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Gary A. Polis; Donald R. Strong

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FOOD WEB COMPLEXITY AND COMMUNITY DYNAMICS

GARY A. POLIS[1,*] AND DONALD R. STRONG[2,†]

[1]Department of Biology, Vanderbilt University, Box 93, Nashville, Tennessee 37235; [2]Bodega Marine Laboratory, University of California, Box 247, Bodega Bay, California 94923

Abstract.—Food webs in nature have multiple, reticulate connections between a diversity of consumers and resources. Such complexity affects web dynamics: it first spreads the direct effects of consumption and productivity throughout the web rather than focusing them at particular "trophic levels." Second, consumer densities are often donor controlled with food from across the trophic spectrum, the herbivore and detrital channels, other habitats, life-history omnivory, and even trophic mutualism. Although consumers usually do not affect these resources, increased numbers often allow consumers to depress other resources to levels lower than if donor-controlled resources were absent. We propose that such donor-controlled and "multichannel" omnivory is a general feature of consumer control and central to food web dynamics. This observation is contrary to the normal practice of inferring dynamics by simplifying webs into a few linear "trophic levels," as per "green world" theories. Such theories do not accommodate common and dynamically important features of real webs such as the ubiquity of donor control and the importance and dynamics of detritus, omnivory, resources crossing habitats, life history, nutrients (as opposed to energy), pathogens, resource defenses, and trophic symbioses. We conclude that trophic cascades and top-down community regulation as envisioned by trophic-level theories are relatively uncommon in nature.

Ecological research has amply demonstrated that food webs in nature contain hundreds to thousands of species, reticulately connected via multiple links of various strength to species in the autotroph and saprophagous channels and in the same and different habitats; omnivorous, age-structured consumers are common. These facts and their dynamic consequences need to be incorporated directly into theory. Nevertheless, much theory still relies on the idealization of "trophic levels" connected in a single linear chain. In this article, we argue that this simplification cannot capture adequately the dynamics of food webs or communities, and highly significant features are neglected by the continual use of such abstractions.

The trophic-level ideal in a simple linear food chain has had great appeal. Trophodynamics (Lindeman 1942) sought to explain the height of the trophic pyramid by reference to a progressive attenuation of energy passing up trophic levels, envisioned as distinct and functionally homogeneous sets of green plants, herbivores, primary carnivores, and, sometimes, secondary carnivores (Slobodkin 1960). This is a "bottom-up" community theory, based on the thermodynamics of energy transfer. In counterpoint, the green world hypothesis (HSS; Hair-

* To whom correspondence should be sent. E-mail: polisga@macpost.vanderbilt.edu.
† E-mail: drstrong@ucdavis.edu.

ston et al. 1960; Slobodkin et al. 1967) is primarily a "top-down" theory, with abundance at each level set, directly or indirectly, by consumers at the top of the chain. Thus, carnivores suppress herbivores, which releases green plants to flourish. The exploitation ecosystem hypothesis (EEH) generalizes HSS to fewer or more than three trophic levels (Fretwell 1977, 1987; Oksanen 1983, 1988, 1991; Oksanen et al. 1981; Hairston and Hairston 1993). Trophic cascades (Power 1990; Carpenter and Kitchell 1993) are examples of food chains that behave roughly according to EEH. Trophodynamics and EEH each rely on the integrity of trophic levels and the existence of a single, albeit different, overwhelming mechanism that imposes structure on ecosystems.

We advocate instead an alternative, more realistic approach that incorporates the diverse array of connections among species to explain community dynamics. We first critique the trophic-level concept and hypotheses derived from it. We then delineate the richness of linkages among species. Finally, we propose a framework of food web and community dynamics that incorporates these factors.

EXPLOITATION ECOSYSTEM HYPOTHESES (EEH)

The exploitation ecosystem hypothesis proposes a conceptual framework of "exploitation ecosystems" where strong consumption leads to alternation of high and low biomass between successive levels. Even numbers of "effective" trophic levels (two or four levels) produce low-standing crops of plants because the herbivore population (level 2) flourishes. Odd numbers (one or three levels) result in the opposite effect: herbivores are suppressed and plants do well. Proponents of EEH differ on subsidiary points, the first being the role of bottom-up effects. For Oksanen-Fretwell, primary productivity sets the number of effective levels (Fretwell 1977, 1987; Oksanen et al. 1981; Oksanen 1983, 1988, 1991). The most productive systems support secondary carnivores, so they have four levels and low-standing crops of plants. Low-productivity systems (e.g., tundra) support only one effective level: plants. More productive habitats (e.g., forests) have three. Productivity is never high enough to support more than three effective levels on land or four in water (Oksanen et al. 1981; Oksanen 1988). Hairston and Hairston (1993) disagree and argue that physical differences between habitats, by affecting plant competition and consumer foraging, cause three levels on land and four in water.

Definitions of trophic levels that follow EEH are distinctive. Oksanen and Fretwell adopt the convention that trophic levels occur only if consumers significantly control the dynamics or biomass of their food species (Oksanen et al. 1981; L. Oksanen 1990; Power 1992a; L. Oksanen, personal communication). Without top-down control, consumers do not comprise an effective trophic level regardless of biomass or the number of species involved (see *Detritus and Its Infusion into the Classic Food Chain*, below). "Only when grazers regulate plants are grazers counted (as a trophic level), and only when predators regulate grazers are they fully counted. . . . Thus, considerations of food chain dynamics do not become stranded in the immense complexity of real food webs" (Fretwell 1987, p. 295). On the other hand, Hairston and Hairston's (1993) trophic levels are

based on energy deriving from primary productivity. Thus, "trophic level interactions . . . weight particular links in the food web for their energetic significance" (p. 385). A trophic level is "a group of organisms acquiring a considerable majority of its energy from the adjacent level nearer the abiotic source" (p. 383).

Despite these differences, EEH advocates all argue that variability in the number of trophic levels exerts profound consequences on community structure and dynamics.

COMPLEX FOOD WEBS AND TROPHIC-LEVEL HYPOTHESES

We provide an overview of crucial and general processes ubiquitous to the dynamics of food webs, concluding that linear food chain theory lacks appreciation of the breadth and diversity of phenomena found in natural webs. Some arguments are developed substantially for the first time in the context of web dynamics, although seeds are well planted in the literature (e.g., the importance of donor control, spatial subsidies, detrital shunts, age-structure effects, dynamics of pathogens; see below). Some points were made earlier (e.g., the importance of plant defenses, the artificiality of trophic levels; Murdoch 1966; Ehrlich and Birch 1967; see below) but are valuable to reexamine in light of recent discoveries.

In particular, we focus on processes incongruous with EEH and other trophic-level models (e.g., omnivory, flow from detrital to herbivore channels). Our tack is to establish that these phenomena are widespread in nature and then show that they often influence population and community dynamics. Our evidence that a phenomenon affects dynamics is based largely on subsets of species in communities. It may be argued that these dynamics only describe interactions among subsets and may not apply to the dynamics of entire communities. In the virtual absence of relevant data on community-level dynamics, the best anyone can do is to marshall existing data based on such subsets (e.g., Sih et al. 1985; Menge and Sutherland 1987; Hairston and Hairston 1993).

Trophic Levels, Reticulate Food Webs, and Energetics

Food webs of most ecosystems are reticulate; that is, they have high connectance and omnivory such that most consumer populations are linked to a variety of resource populations that occur at a wide range of feeding links from primary productivity.

