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TOP-DOWN AND BOTTOM-UP FORCES IN FOOD WEBS: DO PLANTS HAVE PRIMACY?¹

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INTRODUCTION

Ecologists have long debated the importance of trophic interactions in determining distributions and abundances of organisms. Those ecologists who agree that trophic interactions are important still debate whether the primary control is by resources (bottom-up forces) or predators (top-down forces). According to the bottom-up view, organisms on each trophic level are food limited. The top-down view holds that organisms at the top of food chains are food limited, and at successive lower levels, they are alternately predator, then food limited (Bowlby and Roff 1986; see Menge and Sutherland 1976 for a more extreme top-down view; Table 1). Hunter and Price (1992) offers a synthetic framework and sensible advice regarding this controversy. They suggest that ecologists not ask, “Do resources or predators regulate this particular population?,” but rather, “What factors modulate resource limitation and predation in this system, determining when and where predators or resources will dominate in regulating populations?” Here, I review factors that affect the relative strength of top-down and bottom-up forces in food webs. I also discuss methodological problems that color our perceptions of the importance of these forces.

The “top-down” view, first introduced by Hairston, Smith, and Slobodkin (1960) in their famous “the world is green” proposition, predicts that whether or not organisms are predator or resource limited depends on their position in food chains. Hairston et al. (“HSS”) argued that green biomass accumulated (in mature terrestrial communities) because predators kept herbivores in check. This theory had the potential to synthesize opposing views about population regulation held by ecologists with different taxonomic expertise. If herbivores were held in check by their predators and predators were therefore largely food limited, then ecologists studying birds at the third trophic level should be

impressed by competition (MacArthur 1958, Lack 1971), whereas ecologists studying insects at the second trophic level should find their populations responding only vaguely if at all to resource levels (Andrewartha and Birch 1954, Strong 1984).

Some ecologists, however, have found HSS to be not a conciliatory balm, but an irritant for ecology’s growing pains. As an irritant, the HSS theory has been highly productive. Ecologists challenging the assumption that a green world is an edible one have developed the active field of plant defense theory (Feeney 1968, Coley et al. 1985). Ecologists who assert that trophic levels are non-operational concepts with no useful correspondence to reality (Murdoch 1966, Peters 1977, Polis 1991) are provoking thought about why, despite omnivory and the complex linkages of real food webs, manipulations of top predators in communities sometimes trigger chain-like trophic cascades (discussed in *Feedbacks: Issue 2*). Most fundamentally, some ecologists became interested in why the world wasn’t green everywhere. Fretwell, for example, was interested in applying the HSS framework to the Konza Prairie ecosystem, but observed that Kansas was not entirely green (L. Oksanen 1990: 448–449 and *personal communication*). By extending the theory to systems with fewer or more than three trophic levels, Fretwell predicted that where food chains have odd numbers, grazers would be predator limited and landscapes should be filled with lush green vegetation. Where food chains have even numbers of trophic levels, plants would be grazer limited and landscapes should appear barren. Fretwell (1977, 1987) also predicted that trophic levels will be added sequentially as primary productivity increases, so that along large-scale environmental gradients of productivity, landscapes will alternately appear green or barren.

These top-down views, along with later trophic cascade models (Paine 1980, Carpenter et al. 1985), hold that plant standing crops are largely regulated by top-down forces. By their presence or absence, higher trophic levels will determine whether or not conspicuous

¹ For reprints of this Special Feature, see footnote 1, p. 723.

TABLE 1. Views on the relative importance of top-down and bottom-up regulation in food webs in decreasing order of the relative strength attributed to top-down forces.

TOP DOWN
<i>Menge and Sutherland 1976</i> : Food webs are filled with omnivores, with larger species capable of eating most smaller species. Most trophic levels below the top are potentially predator limited. Physical disturbance shortens food chains.
<i>H Hairston, Smith, and Slobodkin 1960</i> : Predators regulate herbivores, releasing plants to attain densities at which they become resource limited. Detritivores and herbivores are predator limited; plants and predators are resource limited.
<i>Fretwell 1977, 1987, Oksanen et al. 1981</i> : Food chains can have fewer or more than three trophic levels. Top trophic levels and those even numbers of steps below them are resource limited; trophic levels odd numbers of steps below the top are predator limited.
CO-LIMITATION BY PREDATORS AND RESOURCES
<i>McQueen et al. 1989</i> : Trophic cascades produced by top-down forces in limnetic lake food webs attenuate before reaching plants.
<i>Getz 1984, Arditi and Ginzburg 1989</i> : Interference (broadly defined) among predators prevents their efficient exploitation of resources, so that prey populations, though reduced by exploitation, can increase with increases in their own resources.
<i>Mittelbach et al. 1988</i> : Predators require different resources as juveniles than as adults. This decoupling prevents predator populations from efficiently tracking resources when increases involve food of only one predator life history stage.
<i>Leibold 1989</i> : Control of prey by consumers diminishes after initial exploitation shifts community dominance to less edible species.
<i>Sinclair and Norton-Griffiths 1979</i> : Starvation-weakened prey become more vulnerable to predation or disease.
<i>Sih 1982, Mittelbach 1988, Power 1984a</i> : Prey in spatial refuges from predation become more food limited.
BOTTOM-UP LIMITATION
<i>White 1978</i> : Plants are not appreciably limited by herbivores except when unusually stressed (for example, by drought). All trophic levels are potentially limited by availability of food resources.

growths of plants accrue in communities. But Hunter and Price (1992) offer a compelling argument for the primacy of bottom-up forces in food webs: "... the removal of higher trophic levels leaves lower levels intact (if perhaps greatly modified), whereas the removal of primary producers leaves no system at all." Fretwell's second proposition, that the potential primary productivity of a region would determine the number of trophic levels it could support, is in accord with Hunter and Price's view that plants ultimately provide "the bottom-up template" for communities. While the number of trophic levels in food chains determines plant standing crops, plant productivity constrains the number of trophic levels. By determining the number of trophic levels in communities, plants,

by their productivity, ultimately constrain the top-down forces that in turn regulate their standing crops.

