboratory studies of predator-prey dynamics in simple microbial food chains provide most of what we know about the consequences of increasing food chain length for population dynamics. For example, Gause (35) emphasized that his simple laboratory systems of infusoria feeding on bacteria corresponded to two-level food chains.

The problem in extracting usable information about the influence of food chain length on dynamics from many studies is that critical controls are either omitted or not reported. This appears to reflect an overriding early interest in the dynamics of predator-prey species pairs per se, rather than an interest in comparing the dynamics of prey with or without their predators. Consequently, there is much information about the dynamics of an assortment of readily culturable predator-prey pairs (46, 153), but critical information about the dynamics of the prey in the absence of the predator is much harder to come by. It is also necessary to follow dynamics for a sufficiently long period of time that reasonable measures of temporal dynamics (e.g. temporal variation in abundance, persistence times) can be compared. It is surprising how few studies meet these minimal requirements. Those that do typically vary in food chain length by only one link, which corresponds to the addition or deletion of a predator.

Experimental Manipulations of Food Chain Length

One common consequence of adding predators to prey populations in simple laboratory systems is a rapid decrease in prey abundance, followed by the extinction of both the predator and prey species, or just the predator (35, 41, 51, 74, 77, 91). Extinctions fall within the range of dynamics predicted by models with nonlinear interactions between species, but those models probably predict the observed extinctions for the wrong reasons. In most cases, extinctions in laboratory systems seem to be correlated with time lags that allow predators to overexploit their prey and drive them to extinction before starving out themselves (35, 73).

The failure of predators and prey to persist in spatially simple laboratory environments is frequently cited as evidence for the importance of spatial refuges or other metapopulation mechanisms in promoting predator-prey coexistence (35, 51). This argument probably overstates the case for the importance of spatial refuges, however, because there are numerous examples of predator-prey pairs that do manage to coexist for long periods of time in simple, spatially homogeneous, laboratory settings (153, 5, 22, 50, 57, 61–63, 74, 92, 135, 152, 155). These persisting systems provide support for the notion that relatively simple models may adequately describe the dynamics of a certain class of food chains.

Prolonged interactions among predators and prey in laboratory settings can produce a variety of dynamics. In microbial systems, one common pattern is an increase in the temporal variation in prey population size in longer food chains. This pattern holds for interactions between bacteria and phage (15, 50, 69, 70), bacteria and protists (21, 57, 152, 155), and protists and protists (6, 62, 63, 73, 92, 135).

In some cases prey dynamics may be relatively unaffected by predators. Luckinbill (75) found no obvious difference between dynamics of the prey species *Colpidium campylum* with and without the predator *Didinium nasutum*. Morin & Lawler (92) also noted a minority of cases where temporal variation in prey dynamics was unaffected by predators. None of these studies has examined the full range of food chain length (from two to four levels) explored theoretically by Pimm & Lawton (120, 121).

An assortment of studies of arthropod predator-prey interactions in laboratory settings describes either sustained oscillations or irregular fluctuations in population size over time (51, 91, 111, 112, 153). Huffaker's (51) classic study of interactions between herbivorous and predatory mites is unusual in that it does describe the dynamics of prey with and without predators. For persisting systems of differing spatial complexity, prey dynamics appeared more variable in shorter food chains without predatory mites. Mitchell et al (91) show that the population dynamics of *Drosophila* become increasingly irregular as parasitoids become more abundant.

Damped oscillations in the abundances of coevolved predators and prey, like those described by Pimentel (111) and others (15, 50, 70), can have multiple causes, including reduced attack rates by predators and increased resistance by hosts. Some studies of interactions between bacteria and viruses in chemostats offer indirect insights into links between dynamics and food chain lengths, which are inferred from well-known evolutionary changes in the bacteria and viruses that tend to decouple the predator-prey interaction. In most cases, bacterial populations initially display erratic temporal fluctuations in abundance as they interact with viruses that function as predators (15, 50, 70). After the bacteria and viruses coevolve for a time, resistant bacteria attain much higher densities and exhibit temporally stable dynamics, which can be interpreted as the dynamics typical of shorter food chains.