"Trophic levels."—We reiterate that the notion that species clearly aggregate into discrete, homogeneous trophic levels is fiction (Darnell 1961; Gallopin 1972; Peters 1977; Levine 1980; Cousins 1987; Hanski 1987; Polis 1991; Hunter and Price 1992; Power 1992*a*). Especially in species-rich systems, groups of species with diets of similar species do not occur (Winemiller 1990; Polis 1991). Omnivory, ontogenetic, and environmentally induced diet shifts and geographical and temporal diet heterogeneity all obscure discrete trophic levels (see below). Even plants do not form a single level; higher plants have diverse crucial trophic and symbiotic connections with heterotrophs (see the appendix), and many phytoplankton are mixotrophic, obtaining energy via photosynthesis, absorption of organic molecules, and ingestion of particles and bacteria (Porter et al. 1985;

Sanders and Porter 1988; also see *Non- and Quasi-Trophic Processes*, below). With increasing diversity and reticulation in webs, trophic levels blur into what Darnell (1961) termed a trophic spectrum (e.g., Winemiller 1990). We suggest that Darnell's species-individualistic and continuous "trophic spectra" are a reasonable alternative to the simplistic construct of homogeneous trophic levels.

Omnivory.—Omnivory, a ubiquitous contravention of the trophic-level concept (Darnell 1961; Rigler 1975; Peters 1977; Polis 1991), must be accommodated to understand community structure and dynamics (Menge and Sutherland 1987; Polis 1994). In detailed studies, most consumers eat five to more than 100 species, coming from a broad range of feeding links away from primary productivity (Walter 1987; Moore et al. 1988; Sprules and Bowerman 1988; Schoener 1989; Winemiller 1990; Hall and Raffaelli 1991; Polis 1991). Intraguild predators (Polis et al. 1989; Spiller and Schoener 1990; Polis and Holt 1992; Rosenheim et al. 1993) and cannibals (Polis 1981, 1991; Elgar and Crespi 1992) eat trophically similar consumers; each can significantly alter prey dynamics and is ubiquitous in webs. Detritivory and saprophagy (see *Detritus and Its Infusion into the Classic Food Chain*, below) are common forms of omnivory (Peterson and Jensen 1911; Darnell 1964; Polis et al. 1989; Polis 1991). Detritus originates diversely throughout the trophic spectrum and does not form one food source or homogeneous trophic level. Most metazoan detritivores are omnivorous intraguild predators, obtaining nutrition both from detritus and microbes and metazoans in detritus.

Omnivory and the dynamics of populations and communities.—Omnivory has two essential effects on the dynamics of consumers, resources, food webs, and communities. First, it diffuses the effects of consumption and productivity across the trophic spectrum, rather than focusing them at particular "trophic levels." It increases web connectance (Sprules and Bowerman 1988; Vadas 1990; Polis 1991; Strong 1992), shunts the flow of energy away from adjacent trophic compartments (Jaeger and Gardner 1988), alters predator-prey dynamics in ways contra to EEH assumptions (discussed later), and thus disrupts or dampens the ecosystem control envisioned by EEH (Menge and Sutherland 1976, 1987; Vadas 1989; Fairweather 1990; Spiller and Schoener 1990; Polis and Holt 1992; Abrams 1993a; Diehl 1993; Polis 1994). As one example, omnivorous crayfish can depress both herbivorous snails (consistent with EEH) and macrophytes (inconsistent) (Lodge et al. 1994).

Second, omnivory can affect dynamics in a way analogous to apparent competition (Holt 1984) (fig. 1A). Feeding on "nonnormal" prey can increase the size of consumer populations (or sustain them during poor periods), thus promoting top-down control and depression of "normal" prey (e.g., Dayton 1984; Polis et al. 1989; Polis 1991; Holt and Lawton 1994). Frugivory, herbivory, granivory, detritivory, and even coprophagy form common subsidies for many predators. Vertebrate carnivores consume amply from the lower web without markedly depleting these resources (Peters 1977; Robertson 1982; Smythe 1986; Herrera 1989; Vadas 1990; Polis 1991). Does energy from fruit help carnivores depress vertebrate prey (e.g., herbivores)? Arthropodivory by seed-eating birds is the norm during breeding, with insect protein crucial to nestlings (Polis 1991; Levey and Stiles 1992). We maintain that arthropodivory by granivores (and, conversely,
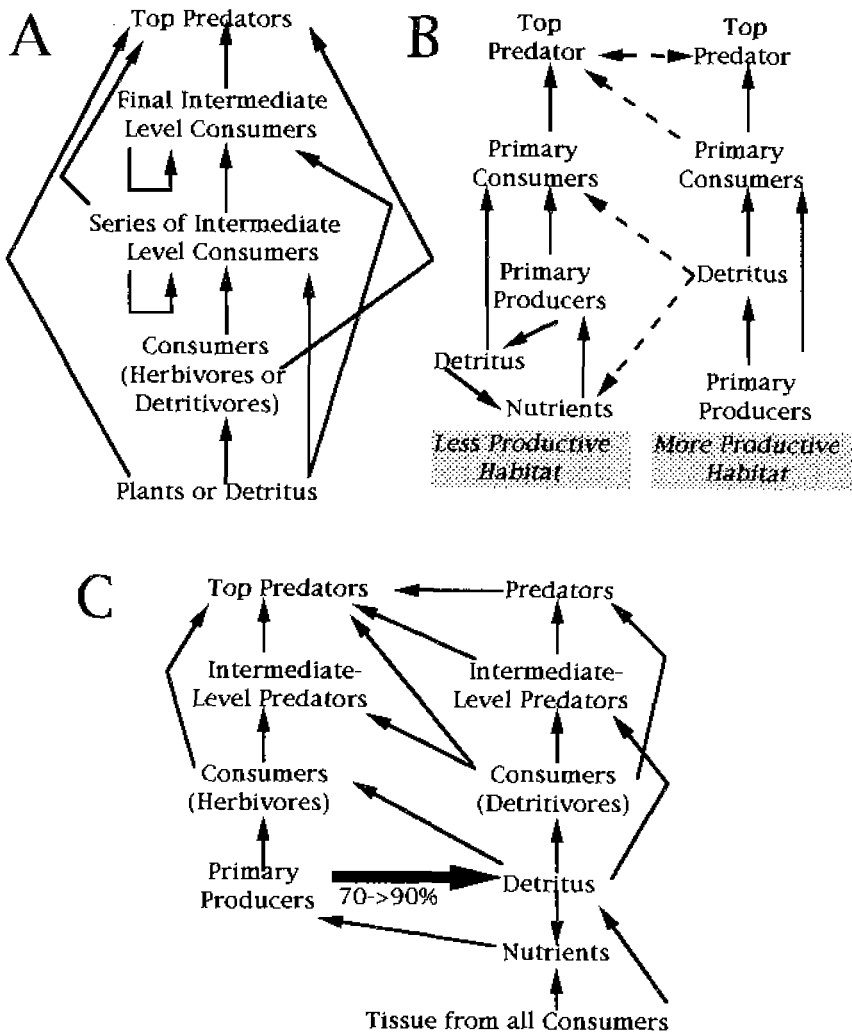
Fig. 1.—A, The dynamics of omnivory. Consumer populations can be increased by eating resources from several different parts of the trophic spectrum. This figure is a gross simplification; multiple omnivorous connections are exemplified in more detail in Polis (1991) and Winemiller (1990). B, Spatial subsidy. Species in one habitat receive energy, detritus, and/or prey from other habitats. Consumers also move among habitats. C, Detrital shunts. Reinfusion of energy from the detrital channel into the "classic," grazer-based food web channel can occur throughout the trophic spectrum.

granivory by arthropodivores) must enhance bird populations and thus reduce seeds (arthropods) to a greater degree than if diets were not so augmented.

How important is energetics?—Hairston and Hairston (1993) use "energetic significance" to determine trophic-level status. Although energy flow is central to understand ecosystem function (DeAngelis 1992; see below and Discussion), an energy-based trophic-level concept is inappropriate if the focus is on community and population dynamics (changes of biomass and abundance). Important links in interaction webs (describing population effects) and descriptive webs (quantifying energy and matter flow) are often not congruent (Paine 1980, 1988; Dayton 1984; Menge and Sutherland 1987; Polis 1994).