The Fretwell model, then, predicts that top-down forces will dominate trophic dynamics, but that food web structure will be set by the fundamental bottom-up attribute of ecosystems, plant productivity. This verbal model, and a number of mathematical models of trophic stacks (Smith 1969, Verhoff and Smith 1971, Sykes 1973, Oksanen et al. 1981, W. M. Getz 1984 and *unpublished manuscript*, Arditi and Ginzburg 1989) incorporate top-down bottom-up dualities. Yet several remain simple enough to accommodate additional real world complexity and still offer interpretable predictions. In real food webs, "a host of biotic and abiotic factors" will modulate the relative strengths of predator control and resource limitation of populations (Hunter and Price 1992). For example, top-down forces will be weakened relative to bottom-up forces by factors that reduce consumer efficiency. Models of stacked trophic levels that capture interactions and feedbacks within and between trophic levels that change consumer efficiency contribute to the synthesis Hunter and Price seek regarding forces in food webs.

CONSUMER EFFICIENCY IN MULTI-TROPHIC LEVEL MODELS

The relative efficacy of top-down vs. bottom-up forces in food webs will depend in part on the efficiency with which consumers can exploit their prey. Interactions among consumers, between consumers and resources, and between nonadjacent trophic levels can affect consumer efficiency, and thereby modify top-down forces in food webs (Fig. 1).

A recent theoretical controversy has set into relief different assumptions in multi-trophic level models about behavioral interactions among predators, and about time scales of prey attack vs. predator population response (Arditi and Ginzburg 1989, Hanski 1991, L. Oksanen, *unpublished manuscript*). L. and T. Oksanen, who formalized and extended Fretwell's food chain dynamic theory (Oksanen et al. 1981, Oksanen 1988, 1990, T. Oksanen 1990a), built their models upon classical predator-prey models (Rosenzweig 1971, 1973) in which attack rates of predators are assumed to depend only on absolute, instantaneous prey density. These prey-dependent models generate vertical predator isoclines (Rosenzweig and MacArthur 1963) (Fig. 2 isocline a), indicating that in three-level food chains, increases in primary productivity should lead to increases in predator but not herbivore abundances (Fig. 3a). If trophic levels are added across productivity gradients, these prey-dependent models predict stepwise accrual of trophic level biomass, in which productivity of resources and consumers are uncorrelated within productivity intervals supporting a given number of

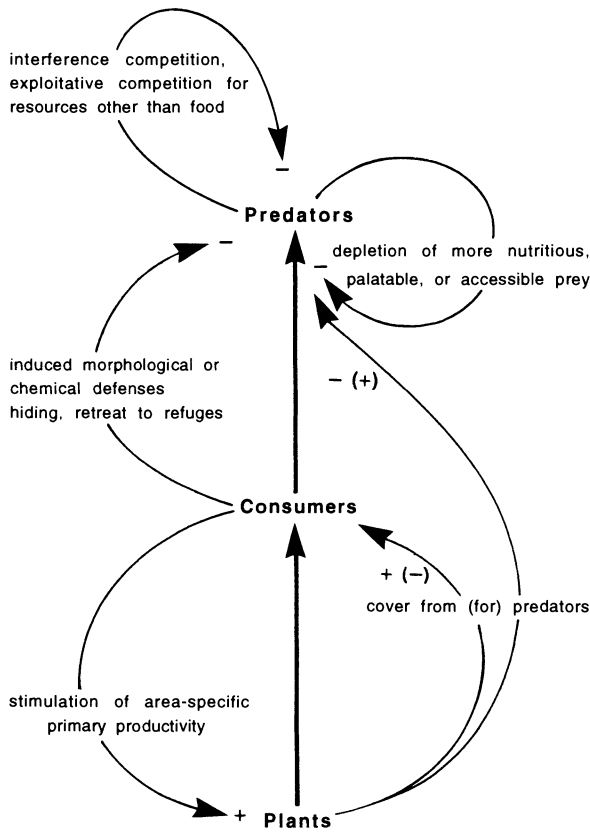


FIG. 1. Mechanisms (curved arrows) modulating top-down and bottom-up forces (straight arrows) in food chains.

levels (Oksanen et al. 1981, Mittelbach et al. 1988: 220, Fig. 1).

Predators may not regulate their food resources efficiently, however, if they fight with each other, are limited by and compete for resources other than food (e.g., shelters, water), cause prey to hide or become better defended, or if time lags occur between prey consumption and the predator's reproductive response (Arditi and Ginzburg 1989, Begon et al. 1990). Some theorists (Getz 1984, Arditi and Ginzburg 1989, Arditi et al. 1990) have argued that in many cases, predator attack rates should scale not to absolute prey density, but to some function of the ratio of prey numbers to the numbers of predators sharing them. Proponents of these ratio-dependent models argue that ratio dependence better captures the dynamics of systems in which predators engage in mutual interference, live in heterogeneous environments, or recruit on slower time scales than they attack their prey (Arditi and Ginzburg 1989, Hanski 1991). These ratio-dependent models produce predator isoclines bent to the right (Fig. 2, isoclines b, c), indicating that consumers and their resources should both increase with ecosystem produc-

tivity (Fig. 3b, c). Correlated increases of consumers and resources have been taken as evidence for the primacy of bottom-up forces in food webs (McQueen et al. 1986, Mittelbach et al. 1988). In the spirit of Hunter and Price, however, we should acknowledge that positive correlations obtain when both top-down and bottom-up forces co-limit populations (Fig. 3b, c). If prey experience only bottom-up control (Fig. 2, isocline d), densities of predators and prey will not necessarily be correlated (Fig. 3d).