It is also worth pointing out that there have been very few efforts to actually estimate the parameters of simple model food chains that correspond to laboratory food chains with more than two trophic levels. Consequently, few strictly quantitative tests of food chain models exist. Some exceptions include the continuous culture studies of Tsuchiya et al (152), Curds (21), and Lenski & Levin (69), and the batch culture studies of Maly (77). Tsuchiya et al (152) concluded that a Monod model with terms for saturation kinetics in resource uptake provided a better fit to their data than did a classic Lotka-Volterra model without saturation kinetics. In practice, the Monod model would have some of the same features as the models elaborated by Pimm & Lawton (120), such as density dependence at the base of the food chain, and the Monod model would differ in the kind of nonlinear functional and numerical responses linking prey-predator dynamics.

Dynamics of predators and prey in natural nonexperimental settings also sometimes yield patterns of greater temporal variation where predators are present (45, 94). Some examples of biological control fall into this category. There are fewer examples of what happens after specialized predators of the herbivores are introduced, but predators appear to accentuate the population fluctuations of organisms as different as California red scale (96) and voles (45). Although a wealth of population dynamic data exists for different kinds of species (20, 162), it is usually impossible to determine the structure of the food chains in which such species are embedded. This makes it impossible to say much about links between observed population dynamics and food web theory in most natural systems.

Although there is a modest amount of data concerning the effects of typical top predators on prey dynamics, few analogous data exist for omnivorous top predators. This is unfortunate, because theory predicts that chains containing omnivores should be much less stable than comparable chains without omnivores (120, 121). Diehl (26) has pointed out the virtual absence of population dynamic information about the prey of omnivores, or the omnivores themselves. Lawler & Morin (63) and Morin & Lawler (92) have compared the dynamics of species in simple food chains with and without omnivorous top predators. They found no consistent effects of omnivores on prey dynamics for two omnivore species feeding on two different prey, a total of four different food chains, but they did find that omnivores often attained higher population densities than did nonomnivorous predators.

To our knowledge, there are no other comparative studies of population dynamics in natural settings for predators that differ with respect to omnivory. Diehl (26) has attempted to survey the relative net impacts of omnivores and nonomnivores in natural communities, but the data do not address dynamics per se. Other surveys of the effects of predators on prey populations, such as that of Sih et al (140), make clear that most experimental studies do not distinguish among types of predators (omnivore or not), and few studies contain the information on long-term dynamics needed to assess stability.

Productivity and Food Chain Length

A handful of researchers have tested whether enrichment destabilizes predator-prey population dynamics in aquatic microcosms and lake enclosures, with mixed results. Luckinbill (73, 74) destabilized protist predator-prey interactions by enriching the bacterial food supply of the prey species. Enrichment improved the nutrient content of the prey, which in turn delayed predator starvation and allowed predators to drive prey populations to extinction. Neill (100) found that adding nutrients to enclosures in an oligotrophic lake improved rotifer recruitment, which supported high densities of midge larvae (*Chaoborus*), which in turn overexploited their alternate crustacean prey. In a study conducted in estuarine enclosures, Björnsen et al (7) showed that correlated oscillations in bacteria and heterotrophic flagellates increased in amplitude when nutrients were added. Analogous responses to increased nutrient supply rates occur in some continuous culture systems (57). Balčiūnas & Lawler (6) enriched basal resources in a microbial food chain, which caused the extinction of the top predator, but not through the "paradox of enrichment" mechanism. Augmenting resources allowed most of the prey to achieve a size refuge from predation. McCauley & Murdoch (86) found no effect of enrichment on population cycles involving *Daphnia* feeding on algae; they suggested that the observed dynamics were driven by time lags in the response of consumers to prey abundance.

Unfortunately, comparable information about the effects of productivity of terrestrial systems is usually unavailable (24), primarily because the long generation times of most terrestrial producers and consumers make it difficult to say much about long-term population dynamics, other than those in rather unique circumstances (141).

Unlike the pattern predicted by the paradox of enrichment, the energy transfer hypothesis suggests that longer food chains should occur in more productive habitats. Pimm & Kitching (118) and Jenkins et al (56) have manipulated productivity in an effort to learn whether productivity affects the number of tropic levels supported in simple tree-hole communities. The results have been mixed. Additions of nutrients above ambient levels actually appeared to reduce the number of trophic levels in one study (118), a result loosely consistent with the paradox of enrichment. In a second study of the same system where nutrient inputs were reduced to two orders of magnitude below ambient levels, food chains again became shorter (56). As noted above, enrichment of laboratory systems tends to destabilize some interactions that are stable at lower levels of enrichment, resulting in either the extinction of species and a concomitant reduction in food chain length, or increasing temporal variation in abundance.