Knowledge of energy flow is insufficient to understand the effects of species interactions in webs (Paine 1988, 1992; Lawton 1989; Polis 1991, 1994), in part because energy flow and biomass production are themselves emergent functions of interactions among populations within the web (Oksanen et al. 1981; DeAngelis 1992; Menge 1992). Consumer regulation of populations need involve little energy transfer and few feeding interactions (e.g., Polis and McCormick 1986; Spiller and Schoener 1988). For example, removing predatory rats increased lizard abundance 3–30 times although lizards formed less than 3% of rat's diet (Towns 1991; D. R. Towns, personal communication). Key regulatory factors may produce much less overall mortality than other factors (Manly 1988). Brief, intense predation episodes may net little energy for the predator but may be central to prey dynamics (e.g., Wilbur et al. 1983; Polis and McCormick 1987; Hall et al. 1990). The consumption of young stages (seeds, eggs, larvae) may provide trivial energy to a consumer but can greatly depress prey abundance. Meiofaunal bottlenecks on settling larvae either by predators, filter, and/or suspension feeders are a key process structuring marine benthic communities (references in Polis et al. 1989). Pathogens and parasites form an extreme example: they take little energy, even when they decimate their host populations (see *Parasites and Pathogens*, below).

The degree of resource suppression is not a function of energy transfer (e.g., Hall et al. 1990). Dayton (1984, fig. 12.1) showed that the species apparently exerting the strongest effects on the structure and dynamics of his Antarctic bottom community would be deemed unimportant from analyses of diet, energy transfer, or biomass. Such discoveries have stimulated many (Paine 1980, 1988, 1992; Dayton 1984; Fairweather 1990; Underwood 1990; Polis 1991, 1994) to argue that, without experimentation, one cannot a priori decide which are strong or weak links. An apparently weak link (in terms of diet or energy transfer) can be a key link dynamically, and an important energetic link may affect dynamics little. No necessary concordance of dynamics with either dietary or energetic measures exists. This insight counters the use of energetics to recognize strong interaction links or to claim, for example, that all land communities are three-tiered because "energy transfers above the third trophic level in terrestrial systems are relatively unimportant" (Hairston and Hairston 1993, p. 384).

Trophic Dynamics of Spatially Subsidized Consumers

Almost all natural systems are open and spatially heterogeneous. Trophic linkages (fig. 1*B*) are common among habitats that differ moderately (e.g., grassland-

forest; littoral-sublittoral or pelagic) or greatly (land-water; photic-aphotic zones) (Polis et al. 1995; Polis and Hurd 1996). Nutrients (e.g., run-off, upwelling, guano), detritus (e.g., leaf fall into water; shore drift), prey (e.g., emerging aquatic insects), or consumers (forage across habitats; migrate) frequently cross habitats.

Spatial coupling can be key to dynamics (Polis et al. 1995; Polis and Hurd 1995a, 1995b, 1996). For instance, arboreal anole populations, subsidized by imported allochthonous insects from light gaps, increase so as to suppress spiders and some predators and herbivores (Dial 1992). Abundance detrital kelp from the sublittoral zone promotes dense intertidal limpet and urchin populations, which then graze noncoralline algae to low cover (Duggins et al. 1989; Bustamante 1994). Allochthonous subsidies commonly influence stream systems: leaf fall subsidizes herbivores, which in turn depress algae (e.g., Rosemond et al. 1993; also see Polis and Hurd 1995a; Polis et al. 1995). These consumers do not affect the rate of import, availability, or dynamics of the allochthonous resources. However, subsidies allow consumers to be more abundant than if supported solely by in situ resources with consequent suppression of in situ resources decoupled from in situ productivity (Holt 1985; T. Oksanen 1990; Polis and Hurd 1995a; Polis et al. 1995). This is archetypal donor control (DeAngelis 1992).

Such dynamics based on subsidized donor control are inconsistent with EEH mechanisms based on in situ productivity (Oksanen et al. 1981; Oksanen 1988; see T. Oksanen 1990). Hairston and Hairston (1993) recognize this problem: "[systems] not well defined" should be "excluded from our consideration because there more than one trophic level depends on an external source of energy" (p. 381). Thus, they do not apply their model to the marine intertidal and subtidal. We see no reason why these habitats qualitatively differ from other habitats in the potential role for allochthonous flow on dynamics. Indeed, spatially subsidized trophic dynamics are widespread (ubiquitous?) across habitat types (Polis et al. 1995; Polis and Hurd 1996).

Detritus and Its Infusion into the Classic Food Chain

Little of the energy fixed by plants passes directly into the grazing food chain— herbivores eating plants and eaten by carnivores–that is the focus of EEH. Herbivores consume about 10% (range: 1%–50%) of production; the rest passes into the detrital chain (Wiegert and Owen 1971; Cousins 1980; Odum and Biever 1984; Patten 1985; Fenchel 1988; Polis 1991; DeAngelis 1992; Hairston and Hairston 1993; G. A. Polis, R. D. Holt, M. Vanni, and A. Rosemond, unpublished manuscript). Most terrestrial ecosystems are not net accumulators of undigested biomass (Hairston et al. 1960), and most plant biomass is thus soon digested by detritivores, with nutrients and energy passing through "functional compartments" comprised of diverse microbes and animals where several factors regulate its flow and control the availability of detritus and detritivores to consumers (Boling et al. 1975; Ambrose 1984; Oberndorfer et al. 1984; Weinberg 1984; Commito and Ambrose 1985; Fletcher et al. 1987; Fenchel 1988; Moore et al. 1988; Crawford 1991). The erroneous assumptions of HSS that grazing chains are generally not cross-linked with and dynamically independent of detrital chains was first pointed out by Wiegert and Owen (1971).

Detrital energy and nutrients reenter grazing chains when detritivores are eaten by predators that also eat herbivores (fig. 1C). Such detrital infusions are common, interweaving energetics and dynamics of biophages and saprophages (Darnell 1961; Wiegert and Owen 1971; Moore and Hunt 1988; Moore et al. 1988; Morton and James 1988; Vadas 1990; Polis 1991, 1994; Forsberg et al. 1993; Vetter 1994; Gaedke et al. 1995; e.g., Hairston and Hairston 1993, tables 1 and 4, figs. 1, 2, and 3; Oksanen et al. 1995; Porter 1995; Vanni 1995). Bypassing herbivores, this linkage can affect herbivore regulation in a manner analogous to spatial subsidies. Predator populations, subsidized by saprophagous prey, can increase and suppress other predators or herbivores. For example, scorpions, deriving 39%–57% of their prey from detritivores, suppress other predators (Polis and McCormick 1986, 1987; Polis 1991).

Detrital infusion to predators in the grazing chain can create the appearance of a simple linear trophic cascade, but with the difference that nutrition from detritivores sustains or elevates predators to levels sufficient to suppress herbivores. For example, in many coastal areas, marine detritus greatly influences the terrestrial web (Polis and Hurd 1995a, 1995b, 1996). Large populations of arthropods eat beached algae and carrion; these detritivores provide >90% of the food for spiders, scorpions, and/or lizards, consumers that reach densities one to two orders of magnitude greater than areas not influenced by detritus. In some areas, abundant spiders suppress insect herbivores, which significantly decreases plant damage (Polis and Hurd 1995a; also see Dial 1992).

The exact effect of detrital shunts depends on the relative benefits for each species and where detritus reenters (to producers, herbivores, intermediate or higher consumers; G. A. Polis, R. D. Holt, M. Vanni, and A. Rosemond, unpublished manuscript). For example, nutrients from detritus greatly influence plant productivity; models show that a 10% reduction in detritus can cause a 50% reduction of plant biomass (DeAngelis 1992). The dynamics of consumer control within the detrital web and those produced by infusion of detritivores into the grazing web are crucial to community structure and dynamics. Neither is considered by EEH.