Other mechanisms leading to ratio-dependent attack rates include declines in the edibility or availability of food. Food quality may decline because of active responses by prey to predators, such as hiding or withdrawing to refuges (Edmunds 1974, Charnov et al. 1976, Sih 1982, Werner et al. 1983, Power 1984a, 1987, Power et al. 1985, Mittelbach 1988, Sih et al. 1988) or the induction of morphological or chemical defenses

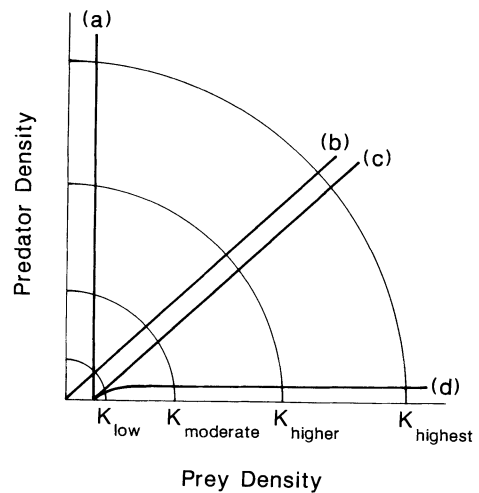


FIG. 2. Phase space showing prey isoclines for low, moderate, higher, and highest productivity environments, and four isoclines of increasingly self-limited predator populations: (a) isocline predicted from Rosenzweig and Oksanen models for predators whose functional response depends only on prey density; (b) isocline generated by the Arditi-Ginzburg model for predators whose functional responses are ratio-dependent; (c) isoclines from the ratio-dependent model of Getz, which can relax the assumption of (b) that predators can reduce prey populations to zero; and (d) an isocline for a predator whose population becomes limited by resources other than prey. All predator types are defined as more efficient as their zero isoclines move nearer to the Y axis. "Efficient" consumers suppress prey populations to low levels, and can maintain viable populations themselves on low standing crops of prey. Some predators, like spiders (Schoener 1989), can persist at low prey densities but have little impact on prey populations. Their zero isoclines are near the Y axis only at low prey density. These predators would not be considered "efficient" in the present sense, as some constraint prevents them from responding to and damping increases of their prey. Modified from Begon et al. (1990).

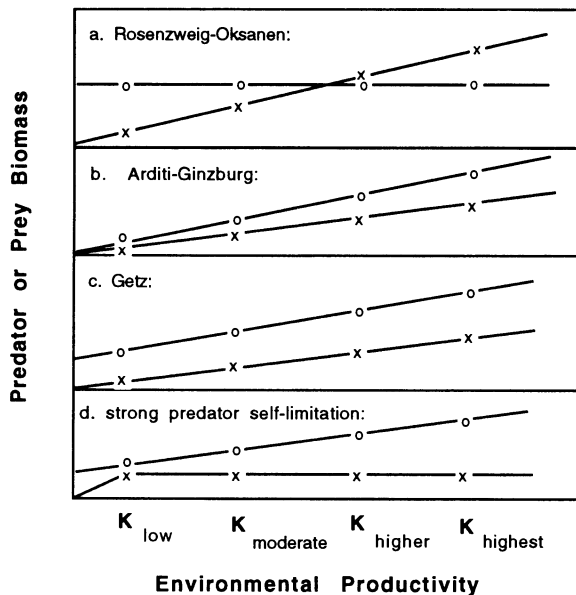


FIG. 3. Patterns of accrual of predator (\times) and prey (\circ) biomass with increasing environmental productivity (or potential carrying capacity, K , for plants in the environment) expected for predators with isoclines a, b, c, and d.

(e.g., Gilbert and Stemberger 1984, Harvell 1984, Haukioja et al. 1985). Even without active responses of prey individuals to predators, prey quality or availability may change with depletion, if predators initially select more available or palatable prey individuals or species, and remaining prey become progressively less nutritious or palatable (Leibold 1989) or harder to find (see the "Losing your marbles" game, Smith 1972: 319, 334–335).

Finally, discrepancies between demographic and behavioral time scales (Arditi and Ginzburg 1989, Hanski 1991), and the decoupling of food availability for one consumer life history stage from the survival or fecundity of another life history stage (Mittelbach et al. 1988, Neill 1988) can reduce consumer efficiency in both tracking and suppressing prey populations. These mechanisms, along with predator interference (broadly defined), will weaken top-down relative to bottom-up forces in food webs.

FEEDBACKS BETWEEN CONSUMERS AND RESOURCES, AND BETWEEN NONADJACENT TROPHIC LEVELS

Two other types of interactions between trophic levels that modulate top-down and bottom-up forces in food webs are (1) nonlinear responses of primary productivity to grazing, and (2) the effect of cover provided by plants on predator–prey interactions.