Although Pimm (117) found no evidence for a correlation between productivity and food chain length in his survey of systems, Persson et al (107) found that more productive lakes tended to support an additional trophic level, up to a point. Lakes with the highest productivity also had slightly shorter food chains. The uncertainty in interpreting such comparative studies comes from the inability to disentangle observed differences in productivity from other factors that might affect food chain length.

Trophic Cascades, Food Chain Length, and Population Dynamics

In evaluating the potential for predation to cause cascading effects, researchers have noted that prey are often resistant to predators, so that predators may not reduce prey biomass enough for a strong cascade to occur (e.g. 66, 68, 128, 156). We use "prey resistance" as a general term to encompass prey inedibility, physical defenses, behavioral defenses, and the use of spatial or temporal refuges. Prey resistance could also affect food chain length, but whether resistance lengthens or shortens food chains depends on the details of how predators and prey interact (2). If most prey are resistant in some way, the amount of biomass available to support predators will be low. Strong resistance consequently decreases the predator's resource base and potentially shortens the food chain (e.g, 6). However, a partial refuge that prevents the predator from overexploiting the prey may ensure sufficient stability of prey production to allow both prey and predators to attain a higher biomass, creating the potential for a longer food chain. Refuges that protect a large portion of the population may result in donor-controlled population dynamics, so called because the refuge prevents predators from strongly affecting prey dynamics, while prey dynamics still influence the predator (23). Such systems are often quite stable.

Elliott et al (28) demonstrated how the presence of a refuge can allow a potentially unstable trophic cascade to persist by preventing the overexploitation of prey. They constructed a tri-trophic food chain of algae, *Daphnia*, and fish in replicated experimental microcosms, plus the shorter food chains of algae alone, and algae plus *Daphnia*. When fish were present, *Daphnia* populations crashed. However if the fish were confined to a cage, they were prevented from overexploiting the *Daphnia*, and all three trophic levels coexisted in the microcosms. Similarly, Takahashi (149) was able to stabilize a host-parasitoid interaction by providing a spatial refuge for the host.

In other systems, cascades are truncated before they reach the lowest trophic levels (13, 104). Pace & Funke (104) found that negative effects of *Daphnia* on protists failed to enhance the abundance of bacteria in lake enclosure experiments, despite the fact that protists are important consumers of bacteria.

Reduced predator efficiency can also counteract the tendency of predators to overexploit prey (59, 97). Spatial heterogeneity can reduce predator efficiency even in the absence of an explicit spatial refuge (that is, space that is available to prey but not to predators, 51, 77, 98, 148, 157). Space per se can also dilute prey so that predator-prey encounters become infrequent, thereby allowing prey to persist (74). Interference among predators can prevent excessive attack rates, and aggregation of predators in dense patches of prey can stabilize predator-prey dynamics by reducing attacks in areas where prey are sparse (31).

The trophic cascade hypothesis has been quite controversial (e.g. 1, 11, 25, 42, 52, 126, 136, 146). Debate has centered on one main issue: Does the cascade hypothesis apply to entire, complex food webs? The answer is probably "rarely," for three reasons. First, omnivory can blur trophic levels and weaken cascading effects, and omnivores are prevalent in many systems (93, 108, 125, 126, 161). Second, strong full-web cascades are unlikely unless the prey within a trophic level are homogeneously edible and available to predators (1, 47, 68, 89, 126). Finally, interference among predators (4, 37) and abiotic forces may weaken cascades by preventing predators from reaching abundances such that they limit prey. All these factors can reduce the strength and extent of cascades in food webs. Top-down effects are evident in many communities, but they vary greatly in magnitude and in the number of food web members affected. This has led some to question the strength of an effect needed before a top-down effect can be legitimately termed a cascade, since the original theory predicted overwhelming top-down effects (25, 47). Nevertheless, few can dispute that trophic cascades can affect the population dynamics of species within single food chains embedded in larger food webs. Cascades are one of the most common and widely recognized indirect effects in nature, and they should retain a central place in ecological theory (reviews: 33, 42, 127, 163; see also 9, 39, 72, 78, 79, 84, 132, 143). Trophic cascades influence population dynamics, and population dynamics potentially determine the number of trophic levels in food chains.