Life-History Omnivory Decouples Resource Consumer Dynamics

Life-history omnivory describes shifts in diet during development, which often are accompanied by ontogenetic changes in habitat. Diet can change substantially either discontinuously (e.g., at metamorphosis) or slowly with growth (Wilbur 1980; Polis 1984, 1988; Werner and Gilliam 1984; Mittlebach et al. 1988; Heatwole 1989; Olson and Olson 1989). Such life histories are widespread; Werner (1988) estimates that 80% of all animal species undergo metamorphosis. Changes in resource use can be dramatic (e.g., predaceous juveniles—plant-feeding adults in parasitoids and many other insects; herbivorous tadpoles and predaceous frogs and toads), with prey size variation as great as three to four orders of magnitude. Even among nonmetamorphic species, diets change greatly with age, with diet differences among age classes often more distinct than those among most species (Polis 1984).

Life-history omnivory can either impede consumer control or amplify resource

suppression via dynamics similar to those of spatial subsidy or detrital shunts. The strength of "coupling" between a consumer stage and its resources depends on the relative resource supply for each stage (R_s) of the consumer species (see Wilbur 1980; we use "resource supply" in the sense that the abundance and renewal rates of food resources set the potential maximum population size of a stage). Stages coming from relatively more productive conditions will tend to have initial abundances (N_s) higher than the maximum supported by the less productive environment they enter (i.e., $N_s > N$ allowed by R_s). This surfeit of consumers entering the next stage should make control of resources more likely. Conversely, stages reduced in numbers by low-resource environments will under-utilize resources of subsequent more productive environments (i.e., $N_s < R_s$), which attenuates the potential for resource control.

Many examples show that stage-specific resource levels (R_s) vary greatly with significant effects on numbers of that stage (N_s). Disparate levels of productivity and mortality are hypothesized to be major forces in the evolution of metamorphosis and habitat shifts (Wilbur 1980, 1988; Werner and Gilliam 1984). Migratory fish grow in the relatively more productive habitat (ocean or freshwater) and reproduce in the less productive habitat (Gross et al. 1988); adult biomass in the less productive habitat is always greater than could be produced by in situ productivity. Larval stages of amphibians (Wilbur 1980; Berven 1990), fish and invertebrates (Olson and Olson 1989), and insects (Prout and McChessney 1985) are often severely food limited, whereas adult stages are not. Widespread "ontogenetic bottlenecks" (Werner and Gilliam 1984) often arise because stage-specific resources (R_s) differ (e.g., Larkin and Smith 1954; Lasenby et al. 1986; Winemiller 1989, 1990; Persson and Greenberg 1990).

Sunfish demonstrate particularly well that resource availability (R_s) at one stage significantly influences resource use and suppression at other stages (Mittlebach and Chesson 1987; Mittlebach et al. 1988; Osenberg et al. 1992; Mittlebach and Osenberg 1993). When resource availability is high for juveniles, adults increase, overexploit, and depress their resources (i.e., $N_s > R_s$); alternatively, when juvenile resources are low, adults do not depress their resources $(N_s < R_s)$. Thus, complex life histories and age structure omnivory can exert diverse effects on food chains, from thwarting top-down control (if $N_s < R_s$) to amplifying it with suppression (if $N_s > R_s$).

Linkage Strength and Type: How Common Is Strong Recipient Control?

For Oksanen-Fretwell dynamics, interactions between trophic levels need to be strong (sensu Paine 1980, 1992) and concurrent. If not, sustained changes in dynamics up or down the food chain between successively linked populations will not occur. Moreover, all links must be "recipient controlled" (Juliano and Lawton 1990; DeAngelis 1992; Hawkins 1992); that is, consumers substantially depress populations of "donors" (resources). If a link is weak or only donor controlled (consumers do not affect resource renewal rate), predation effects will not cascade down the web. For the reasons sketched below, we argue that most links are donor controlled rather than recipient controlled. Hawkins (1992) maintains that most parasitoid-host links (which include about half of all multicellular

species) are donor controlled; that is, parasitoids rarely regulate host populations (also see Stiling 1988).

Some criteria for effective recipient control (also see Menge and Sutherland 1987; Skogland 1991; Hawkins 1992; Hunter and Price 1992; Power 1992a; Strong 1992; Abrams 1993; Polis 1994) are as follows. First, consumer protections should not greatly limit the ability of consumers to depress their resources. Resources should be uniformly edible—that is, without effective defenses, refuges, or escape in size. Further, consumption should not promote a progressive decline in edibility or catchability—that is, no resource depression (Charnov et al. 1976)—that makes consumers less effective in reducing resource populations (see Menge and Sutherland 1987; Leibold 1989; and *Protections against Consumers*, below).

Second, consumers respond to increases in resources with increased consumption. Functionally, consumers should not become saturated. Numerically, the consumer's reproductive response to increases in resource level should occur without great time lags (Carpenter and Kitchell 1993). (The next three conditions also mediate consumer response to changing resource levels.)

Third, extrinsic factors do not greatly limit the numerical response of consumer populations. Shortage of resources other than food (e.g., shelter, water), stressful abiotic factors, disturbance, temporal variability, and spatial heterogeneity should not keep populations so low as to prevent responses to prey increases. When so impeded, consumer numbers are below that set by resources and are less likely to exert recipient control (Andrewartha and Birch 1954; Ehrlich and Birch 1967; Menge and Sutherland 1987).

Fourth, "relative food shortage" should be infrequent. This describes the inherent difficulties of consumers to find, capture, or process the resource population (Andrewartha and Birch 1954) owing to, for example, severely limited foraging time, inefficiency at higher prey densities, or inability to handle sufficient prey for reproduction. Relative food shortages arise from abiotic (e.g., temperature) or biotic (e.g., predator avoidance) factors. If prey are widely distributed or sparse, foraging time per se may be too short. Relative food shortage appears common in many systems (Andrewartha and Browning 1961; White 1978; Polis and McCormick 1987; Schmitz 1992; Abrams 1993; Cronin and Strong 1993.) It changes both numerical and functional responses of consumers and partially underlies the observed high frequency of food limitation in consumers but without obvious resource depletion—one explanation why recipient control is apparently rare (Polis and McCormick 1987).

Fifth, interference and direct density dependence of consumers should not disrupt control. Exploitation ecosystem hypothesis models (Oksanen et al. 1981; Oksanen 1988) assume that the growth rate of consumer populations is affected only through resource depletion. Strongly density-dependent consumer mortality interferes with top-down food chain dynamics (Gatto 1991). Many forms of interference, both intra- and inter-specific, can produce density dependence, constraining the regulatory potential of consumers by limiting their populations below numbers that exert recipient control (Hassell 1978; Beddington et al. 1978; Polis 1981, 1988; Arditi and Ginzburg 1989; Polis et al. 1989; Skogland 1991). For example, interference can limit the use of spiders and some parasitoids and insect

predators as effective biocontrol agents (Riechert and Lockley 1984; Ehler 1992; Rosenheim et al. 1993).

Finally, consumer-resource dynamics are not heavily influenced by other sources of energy to consumers. Subsidies to consumers from other habitats, life-history omnivory, or detrital shunts (see above) should not disrupt density-dependent (regulatory) responses of consumers to their resources (Polis et al. 1995).

The above conditions mediate and limit consumer ability to regulate resources. We suggest that all conditions necessary for successive links to be recipient controlled and in phase rarely co-occur, which thus prevents trophic cascades from being a common factor in the dynamics of natural webs (Strong 1992; Polis 1994; also see DeMelo et al. 1992). Models reinforce this position; with the addition of reasonable biological realities, strong top-down control is often lost (Jaeger and Gardner 1988; Leibold 1989; T. Oksanen 1990; Gatto 1991; Abrams 1992, 1993). Although strong individual resource-consumer links do occur, neither productivity nor consumption necessarily propagate linearly up or down a web.