Some early multitrophic-level models incorporated feedbacks between plants and consumers when nutrients are conserved and recycled within the system (Smith 1969, Verhoff and Smith 1971, Sykes 1973). Nutrient recycling and other positive indirect effects of grazing on plants produce hump-shaped relationships between grazing pressure and growth rates of phytoplankton (Miura et al. 1978, Seale 1980, Sterner 1986, Carpenter and Kitchell 1988), periphyton (Flint and Goldman 1975, Lamberti and Resh 1983, Power 1983, 1990a, Carpenter and Lodge 1986, Lodge 1991), and terrestrial graminoids (McNaughton 1985, Jefferies 1988). At low grazing pressures, plant losses may be offset by growth stimulated by recycling of nutrients (Seale 1980, Sterner 1986) or removing senescent tissues (McNaughton 1976), overgrowths, or sediments (Power 1990a), and area-specific primary productivity may exceed that of ungrazed vegetation. As grazing increases, however, plant biomass losses will reach levels that cannot be offset by stimulated growth, and area-specific primary productivity will decline. Highly nonlinear relationships between grazing pressure and plant renewal could decouple and destabilize top-down trophic control in real food webs, making plant standing crops under different trophic regimes difficult or impossible to predict (Hastings and Powell 1991). This may occur in some limnetic lake food webs, where cascading responses linking higher trophic levels attenuate before reaching phytoplankton (McQueen et al. 1986, 1989).

Finally, predator–prey interactions change with availability of cover, and plants, as they accumulate, provide cover (Crowder and Cooper 1982, Savino and Stein 1982, Carpenter and Lodge 1986, Power 1990b). How will such dynamic feedbacks (Mangel and Clark 1988) affect community patterns, shifting the balance of top-down and bottom-up forces in food webs? While they are among the factors discussed in the verbal model of Hunter and Price (1992), feedbacks between non-adjacent trophic levels have not yet been incorporated into published mathematical food-chain dynamics theory, although a recent model developed by W. M. Getz (*unpublished manuscript*) has the generality and flexibility to capture such features.

In summary, there appear to be a small number of verbal and mathematical models, to which Hunter and Price have made a thoughtful contribution, that can accommodate synthetic, flexible views of changing, context-dependent roles of top-down and bottom-up forces in food webs. As is common in ecology, however, our ability to explore the assumptions and predictions of these models with field data lags far behind. Real world tests of even the simpler models, such as the Fretwell-Oksanen model of food-chain dynamics, require resolution of some serious methodological issues.

First, can the independent and dependent variables of models (local primary productivity and trophic level biomass for the Fretwell-Oksanen model) be quantified in nature? When should we evaluate trophic level biomass, given that communities are subject to periodic disturbances, and may not be in fully recovered, "equilibrium" states? How should we spatially circumscribe communities for this analysis, when home ranges of co-occurring consumers can be markedly different, and for some, can be larger than the scale of spatial heterogeneity in primary productivity? Finally, how can we test predictions when dynamic feedbacks, such as nonlinear responses of plant growth to grazing, or changes in predator-prey dynamics with structural changes accompanying plant growth, may make outcomes highly time dependent? Below, I will briefly illustrate these issues with results and observations from natural systems, with emphasis on river food webs.

Issue 1: Positioning food webs along productivity gradients

To compare top-down and bottom-up forces in food webs under different productivity regimes, we need to circumscribe and quantify the major sources of energy fueling particular communities. This task is entangled in issues of spatio-temporal scale that complicate the correlations of primary productivity, annual primary production, and plant standing crops. In some cases, fairly coarse-grained approximations based on strong correlations of annual primary production with supply rates of limiting factors may suffice. Rosenzweig (1968) predicted net aboveground annual primary production in terrestrial communities from annual actual evapotranspiration, which takes into account both water availability and solar radiation. In arid areas like African savannahs, annual precipitation may suffice to predict primary production empirically (Coe et al. 1976). Temperate lakes are often phosphorus limited, and spring phosphorus has been a good predictor of mean summer chlorophyll across much of North America (Dillon and Rigler 1974). Forest canopy over rivers limits sunlight reaching the bed. Canopy density strongly correlates with primary production in rivers and streams in Panama (Power 1983, 1984b), Oregon (Hawkins et al. 1982), North Carolina (Lowe et al. 1986), and California (Feminella et al. 1989).

These coarse, empirical predictions may miss crucial mechanistic details, however. In lakes, much algal growth may be fueled by the extremely rapid uptake of phosphorus by phytoplankton cells near the leaky oral grooves of zooplankton (Lehman and Scavia 1982, Lehman 1984). Grazing armored catfish remove sediments from patches of riverbed, stimulating primary productivity and increasing standing crops of attached algae (Power 1990a). Ungulate grazing in the Serengeti

(McNaughton 1976, 1985) and goose grazing in the Canadian Arctic (Jeffries 1988) have stimulatory local effects on graminoid growth. Grazers that unbury nitrogen-fixing cyanobacteria have been shown to increase ecosystem primary production in arctic marches (Bazely and Jeffries 1989) and are postulated to do so in Ozark rivers (Power et al. 1988). Do these internal recycling and physiological processes substantially alter energy flow through food webs, or are extrinsic environmental and climatic controls overwhelmingly important, and hence sufficient to characterize ecosystem productivity?

On a larger spatio-temporal scale, food webs in aquatic habitats adjacent to land (rivers, lakes, estuaries) are fueled by both autochthonous primary production of aquatic plants, and detritus from both autochthonous (local aquatic) and allochthonous (terrestrial) sources (Boling et al. 1975, Minshall 1978, Webster 1983, Petersen et al. 1989). Algae are generally higher quality food than detritus for tadpoles (S. Kupperberg et al., *unpublished manuscript*), insects (Cummins and Klug 1979, Fuller et al. 1986, Mayer and Likens 1987), and fish (Power 1983, 1984c, 1990a). However, the quantitative and qualitative importance of allochthonous and autochthonous energy sources for river communities change seasonally, for example, with the flush and fall of terrestrial leaves (Boling et al. 1975, Cummins et al. 1983). Seasonal energy inventories for streams based on biochemically available detritus and in situ primary production are not yet available (Bowlby and Roff 1986), and would be difficult to construct. They would help, however, in determining the degree to which energy flux in river food webs can be assessed without consideration of inputs from and losses to watersheds. Similar considerations apply to any habitat with a high edge to area ratio.