Recent work also suggests that effects of enrichment on the abundance of species in different trophic levels will depend on the trophic level considered and on food chain length, as suggested by Fretwell (32) and Oksanen et al (103). Wootton & Power (164) have shown that increased algal productivity in stream systems has no effect on the abundance of grazers, but significantly increases the abundance of small predators that feed on grazers. Where food chains are one level longer, and larger predators depress the abundance of small predators, grazers become more abundant, while algal abundance is depressed.

Complexity and Dynamics

Rigorous experimental tests of effects of food web complexity on stability should manipulate species richness and/or connectance independently of other potentially correlated factors. Unfortunately, many field studies confound differences in species richness with differences in successional age, so that the factors contributing to differences among communities remain somewhat ambiguous (e.g. 53, 87, 95, 110). Important exceptions include the microcosm studies of Hairston et al (41), Tsuchiya et al (152), Luckinbill (75), and Lawler (61, 62) that directly created increases in species richness while measuring the stability of relatively simple laboratory communities of bacteria and protists. Hairston et al (41) found that increased bacterial diversity enhanced the stability of bactivorous *Paramecium* spp., but communities containing three species of *Paramecium* appeared less stable than those containing fewer species. Addition of the predators *Didinium* and *Woodruffia* also destabilized the communities, although these predators can sometimes coexist with prey for long periods under other conditions (73, 74, 135). Hairston et al could not resolve, from this study, whether diversity and stability were related, and they called for more experiments. With the exception of a handful of studies, the call went largely unheeded. Tsuchiya et al (152) found that the inclusion of a third trophic level stabilized an unstable competitive interaction between two species of bacteria. Luckinbill (75) and Lawler (62) both found that the addition of an alternate prey destabilized a previously stable interaction between different protist predator-prey pairs. In a different study, Lawler (61) assembled food webs of differing complexity (2, 4, and 8 protist species) from pairs of predators and prey that were known to be stable. Frequencies of extinctions were significantly higher in the more complex communities, suggesting that more complex communities were indeed less stable. Resurgent interest in the structure and dynamics of food webs has prompted renewed calls for experimental studies of stability and complexity (67, 88, 119). The recent experiments by Naeem et al (99) and Tilman & Downing (151) have examined various aspects of the performance of ecosystems with different degrees of species richness. Because most of the species in these terrestrial systems are relatively long-lived, these experiments have not directly addressed the issue of how complexity affects population dynamics. They have suggested that the ability of communities to absorb carbon dioxide (99) or retain biomass in the face of environmental perturbations (151) is positively related to initial species richness and food web complexity.

Some field studies of relations between complexity and stability have measured how communities of relatively long-lived organisms respond to various perturbations (e.g. 53, 54, 87, 110). Other studies estimated temporal variation in the attributes of communities of different complexity, to measure dynamic correlates of complexity (e.g. 95, 109, 159, 160). These studies have yielded interesting results, but they have their limitations. Logistic constraints common to most field studies limit replication, and experimental time scales are typically too brief (relative to the generation time of key organisms) to permit assessment of stability (20).

Complex natural food webs are reticulate in structure, so that one population can affect another through many indirect pathways. We reviewed the potential consequences of one type of indirect effect, trophic cascades, above. Other indirect effects include consumptive competition, apparent competition, indirect mutualisms, and interaction modifications. The implications of these various indirect effects for community structure and population dynamics have been reviewed recently by Wootton (163), so we will not duplicate that effort here. However, it is worth pointing out that as food webs become more species rich and connected, more potential pathways of indirect effects arise. Indirect effects complicate the predictions of population dynamics. Nevertheless, ecologists have made progress in identifying the food web structures that produce indirect effects. In many cases, empirical studies of trophic cascades, competition, and apparent competition have verified theoretical predictions about how these processes influence population dynamics (163).