Parasites and Pathogens

Disease and parasitism are ubiquitous. Virus, rickettsia, bacteria, fungi, and metazoan parasites often are crucial to host dynamics. They can cause catastrophic pandemics, destroy populations (e.g., Davis 1986; Dobson and Hudson 1986; Lessios 1988; Burdon and Leather 1990; Kohler and Wiley 1992), depress densities, generate periodic cycles (Anderson and May 1978a, 1978b, 1982; McDonald et al. 1989), and/or decrease the host's ability to use resources, resist predation, or compete (Price et al. 1986; Toft 1991).

Population regulation and energetics of disease-host links are quite different from EEH consumer-resource links. No disease "trophic level" forms, and virtually no disease biomass results even after heavy mortality (Anderson and May 1978a, 1978b; Holt 1984; Burdon 1987; Loye and Zuk 1991; Toft 1991). Great changes in dynamics, abundance, and biomass occur but with negligible energetic transfer between the exploitative agent and its resource. This clearly contradicts Hairston and Hairston's (1993) energetic-based view of trophic dynamics and Oksanen's models of relative biomass allocation to top trophic levels.

Why do pathogens not decimate all hosts—that is, what limits their abundance? Known limiting factors include host defenses (Fritz and Simms 1992), decrease in virulence (Fenner and Ratcliffe 1965), transmission and alternative hosts (Thompson 1994), and various combinations of factors that lead to self-regulation or relative food (i.e., host) shortage (e.g., constraints on transmission) (Levins and Pimental 1981; Price et al. 1986; Dwyer et al. 1990). In contrast to the conditions described by EEH models, neither diseases nor parasites are known to be controlled by their own natural enemies (Anderson and May 1978b, 1982; Burdon 1987).

Nutrients

Inorganic nutrients and water, crucial to plant distribution and abundance, are central to web dynamics because they determine primary productivity and the

strength of "bottom-up" factors (Carpenter et al. 1992; DeAngelis 1992; Hunter and Price 1992; Power 1992a; Sullivan et al. 1993). These resources are a large part of why the world is "green" or barren. The specific resources that limit plants vary (e.g., water in deserts, light in shaded areas), but inorganic nutrients limit productivity across many habitats. Nutrients affect "greenness," or the lack thereof, in lakes (Schindler 1977; Vanni 1987, 1995; Sterner 1990; Carpenter et al. 1992), streams (Elwood et al. 1981; Peterson et al. 1985, 1993; Rosemond et al. 1993), oceans (Glynn 1988; Howarth 1988; Barry and Dayton 1991; Wells 1994), bays (D'Elia 1988), coral reefs (D'Elia 1988; Williams and Carpenter 1988), the rocky intertidal (Bosman and Hockey 1986; Bosman et al. 1987), salt marshes (Vince et al. 1981), and on land from forests to fields (Siegfried 1982; Strauss 1987; Ryan and Watkins 1989; Pastor and Naiman 1992). Nutrient limitation is important on temporal and spatial scales ranging from very small (e.g., cell-cell competition) to large (annual lake production) (Tilman 1982).

Nutrients affect dynamics over all the community. Seasonally pulsed nutrients from upwelling and turnover produce massive increases in marine (Glynn 1988; Barry and Dayton 1991) and lake (Carpenter et al. 1992) secondary productivity. Nutrient availability influences community structure and secondary productivity in the intertidal region (Bosman and Hockey 1986; Bosman et al. 1987; Menge 1992) and on land (e.g., Hurd and Wolf 1974; Price et al. 1980; Siegfried 1982; Burger 1985; Strauss 1987; Ryan and Watkins 1989).

The commonness of nutrients and water as explanations for food web variation contradicts EEH's focus on energy. We suggest that EEH cannot easily incorporate nutrients. Even if nutrients were considered only as a requisite for plant growth and the predictions extrapolated back to include them as a "trophic level" below plants, interactive effects would likely preclude any straightforward application. Light, water, and herbivores interact with nutrients to affect productivity in complex ways: productivity neither simply nor directly increases with nutrient availability (e.g., Vanni and Temte 1990; Rosemond et al. 1993). Thus, nutrients cannot be simply grafted as another trophic level below plants.

Non- and Quasi-Trophic Processes

We question the assumption that feeding links are the major factor structuring ecosystems. We suggest that this notion belies the importance of other interactions that do not involve energy transfer (e.g., mutualism, interference, habitat modification). Such interactions can produce the appearance of trophic cascades arising from predation but that actually propagate nontrophically through the web (Abrams 1987; Fairweather 1990). Here, we outline two processes whereby substantial flow of energy and nutrients occur among organisms but without standard feeding.

Symbiotic transfer of energy and nutrient among organisms.—Symbiotic interactions among plants, animals, microbes, and fungi are common (see the appendix). Ranging from mutualistic to parasitic, they exert profound effects. Plants are embedded in trophic spectra as continuous as those of any organism; the notion that herbivores are the only heterotrophs that significantly influence plants

is false (see the appendix). Land plants are especially abetted by symbioses: microbes, cryptozoa, and animals greatly facilitate plants, attenuate herbivory, and are a big part of why the world is green. Pollination and seed dispersal are general and profoundly important trophic symbioses of land ecosystems (Regal 1977; Wilson 1993).

Microbes are crucial to plant function and integral to web dynamics. N-Fixing bacteria (Bentley and Johnson 1991) and endophytic fungi (Allen 1991; Carroll 1991; Clay 1991) are common symbionts that aid plants greatly via herbivore protection or increased competitive ability (Harley 1989). Mutualism is one end of a gradient; many fungal-plant links are antagonistic (Wilson 1993), and competition between mycorrhizae and other herbivores is potentially great (Jones and Last 1991). Mycorrhizae also link plants to one another as they carry inorganic nutrients and often extract substantial amounts of fixed carbon (Allen 1980). Single plant taxa can have many fungal associates; even different genera are linked by mycorrhizae and potentially exploit each other (Read 1984; Trappe and Luoma 1991). Symbionts are not all minute—10%-20% of land plant taxa root-graft, thus effectively parasitizing one another (Atsatt 1983).

Metazoan animals also engage extensively in trophic symbioses with autotrophs. Invertebrates from a diversity of phyla rely on symbioses with single-celled algae. Perhaps most famous is the relationship between zooxanthellae dinoflagellates and reef-building corals, which supports a diverse and biomass-rich ecosystem. Symbionts nurture their animal hosts with carbohydrates and/or calcium carbonate.

Nontrophic uptake of energy and nutrients: the antithesis of trophic levels.—Dissolved organic matter (DOM) is produced by detritus (Lehman 1984; Fenchel 1988; Hessen et al. 1990), exudates, and metabolites from "leaky membranes," excretion, and defecation (Thomas 1990). Dissolved organic matter contains organics (sugars, carboxylic acids, carbohydrates) and nutrients (N, P). "Auto-" and heterotrophs from monera to protists to metazoa absorb DOM. Although not classically trophic (Odum and Biever 1984), such uptake is apparently widespread and important in aquatic systems (Odum and Biever 1984; Wetzel 1984; Fenchel 1988; Hessen et al. 1990; Reid 1991). Thomas (1990) questions the assumption that all higher eukaryotes obtain energy entirely by eating organisms. Note that neither classic consumption nor recipient control occurs: "absorption" is donor controlled—renewable resources are harvested without a direct effect on the dynamics of DOM donors.

Many consumers normally provide requisite nutrients to plants as inorganic N and P via excretion, cell leakage, or defecation (Meyer and Schultz 1985; Sterner 1990; Pastor and Naiman 1992). This process influences population dynamics and can facilitate aquatic trophic cascades (Carpenter et al. 1992; Vanni 1990, 1995). This nontrophic and positive involvement of herbivores in plant dynamics is at odds with the simple sequential suppression by EEH herbivores. Substantial interplay among nutrients, productivity, and suppression is evident even in simple webs (Elliott et al. 1983; DeAngelis 1992; Leibold and Wilbur 1992; Pastor and Naiman 1992; Lawler and Morin 1993).