Issue 2: Quantifying trophic level biomass: the problem of omnivory

If spatial variation in ecosystem productivity is sufficiently clear and consistent so that communities can be ordered along productivity gradients, can the dependent variable of food chain dynamics theory, trophic level biomass, be quantified? Can trophic levels be distinguished and counted in real food webs, or are their boundaries obscured by omnivory? Reasonably thorough descriptions of food web linkages based on dietary analyses, observations of predation or predator-specific damage, and other natural history information reveal seemingly limitless complexity, even in "depauperate" arctic (Summerhayes and Elton 1923) and desert (Polis 1991) communities (see also Paine 1988). Not only is omnivory rampant, but species undergo ontogenetic diet shifts that make them difficult

to position in food webs, let alone food chains (Werner and Gilliam 1984, Paine 1988).

Despite this complexity, experimental studies of a variety of aquatic systems indicate that even complex, highly interconnected webs can respond to perturbations of higher trophic levels with chain-like dynamics. Chains of strong trophic links in communities are revealed when removing or adding top predators triggers trophic cascades (Paine 1980). For example, when sea otters are exterminated, sea urchin populations explode and mow down nearshore kelp beds (Estes and Palmisano 1974, Estes et al. 1978). When piscivorous fish are removed from Midwestern lakes, planktivorous fish increase, graze down zooplankton, and release phytoplankton to produce algal blooms (Carpenter et al. 1985). Changes in top predators produced trophic cascades in wading pools (Hurlbert and Mulla 1981), ponds (Spencer and King 1984), lakes (Stenson et al. 1978, Shapiro 1979, Henrikson et al. 1980, Shapiro and Wright 1984, Carpenter et al. 1985, 1987, 1990, Carpenter 1988, Carpenter and Kitchell 1988, Northcote 1988, Hanson and Butler 1990), rivers (Power et al. 1985, 1989, Matthews et al. 1987, Power 1987, 1990c, Northcote 1988), and intertidal and offshore marine communities (Paine and Vadas 1969, Mann and Breen 1972, Estes and Palmisano 1974, Mann 1977, Paine 1980, Breen et al. 1982, Duggins 1988, Wootton 1992).

Communities that exhibit trophic cascades have at least one species or guild per trophic level with sufficiently strong potential effects on their resources in the next lower trophic level to produce chain-like, rather than indeterminate web-like responses following perturbations of higher trophic levels. Experimental results have shown that a major artery in the Eel River food web linking fish to small predators to algivores to algae showed chain-like, rather than web-like dynamics despite omnivory of several of the constituent species (Power 1990c). The biological features of species responsible for producing cascades in this river food web include the predator-specific defense of the predominant herbivores, midge larvae whose algal retreats protect them against fish on the fourth trophic level, but not against invertebrate predators and fish fry on the third trophic level. (Power 1990c, Power et al., *in press*).

The widespread occurrence of trophic cascades, at least in aquatic habitats, suggests that trophic levels may as abstractions have sufficient correspondence to reality to be useful dependent variables in comparisons of trophic structure along productivity gradients. Fretwell (1977, 1987) and Oksanen (Oksanen et al. 1981, Oksanen 1990) distinguish between trophic levels that are dynamically or functionally significant, and those represented by predators too rare or too transient to

exert measurable impact on prey populations. It is crucial for testing food chain dynamics theory that we distinguish between trophic levels present only in descriptive webs, and trophic levels that are functionally present. "Functionally significant" top trophic levels can be operationally defined, *sensu* Murdoch (1966), following the experimental approach advocated by Paine (1977). Top trophic level n is "functionally significant" (i.e., can be counted as present in the interaction web) if removing n measurably increases densities of organisms or resources at level $n - 1$. In a cascading system with at least three trophic levels, these changes will suppress populations or resources at level $n - 2$. Similarly, the world is operationally "green" (*sensu* Fretwell 1977, 1987) if removing herbivores does not increase plant biomass, but adding limiting resources does. If the converse applies, the world is operationally "barren." If adding resources or removing herbivores both increase plant standing crops, then the world is in an intermediate state (i.e., consumers and resources co-limit plants).

Note that the operational definition of trophic level applies in webs with strong top-down forces, or with mixed top-down bottom-up control over populations. Webs in which all producers and consumers are resource limited would be classified in this Fretwellian scheme as systems with one functional trophic level.

Issue 3: When to evaluate communities: the problem of incomplete recovery from disturbance

If trophic levels are sufficiently countable so that food chain dynamics is a meaningful subject for research, what are the appropriate temporal and spatial scales for study? In most natural communities, densities of active individuals drop sharply during inclement seasons (temperate winters), or following major disturbances (floods, fire, landslides). As communities recover, community structure and accrual of trophic level biomass may reflect historical accident, differential dispersal capabilities, and population growth rates of early colonists or those residual species that survived the period of stress. Variable initial conditions and events early in the recovery period could produce transient assemblages (once called "early successional seres"; McIntosh 1985) that differ from the type of community that local conditions could eventually support (Drake 1990). Following seasonal or aseasonal disturbances, how long is long enough to assume that all trophic levels that can be supported by the local ecosystem have in fact arrived? Connell and Sousa (1983) propose that pre- and post-disturbance records at least as long as the turnover time of the longest lived species in an assemblage are the minimum required to

assume that a community perturbed from "equilibrium" has regained it.