SYNTHESIS

Kinds of Experiments/Studies That Are Needed

This review should make clear the pressing need for more experimental studies of the effects of food web architecture and energetics on the dynamics of populations. Population dynamic data must be collected over many generations of the focal organisms in order to address basic questions about stability. This requirement will necessarily exclude most long-lived organisms from studies that attempt to link food web structure to population dynamics. Despite that limitation, meaningful data on the dynamics of real species in food webs of known structure can be collected and compared. With somewhat more effort, it should be possible to estimate the parameters of simple food web models that correspond to the kinds of food webs that can be assembled in ecological experiments. Such efforts are critically needed to assess whether the models used to explore the dynamics of food webs and food chains depart in important ways from the dynamics of systems assembled from real species.

The length of experimental food chains examined so far is extremely limited. There seems to be little problem in building short chains with two or three levels in laboratory microcosms. Experimental studies of chains with four or more levels in laboratory microcosms are nonexistent. It is unclear whether such chains will persist long enough, in general, for studies of their long-term dynamics to be feasible, or whether the intrinsic interest in the dynamics of such systems has gone unrecognized. Long chains clearly exist in nature. What we don't know is whether those longer natural chains can only persist when embedded in a more complex food web, and if that is the case, why it might be so. Much the same case can be made for studies of how complexity affects dynamics. The range of species richness explored in these studies is very small, generally a mere handful of species. Species richness in most laboratory microcosms falls several orders of magnitude below the complexity of even the more depauperate natural communities. If effects of complexity on dynamics are a nonlinear function of species richness, the few studies completed so far are likely to yield a very uncertain estimate of relations between complexity, dynamics, and ecosystem functions. Much important work remains to be done to test food web theory. That work is needed both to expand the information base about dynamics of real species in webs of known configuration and to test the very tentative generalizations that we outline below.

Emerging Generalizations

1. *Food Chain Length and Population Dynamics* The limited evidence available suggests that population dynamics become more variable, and in some sense less stable, as food chains increase in length. There are occasional examples of trends in the opposite direction, but these seem to be cases where time lags create variable dynamics in prey populations even in the absence of predators. This pattern suggests that the precise details of the models used to represent food chains may matter very little, as long as a qualitative agreement between food chain structure and dynamics is all that is desired.

2. *Omnivory and Dynamics* Evidence is insufficient to say whether food chains with omnivores are less stable than chains without omnivores. One intriguing pattern is that omnivores appear to attain consistently higher, and occasionally more stable, population sizes than do predators that feed on a single trophic level. Much more work needs to be done to determine whether any of these patterns are general.

3. *Productivity and Food Chains* The effects of various kinds of enrichment on population dynamics and the length of food chains are complex. In the majority of laboratory studies, enrichment is destabilizing, causing a partial or

complete collapse of the food chain and a net decrease in food chain length. Such responses support the basic mechanisms underlying the paradox of enrichment, although some important exceptions do occur. Reductions in nutrient inputs in some systems also cause a reduction in the number of trophic levels, which suggests that energy availability does play some role in the setting the length of food chains. This raises a new paradox, delineated by the observation that increases or decreases in productivity appear to have the same negative effect on the length of food chains. The tentative resolution of this paradox is that food chains collapse for different reasons. Reductions in energy input make it impossible for species on higher trophic levels to obtain enough energy to persist. Increases in energy input destabilize the dynamics of populations in food chains to the point where one or more trophic levels go extinct. It is unclear whether natural food chains contain species that have coevolved to interact stably at some characteristic level of productivity, or whether natural chains persist despite any departures from stable dynamics forced by energetic constraints.

4. *Trophic Cascades* Trophic cascades are a natural consequence of interactions in simple linear food chains. In some situations, cascades are truncated after one or two trophic levels, for a variety of reasons that require further exploration. More work needs to be done to test current ideas about how departures from simple linear food chain architectures will influence the appearance and propagation of cascades in real systems.

5. *Complexity and Dynamics* Very modest increases in the complexity of simple food webs lead to decreases in stability, as is shown by the extinctions of species in more complex communities that readily persist in less complex subsets of the same communities. In at least one case, the mechanism responsible for the decreased stability is a kind of indirect effect, apparent competition. Similar mechanisms seem plausible in related systems. Models suggest that increases in the stability of community- or ecosystem-level responses with increasing complexity are not at odds with the apparent decreased stability of population dynamics (58). It will be particularly interesting to explore whether the dynamics of populations and ecosystem processes are tightly linked or only loosely correlated in systems composed of real species.

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