Protections against Consumers

The exploitation ecosystem hypothesis requires that entire sets of similar species in a "trophic level" are highly and equally vulnerable to depletion by consumers. When resources vary in edibility or vulnerability, EEH dynamics do not occur, since consumers cannot eat protected resources (Arditi and Ginzburg 1989; Leibold 1989; Lawler and Morin 1995), and consumer-resource dynamics become donor controlled (White 1978). In fact, many (most?) species have substantial defenses and size- or ecologically based refuges that impede the ability of consumers to depress them. As previously argued (Murdoch 1966; Rigler 1975; Peters 1977), plants and animals are successful because evolution has produced adaptations protecting them from consumers. That is, their success arises from their intrinsic biology and is not necessarily dependent on extrinsic, higher-level control of their consumers by predators.

Protections against consumption.—Vascular and many nonvascular plants are protected well against herbivory. Lignocellulose, phenols, terpenoids, and other noxious compounds (Futuyma 1983; Feeny 1992; Rosenthal and Berenbaum 1992) all appeared early in the history of land plants and shaped the evolution of food webs (Ehrlich and Raven 1964; Swain 1978). On land, the premier protection is lignocellulose, indigestible by animals. Cellulose is hydrolyzed only by enzymes of bacteria and fungi (Gibson 1968); lignin is digested very slowly, only by fungi (Melillo et al. 1982). Lignin protects well against insects (Coley and Aide 1991) and diseases (Loehle 1988). Lignocellulose is the largest product of net primary productivity (NPP) for land plants (Leith 1975) and comprises the greatest fraction of tissue (Aber and Melillo 1991). Thus, most NPP enters the detrital channel.

Protein, lipids, and other essential dietary components are scarce relative to lignocellulose in plants other than algae, the more so the woodier the plant (Lieth and Whittaker 1975; Demment and Van Soest 1985). The biomass and productivity potentially nutritious to herbivores range from little in coniferous (<2%) and broadleaf (<3%) forests, to intermediate in grasslands (McNaughton et al. 1989), to most (>90%) in algae (Waslien 1979).

Cellulose is digested with or without microbial aid by very few of the most species-rich group of terrestrial herbivores, the arthropods; none utilize lignin (Martin 1987, 1991). Contrary to EEH, not the calories of NPP but protein, nitrogen, and water content of plants limit growth and reproduction of herbivorous insects (Southwood 1973; Slansky and Rodriquez 1987; White 1993). Likewise, little cellulose and no lignin are digested by mammals, and none can subsist on the highly fibrous plant material low in water and N that comprises most biomass of land plants (Demment 1982). (The limited amount of cellulose ultimately assimilated by mammalian herbivores passes through a complex of protozoa and microbes [Hungate 1966] that certainly constitutes more than a single herbivore trophic level.)

In contrast to higher plants, algae have no lignin and are typically <10% cellulose (Waslien 1979). This feature together with fewer noxious compounds (Porter 1977) make some algal plankton (naked green algae, nanoflagellates, crysophytes, dinoflagellates, and certain diatoms) unusually vulnerable and nutritious to herbi-

vores; these are the basal species of the aquatic trophic cascades. Other phyto-plankton have constitutive defenses: spines, large size, and coloniality interfere with filter feeding and ingestion, and mucilaginous sheaths inhibit digestion (Porter 1977; Porter and McDonough 1984; Leibold 1989). Blue-green algae are often toxic (Porter and Orcutt 1980). Even in small concentrations, defended algae can greatly reduce cladoceran filtering rates, potentially short-circuiting the EEH behavior of trophic cascades (Lampert 1982; Gliwicz 1990).

Animal prey across the trophic spectrum also have potent defenses (Ehrlich and Raven 1964; Duffey et al. 1986; Harvell 1990; Hay and Steinberg 1992; Rowell-Rahier and Pasteels 1992). Chemical, constitutive, and/or behavioral defenses and prey escape are common reasons that predators often do not depress resources (Charnov et al. 1976; Menge and Sutherland 1987; Skogland 1991; Abrams 1993).

Environmental heterogeneity.—Spatial and temporal heterogeneity provide great protection to resources and can disrupt their regulation by consumers (Caswell 1978; Arditi and Ginzburg 1989; Hunter and Price 1992; Menge 1992; Power 1992*b;* Hastings 1993). Insects are protected substantially from enemies by refuges generated by the physical and chemical heterogeneity of plants (Price et al. 1980; Hawkins and Gross 1992). For ungulates, seasonality, nomadism, refuges from predation, and differences in the vulnerability of age classes can inhibit prey depression (Skogland 1991; Boutin 1992). Different plants and parts of the same plant vary as much as species in vulnerability and quality to foragers (Demment and Van Soest 1985; Owen-Smith and Cooper 1987; Bryant et al. 1991; Gross et al. 1993; Owen-Smith et al. 1993). Higher plants are "modular" and "differentiated," which provides variable responses to herbivory (Haukioja 1991) and confers substantial protection (Hunter and Price 1992; Strong 1992).

Aquatic Trophic Cascades: Exceptions That Prove the Rule

The discovery of trophic cascades (TCs) by Hrbacek et al. (1961) and their elucidation in freshwater (Brooks and Dodson 1965; Shapiro and Wright 1984; Persson et al. 1988, 1992; Power 1990; Vanni and Findlay 1990; Vanni et al. 1990; Carpenter and Kitchell 1993) and marine systems (Paine and Vadas 1969; Estes and Palmisano 1974; Paine 1980) are a high achievement of community ecology. In these systems, carnivores greatly reduce their prey populations, and this influence has dramatic ecosystem manifestation one or even two links down the chain. Certainly, the intense top-down forces in these algal-based chains provide the best example to date of EEH dynamics. We suggest that, nonetheless, TCs are generally uncommon, except under a set of restrictive conditions that occur in some aquatic systems.

It is a major challenge to sort out the dynamic forms of aquatic TCs: which systems are dominated by TCs and which are not, what other forces come into play, and why (Crowder et al. 1988; McQueen et al. 1989; Carney and Elser 1990; Carpenter and Kitchell 1992; De Melo et al. 1992; Power 1992; Strong 1992). We suggest that a pivotal element is the exceptionally higher edibility, nutritiousness, and vulnerability to herbivores of algae at the base of aquatic TCs. This subset of algae lacks the effective chemical or physical defenses of higher land plants

and other phytoplankton (see *Protections against Consumers,* above; Porter 1977). The most general algal defenses (long spines; thick rigid cell walls; agglutination into colonies too large to ingest; and the toxins and repellents of chrysophytes, dinoflagellates, and cyanobacteria) are believed to be largely absent from TC algae. A great challenge is to understand the dynamic and community effects of "inedible," "resistant," and other less nutritious algae (McCauley et al. 1988; Leibold 1989; Gliwicz 1990; Sarnelle 1993).

The crucial link in aquatic TCs derives from the extraordinary grazing efficiency of large Crustacea, especially *Daphnia,* and their own high vulnerability to fish in the relatively homogeneous aquatic medium of the water column. Indeed, Neill (1992, p. 214) reasons that not just one but a series of keystone-like species co-occur in the TCs of lakes—"distinctive phylogenetic groups" of size-structured, limnetic phyto- and zooplankton, fish, and so forth, that predispose a trophic organization likely to cascade. Neill considers that such an assemblage is unlikely to occur in oceans or on land. We concur and extend this reasoning to the proposition that TCs are generally uncommon because they depend on a set of restrictive conditions: strong, consecutive, recipient-controlled links occurring concurrently and in phase (see *Linkage Strength and Type,* above).

Another challenge is to understand the degree that external factors promote the occurrence of aquatic TCs—for example, life-history omnivory and allochthonous subsidies of piscivorous fish by non-TC prey (see previous discussion). In the TCs that occur in the water column of Wisconsin lakes, most food of the top consumer (adult bass) is littoral in origin, and juvenile bass primarily eat non-TC prey (plankton and insects) (Carpenter and Kitchell 1993; Schindler et al. 1995). Steelhead mature on marine foods, then migrate to California rivers where they initiate strong TCs if conditions are suitable (Power 1990).