In intertidal and terrestrial ecosystems, extensive regional disturbances are rare, and local disturbances typically create mosaics of patches that vary in age (time since disturbance) (Paine and Levin 1981, Sousa 1985). When such mosaics occur within reasonably uniform productivity regimes, the structures of assemblages with different recovery times could be compared. These comparisons, however, would be confounded if mobile elements from older communities influenced younger communities or vice versa; the impacts of variation in space and time could not be easily separated. Re-assembly of intertidal or terrestrial communities following large-scale disturbances would be useful in isolating the effects of recovery time on community structure, but is rarely documented (Drake 1990, but see Dammerman's data on refaunation of Krakatau, 1948, cited in MacArthur and Wilson 1967).

In many ways, rivers are perfect systems for comparative studies of community recovery under different productivity regimes. Floods frequently reset river communities by scouring biota out of long reaches of channel (Bilby 1977, Siegfried and Knight 1977, Gray and Fisher 1981, Fisher et al. 1982, Kimmerer and Allen 1982, Fisher 1983, Ross and Baker 1983, Molles 1985, Matthews 1986, Harvey 1987, Power and Stewart 1987, Erman et al. 1988). While the attainment of equilibrium becomes a somewhat existential issue for communities so frequently and regularly reset (Resh et al. 1988), the large scale of disturbance of river systems allows trophic level recovery to be compared among communities that vary in productivity, but not in age (time since disturbance).

Large regional storms trigger floods of rivers in different watersheds so that systems with different extrinsic productivities are reset simultaneously. Contrasts in the accrual of trophic-level biomass by communities recovering simultaneously in productive and unproductive rivers are not, therefore, confounded by time-dependent factors (e.g., recovery time, seasonal phenologies of species, year-to-year variation in climate). Moreover, organisms in flood-prone rivers have had long histories of exposure to floods, and are constituted of species, many with short generation times, that can recover quickly. An example is the flood-adapted insect fauna of desert streams (Gray and Fisher 1981, Fisher 1983). When flooding and low flow seasons are predictable, as in rivers in Mediterranean climates, ecologists can, year after year, repeatedly observe how productivity influences assembly rates and the final patterns that are established before the next series of winter floods resets rivers, and renews the seasonal cycle.

The Eel River of northern California, under a Med-

iterranean climatic regime, generally experiences predictable winter flooding and summer drought. After scouring winter flows subside in the spring, filamentous green macroalgae (*Cladophora*) grow to lengths of several metres before animal densities build up. At this time, the food chain appears to have only one functionally significant trophic level, and the river turns green. By summer, high densities of tuft-weaving midge larvae (Chironomidae) infest *Cladophora* except where large fish are experimentally or naturally excluded. Enclosure-exclosure experiments in the summer of 1989 showed that larger fish consume fish fry and predatory insects, which feed in turn on the chironomid larvae. Where fish were present (as the fourth trophic level), midges reduced algae to low, prostrate webs. Where the absence of fish released small predators, they suppressed chironomids, and algal standing crops remained higher and became dominated by nitrogen-fixing species (Power 1990c).

Variable disturbance, however, can produce significant year-to-year variation in the dynamics and strength of top-down forces in this food web. In the summer of 1990, an unseasonably late flood in June scoured away extensive *Cladophora* growths. The macroalga never recovered, and midge densities remained orders of magnitude lower than during the three previous summer seasons. Enclosure-exclosure manipulations of fish in the relatively barren 1990 river channel produced no conspicuous trophic cascades. This year-to-year variation in the strength of top-down trophic control reveals one mechanism that modulates control of community structure by fish as potential top predators in the Eel River. As discussed above, when fish exert trophic control at the fourth trophic level, it is because a key herbivore can evade large fish, but remains susceptible to small invertebrate predators and fish fry (Power 1990c, Power et al., *in press*). The raw material for the fish-specific defense of midges is *Cladophora*. When *Cladophora* failed to recover from the flood, midge densities remained low. The 1989-1990 contrast in top-down control by fish in the Eel River serves to further support Hunter and Price's contention that plants have primacy in establishing the directionality of forces in food webs.

Issue 4: Spatial circumscription of communities

What to circumscribe for study of "an ecological community" is one of the great unsolved methodological issues of community ecology (Crowley 1978, McIntosh 1985, Underwood 1986, Krebs 1989). Suggestions range from the classical approach of using plant associations to delimit communities, favored by Hunter and Price (1992), to the intriguing, process-based, but in practice difficult suggestion by Cousins (1990) to delimit ecosystems according to the home ranges of

top predators. Spatial scale issues have already infiltrated the previous discussion here of circumscription of productivity regimes, of which consumers or trophic levels to count, and of time dependencies in food webs. Spatial scale considerations also arise when we attempt to determine the "grain" of heterogeneity in primary productivity relative to the foraging ranges of consumers.

The relative importance of behavioral vs. demographic processes in establishing densities of consumers along productivity gradients depends on whether productivity varies in a fine-grained or coarse-grained fashion, relative to the mobility of consumers. In the original Fretwell-Oksanen models, environmental productivity was envisioned as varying on a large, regional scale, so that consumers generally experienced only one level. Many habitats, however, contain patches that vary markedly in productivity, and are small enough so that consumers cross frequently from one productivity regime into another (Power 1984*b*, Holt 1985, T. Oksanen 1990*a*). When patches of different productivity are smaller than home ranges of consumers, consumer behavior affects their instantaneous density in any given patch (Fretwell and Lucas 1970, Holt 1985, T. Oksanen 1990*a*). Consumers moving between productive patches may opportunistically consume food items in intervening barren habitats. In other words, consumers whose population densities are not constrained by the low productivity of barren patches will nonetheless supplement top-down forces within them. This "spill-over" exploitation will alter patterns of trophic level biomass from patterns predicted by Oksanen et al. (1981) (T. Oksanen 1990*a*). In contrast, when patches are large relative to consumer dispersal capabilities, consumer densities are determined primarily by their local birth and death rates, both subject to local top-down and bottom-up controls. Because some members of communities are larger or more mobile than others, these demographic controls may determine local densities of some but not all of the interacting species in heterogeneous habitats. The issues of consumer spill-over and trophic level accrual patterns under fine-grained heterogeneity in productivity are complex and probably apply to many systems in the real world.