Detritivory, so common in most systems (see *Detritus and Its Infusion into the Classic Food Chain,* above), is apparently unimportant to aquatic TCs. There is little autochthonous plant detritus, owing to a very low content of undigestible cellulose and lignin in aquatic algae. Moreover, consumer feces are relatively low in undigestible detritus but high in DOM. We speculate that the relatively low rates of algal detrital production, the greater influence of DOM, and the rapidly cycling nutrients potentiate strong top-down effects in aquatic systems that cascade.

A valuable lesson of lake TCs is that bottom-up influences are a function of nutrient rather than energy limitation (also see *Nutrients,* above). Nutrients are intricately tied with nontrophic influences of specific consumers, and these influences vary by habitat. In aquatic TCs, defecation and leakage by animals directly and rapidly regenerate the nutrients needed by phytoplankton (Sterner 1990; Carpenter et al. 1992; Vanni 1995). Because refractory particulate plant detritus is scarce, nutrient recycling between autotrophs and consumers does not often involve intermediate decomposer species as is common on land. Nutrient availability and recycling rate are key determinants of productivity; each differs by habitat (Carpenter et al. 1992)—pelagic nutrients cycle rapidly relative to those in the benthic or on land. Trophic cascades in lakes may depend on rapid cycling of P through higher levels. Further, physiological distinctions between animal species

determine whether N or P is more limiting and thus determine the very existence of TCs (Sterner 1990; Carpenter et al. 1992; Peterson et al. 1993; Vanni 1995). Nutrient state is a major factor in lake TCs. Oligotrophic conditions usually preclude rapid phytoplankton growth, proper grazers, and tight nutrient coupling between animals and plants. Cyanobacteria in eutrophic lakes appear sufficiently resistant to the levels of grazing necessary to produce TCs (Carney 1990; Carney and Elser 1990; Gliwicz 1990; Elser and Goldman 1991).

DISCUSSION

Many of the factors delineated above are ubiquitous and important in nature but do not fit well into theory based on trophic levels. We reexamine the practice of categorizing species interactions by erecting linearly arranged trophic levels as a starting point to model natural communities. We feel that such a simplified approach is artificial and, by its very nature, limits our understanding. Neither herbivores nor their consumers need regulate or be regulated in the simple fashion assumed by green world theory (by either predators or interspecific competition for resources). We question the green world assumption that the profusion of plant detritus is a consequence of herbivores being suppressed by predators. The relative absence of protections of algae against herbivory make the aquatic trophic cascade a poor model of terrestrial food webs, in which the lion's share of plant productivity is extremely well protected against herbivores. The low nutritive value of lignocellulose, the myriad noxious phytochemicals, and the complex growth form of higher plants are at least as important reasons for the profusion of plant detritus as the postulated herbivore suppression by predators of green world theories.

A Proposed Framework for Food Web Dynamics

We offer a framework in the context of functioning community webs as an alternative to theories based on discrete trophic levels. Substantial evidence indicates that most webs are reticulate and species are highly interconnected; many (most?) consumers are omnivorous on foods (frequently on both plants and animals) across the trophic spectrum during their life history; most resources are eaten by many species across the trophic spectrum; plants are linked to a variety of species via trophic mutualism; most primary productivity becomes detritus directly; detrital biomass reenters the autotroph channel of the web when detritivores and/or their predators are eaten by consumers that also eat species in the herbivore channel; species are often subsidized by food from other habitats.

We propose that such trophic complexity pervades and generally underlies web dynamics. High connectance diffuses the direct effects of consumption and productivity throughout the trophic spectrum. Thus, consumer and resource dynamics affect and are affected by species at multiple positions along the trophic spectrum rather than interacting only with particular "trophic levels." An extremely important aspect of such complexity is the mixture of donor and recipient control. Consumer density is elevated, and consumers often persist by eating resources whose abundance they do not influence.

We illustrate by focusing on top-down interactions. Some consumers do control some resources and, occasionally, produce trophic cascades. We suggest that such control is often enabled by omnivorous feeding and various consumer subsidies that are usually donor controlled. Here, the transfer of energy and nutrition affects dynamics; numerical increases in consumer abundance occurs from eating diverse resources across the trophic spectrum in the autotroph channel, from detritivores and detritus from the saprovore channel, from other habitats, and across their life history. Consumers, so augmented, exert recipient control to depress particular resources below levels set by the nutrition traveling through any particular consumer-resource link (analogous to the effects of apparent competition; see earlier discussion). Top-down effects arising from such donor-controlled, "multichannel" omnivory are depicted in figure 2. We suggest that strong consumer-mediated dynamics occur precisely *because* webs are reticulate and groups of species do not form homogenous, discrete entities.

Certain factors influence our model. First, the relative amount of donor-controlled input to consumers should increase with the fraction of resource production that is unavailable to consumers, so they cannot affect resource renewal rates (e.g., resources produced in refuges, in different habitats, during periods when consumers are inactive, or those whose life history places them away from consumers for part of their cycle). Second, predators toward the top of the web should benefit relatively more from donor-controlled feeding and subsidies than those lower in the web. Relatively large, top predators often migrate or have the mobility to forage across habitat boundaries; their size promotes omnivory on smaller prey across the trophic spectrum and often produces substantial life-history omnivory (Darnell 1961; Peters 1977; Polis 1984, 1991; Werner and Gilliam 1984; Menge and Sutherland 1987; Sprules and Bowerman 1988; Schoener 1989; Polis et al. 1989, 1995; Vadas 1990; Winemiller 1990; Cohen et al. 1993; Diehl 1993). Third, spatial subsidies (food, nutrients) from other habitats should be greater where strong transport agents (currents, winds) occur (e.g., aeolian environments), in heterogeneous environments, where ecotones are common, and where relatively lower-productivity habitats are juxtaposed to those with higher productivity (aphotic and benthic zones; land and water; coastal zones on oceans, lakes, and streams; caves; forests next to grasslands; see Polis and Hurd 1995*a*, 1996; Polis et al. 1995). Fourth, detrital shunts are most important when the relative amount of productivity eaten by herbivores is low versus the amount that enters detrital channels. The fraction of productivity eaten by herbivores decreases with herbivore inability to respond functionally or numerically, with consumer control on major herbivores or with effective plant defenses.