Herbivore mobility may, on the other hand, simplify trophic structure despite fine-grained heterogeneity in primary production. Where herbivores are mobile, smart (i.e., capable of closely tracking a food resource that fluctuates in space and time), and well defended from their predators, a two-trophic-level system may extend over an impressive range of primary productivity. Armored catfish in the Rio Frijoles of central Panama feed on attached algae. During a study period of 28 mo, catfish tracked algal productivity nearly

quantitatively over a 3-km river reach. In moderately sunny pools where algal accrual was seven times faster than in the darker pools, catfish densities, biomass, and collective grazing rates were, on average, six to seven times higher (Power 1984*b*). Somatic growth rates of immature catfish and survivorship of all catfish were also not statistically distinguishable in sunny, crowded and dark, uncrowded pools. Catfish distributions closely match predictions of the ideal free distribution model (Fretwell and Lucas 1970), which also correspond to the vertical consumer isoclines predicted by Rosenzweig's models for systems with strong top-down control. As a result of their close tracking of spatial variation in algal productivity, catfish maintained constant, uniform, scant standing crops of algae in >50 pools distributed over a 3-km reach of river, despite a heterogeneous forest canopy that caused primary productivity to vary as much as 17-fold among these pools (Power 1981, 1984*b*).

Armored catfish remained at the top of the Rio Frijoles food chain even in reaches with high primary productivity because their dermal armor and impressive spines defend them from swimming, gape-limited predators. These defenses were not effective against herons and kingfishers, and catfish avoided shallow (<20 cm deep) water, where these birds fished (Power 1984*a*, Power et al. 1989). Consequently, green bands of algae accumulated along the shallow river margins, while deeper substrates appeared barren. In the Rio Frijoles, water depth, which affected the susceptibility of fish to birds, rather than primary productivity, determined where a third trophic level was added to the food chain (Power 1987). In larger rivers like the Amazon, armored catfish are susceptible to swimming predators (caiman, arapaima) (Lowe-McConnell 1987). There, trophic structure may be less determined by depth and more related to primary productivity, although this prediction remains uninvestigated.

While prey or predator adaptations may locally determine who is at the top of the functionally dominant food chain and hence how long it is, it is the mobility, voracity, and tracking ability of top consumers, relative to the patch size of their resources, that influences the strength of top-down, relative to bottom-up, forces in food webs.

*Inferences from trophic level biomass
accrual across regional
productivity gradients*

Despite the difficult methodological issues facing ecologists attempting to measure forces in food webs, some have forged ahead to draw inferences from large-scale ecosystem patterns. Oksanen and colleagues (Oksanen et al. 1981, Oksanen 1983, Moen and Oksanen, *in press*) and McNaughton et al. (1989) have both

reviewed global data on correlations between herbivore biomass and plant production. Under Fretwell's theory of top-down trophic control, herbivores should increase along large-scale primary productivity gradients in two-level food chains; they should not increase in three-level food chains, and they should first increase, then plateau, if increased ecosystem productivity produces a transition from a two- to a three-level system (Oksanen et al. 1981). In a data set compiled from studies of deserts, tundra, temperate and tropical grasslands and forests, and salt marshes, McNaughton et al. (1989) found strong positive correlations of herbivore biomass, consumption, and secondary productivity with net aboveground primary productivity over the entire surveyed range of $125\text{--}29,000\text{ kJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. Moen and Oksanen (*in press*) re-examined their data set, and also found a strong positive correlation below primary productivities of $7000\text{ kJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. Above this productivity threshold, however, herbivore density increased more slowly with primary productivity, which Moen and Oksanen interpret as evidence for the addition of a third functionally significant trophic level (producing an HSS system) at the higher range of primary productivities. Depending on root:shoot allocations of plants, $7000\text{ kJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ may be close to the total annual primary productivity originally predicted by Oksanen et al. (1981) to mark the threshold at which three trophic levels would be added to food chains. More data, both on the accrual of biomass by producers and carnivores as well as herbivores along productivity gradients, and from ecosystems with very low and very high primary productivities, are needed to test these interpretations. In particular, data from systems free of major human impacts are required (L. Oksanen, *personal communication*).

The model formalizing Fretwell's ideas (Oksanen et al. 1981) predicts stepped patterns of biomass accrual in given trophic levels along productivity (Fig. 4b). Within productivity intervals that support n trophic levels, increases in primary productivity should produce biomass increases in levels n and $n - 2$, while level $n - 1$ is held at a constant level by exploitation. Therefore, consumer and resource densities should not be correlated within these ranges of primary productivity. Consumer and resource abundances, however, often co-vary positively with increasing productivity (Valiela et al. 1975, Fuller et al. 1986, McQueen et al. 1986, Perrin et al. 1987, Mittelbach et al. 1988). Patterns of positive covariance of consumers and resources have been cited as support for the view that populations are regulated from the bottom up by resource supplies (McQueen et al. 1986, 1989, but see earlier discussion of co-limitation by predators and resources).

In surveys of natural systems, a stepped pattern of

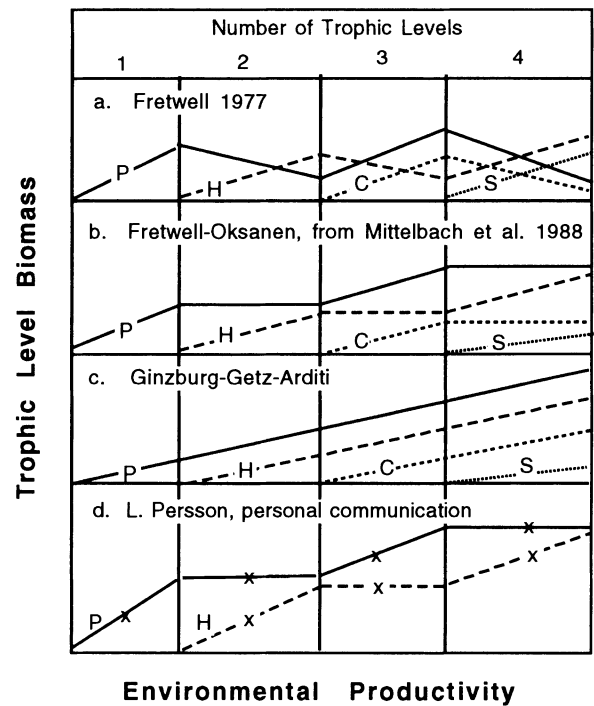


FIG. 4. Patterns of trophic level biomass accrual expected along environmental productivity gradients under pure top-down models (Fretwell and Oksanen) (a, b) and joint control by predators and resources (Arditi-Ginzburg and Getz models) (c). "P" represents primary producers, "H" herbivores, "C" primary consumers that eat herbivores, and "S" secondary carnivores that eat primary carnivores. In (d), crosses represent positions along the gradient of hypothetical biomass samples taken for producers and herbivores. The positive covariance of consumers and resources predicted by the third model could be mistakenly inferred from a pattern that in reality was stepped if regions where populations plateau are undersampled, and if transitions between n and $n + 1$ trophic levels are undetected (Mittelbach et al. 1988; L. Persson, *personal communication*).

trophic biomass accrual produced by strong top-down forces could look like a continuously positive correlation expected under bottom-up control if regions where consumer densities plateau with increasing productivity are undersampled (Fig. 4d; L. Persson, *personal communication*). As Mittelbach et al. (1988) point out, the critical observation to determine whether top-down control is strong is to see whether resource and consumer densities remain uncorrelated if productivity varies, but the number of functionally significant trophic levels remains fixed. It is usually impossible to determine the number of functionally significant trophic levels from observation alone (Issue 2). Therefore, experimental analyses of food webs in which trophic structure is known because it has been manipulated will be essential for inferences about relative strengths of top-down and bottom-up forces from observation

of responses of higher trophic levels to changes in primary productivity. Experimental analyses of the relationships of primary productivity and trophic structure are well underway in lakes and ponds (e.g., Hrbacek et al. 1961, Arruda 1979, Shapiro 1979, Shapiro and Wright 1984, Carpenter et al. 1985, 1987, Ranta et al. 1987, Persson et al. 1988) and tundra-taiga ecosystems (Hansson 1979, Batzli et al. 1980, Oksanen and Oksanen 1981, L. Oksanen 1988, T. Oksanen 1990*b*; Moen et al., *in press*); and are beginning in marshes (Valiela et al. 1975, Jeffries 1988, Bazely and Jeffries 1989), rivers (Power 1984*b*, Peterson et al. 1985, Feminella et al. 1989, Johnston et al. 1990), terrestrial grasslands (McNaughton 1976, 1985); and marine ecosystems (Littler and Murray 1975, Hay 1981, Wootton 1991).

CONCLUSIONS

Plants have obvious primacy in food webs; in particular, their primary productivity is a fundamental control of higher trophic levels. Other plant attributes, such as architecture (e.g., Bernays and Graham 1988, Kareiva and Sahakian 1990) or chemical constituents (e.g., Price et al. 1980, Price and Clancy 1986) clearly also have strong effects on the performances and interactions of higher trophic levels. These other attributes, however, are often molded or constrained by plant growth rates, in either physiological or evolutionary time (Bloom et al. 1985, Coley et al. 1985, L. Oksanen 1990).

Food chain dynamics models linking primary productivity to trophic structure are exciting, because different assumptions about mechanisms lead to distinguishably different predictions about ecosystem level patterns. For example, if consumers affect their own functional response, their densities should correlate with those of resources over large-scale gradients of ecosystem productivity. If instead the classical assumption that predator attack rates depend only on prey density is correct, consumer and resource density should remain uncorrelated across productivity gradients, until food chain length changes. It is quite uncommon in ecology for simple (and observable) differences in the behavioral and population dynamics mechanisms assumed by different models to lead to widely divergent predictions about large-scale community-level patterns.

Despite the growing enthusiasm for multi-trophic level investigations, most ecologists would agree that there are real difficulties in applying food web theories to the real world. We need to resolve methodological issues concerning appropriate spatio-temporal scales, agree upon operational definitions for concepts like trophic levels, and evaluate the assumptions of the variety of available models of top-down and bottom-up forces, to decide which apply in which settings.

Perhaps most challenging, we must also devise testable theory that can address dynamic feedbacks between adjacent and nonadjacent trophic levels (e.g., when is primary productivity a dependent variable, responding to top-down forces? How will accruing plant cover affect predator-prey interactions?). These feedbacks may create indeterminacies that will impede the test of mechanistic food web models (Sykes 1984, Hastings and Powell 1991), but they are too pervasive to ignore.

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