Our model is congruent with many aspects of the Menge-Sutherland (1976, 1987) model (M-S). They postulate that consumption intensity varies with trophic position to produce a gradient in consumer control. Intensity increases monotonically toward the bottom of webs as higher-level consumers tend to be more omnivorous; thus, lower-level species are eaten by more species than those toward the top. If donor-controlled subsidies varied with trophic position so consumers toward the top received more than those at the bottom, our model would be consistent with M-S dynamics. As outlined above, we suggest that top consum-
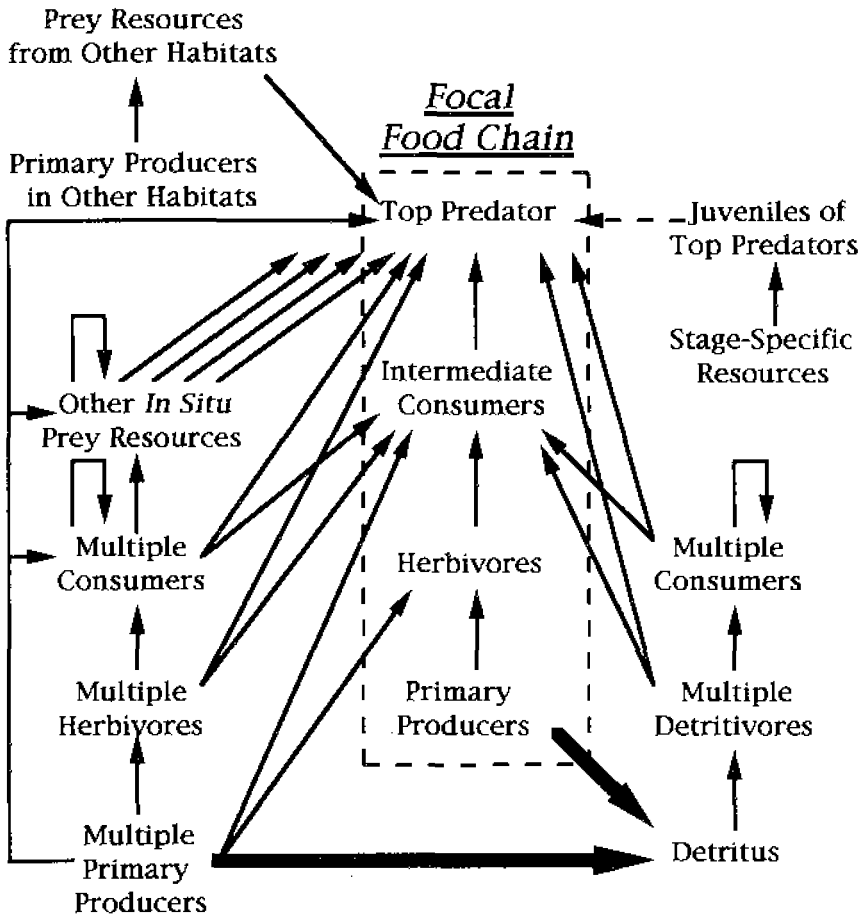
FIG. 2.—Top-down effects arising from "multichannel" omnivory. The abundance and biomass of consumers in the focal food chain is increased from energy arising from many sources outside the focal chain: omnivorous feeding on other in situ resources, resources from the detrital channel, allochthonous resources from other habitats, and life-history omnivory. So subsidized, consumers potentially depress their resources; occasionally trophic cascades occur.

ers are relatively more omnivorous (also suggested in Cohen et al. 1990, 1993) and subsidized, which increases their numbers, strengthens their effects on species lower in the trophic spectrum, and moves community structure away from ESS-type dynamics toward M-S dynamics. However, we caution that consumers at many positions are subsidized (e.g., by allochthonous prey [Polis et al. 1995] or by food from the detrital channel [Rosemond et al. 1993, Porter 1995]), sometimes with great effects on dynamics (see earlier discussion). Thus, we can only speculate on the relative patterns of donor-controlled subsidies as a function of trophic position. Nevertheless, multichannel omnivory and various subsidies promote the type of top-down control envisioned by M-S.

In spite of our antipathy to the trophic-level concept, our donor-controlled model of top-down control could be integrated into EEH. For example, subsidized or multichannel consumers can initiate trophic cascades qualitatively consistent with EEH (e.g., Power 1990; Dial 1992; Carpenter and Kitchell 1993; Polis and Hurd 1995*a;* Schindler et al. 1995; note that in these cases energy does not flow to consumers per EEH mechanisms; see previous discussion). Incorporating various donor-controlled links (e.g., detrital shunts, spatial subsidies) would enrich EEH and make it more realistic (e.g., see T. Oksanen 1990).

High connectance affects other dynamics. For example, even in a simple configuration of omnivory via intraguild predation, top predators may increase or decrease resource abundance depending on the relative strengths of direct and indirect interactions (Polis and Holt 1992). At the consumer level, omnivory can diversify trophic linkages during food abundance and tide populations through lean times; alternative foods also lessen consumer dependence on any one resource, which thus possibly promotes stability and persistence ("risk spreading") (Cope 1896; den Boer 1968; Reddingius 1971; Crawford 1987; Polis et al. 1989; Polis 1991, 1994; Morin and Lawler 1995).

In 1961, Darnell explicitly recognized many of these concepts:

Evidently . . . consumers exhibit a broad disregard for narrow trophic lines. In fact, the ability of a given species to utilize alternative foods (often from different "trophic levels") appears to be one of the main buffering factors which tend to stabilize population levels in complex natural communities. To ignore the inherent diversity and the system of alternatives would seem to be overlooking the very essence of trophic integration involved in community balance. (P. 566)

How to Proceed

What is most needed are more tests in a variety of systems of trophically mediated hypotheses, particularly those that manipulate major elements. Productive avenues will combine consumer-resource dynamics with other important facets of functioning ecosystems—for example, spatial flows, omnivory, life-history omnivory, detrital shunts, community effects of nutrients, variability in resource edibility, indirect effects, and trophic symbioses.

Our model outlined here could be tested by increasing or decreasing input from various energy sources/channels that support consumer populations and determine subsequent changes in consumer abundance, predation intensity, and the dynamics of specific consumer-resource links. For spatial subsidies, one might manipulate the flow from a subsidizing habitat to another. For detrital shunts, remove or add detritus to analyze how this affects the numerical response of multichannel consumers and subsequent effects on prey in the herbivore channel; alternatively, nutrients could be added to facilitate detrital decomposition and the production of detritivorous prey. For age-structure omnivory, alter resource availability at one stage of a consumer and monitor interactions with resources at a second stage. The importance of omnivory to consumer control of resources can be assessed by determining the response of specific prey to manipulations of alternative prey. Other tests would manipulate or substitute multichannel, subsidized predators and those using resources more narrowly. Experiments should

be complemented with natural history observations (Polis et al., in press) and the judicious use of comparative community data (e.g., Menge 1992).

The design of experiments must be well considered. Most experiments manipulate subsets of communities, and it could always be argued that resultant dynamics confer little about the entire communities. Such an argument would make it fruitless to test community-level hypotheses with anything less than manipulations of whole-web components (i.e., "trophic levels"), such as all autotrophs, all detritus, all herbivores, or all consumers of herbivores. However, operational considerations make it problematic to design and conduct experiments of hypotheses dealing with trophic levels as discrete entities. What should be manipulated: an important species, a key guild of "trophic species" (species that feed, and are fed upon, in a similar manner), or all species (or guilds) forming or eating a key resource? To what trophic level do we assign species (e.g., ubiquitous omnivores and intraguild predators) that can exert direct and indirect effects that oppose each other? Even if trophic levels were real, indirect effects might obscure clear results, particularly when entire groups are manipulated.

CONCLUSIONS

Myriad factors impinge on species populations and contribute to food web structure. We attempt to incorporate conceptually some of these factors into a general framework that elevates donor-controlled, "multichannel omnivory" into a central position to understand consumer-resource and web dynamics and the structure of communities. One of our central messages is that complexity, no matter how inconvenient to theory, may be the important signal driving community and web dynamics and not just irrelevant noise. Besides the diversity of direct trophic connections observed in food webs, species in nature also are interconnected via a vast number of other direct (e.g., symbiosis) and indirect links that may reinforce or counter direct trophic ones (Bender et al. 1984; Price et al. 1986; Abrams 1987; Yodzis 1988, 1995; Fairweather 1990; Strauss 1991; Polis and Holt 1992; Menge 1995). In real webs with 10^2–10^4 species, an astronomical number of direct and indirect, weak and strong, trophic and nontrophic, and positive and negative links operate. Our task as community ecologists is clear, although not easy or without major challenges: we need to continue to rethink, quantify, model, and test the interplay between complexity and dynamics. Only when we embrace complexity and variability will we truly understand natural systems.

APPENDIX

Trophic and Symbiotic Interactions of Plants

Most higher plants are enmeshed in continuous and overlapping interactions with a diversity of organisms that are autotrophic, saprotrophic, and holotrophic. Symbioses involving the transfer of organic molecules and nutrients to and from plants range from mutualistic and commensalistic, through relatively neutral, to amensalistic and reciprocally antagonistic. Such interactions frequently and significantly influence the dynamics of plants and their symbionts. The rich array of interactions leads to highly reticulate interconnections of plants with other species throughout the web in contradiction to the concept of discrete and homogeneous trophic levels.

I. Classical Coevolution of Angiosperms, Arthropods, and Vertebrates
   A. Pollination and seed dispersal mutualisms are fundamental to terrestrial ecosystems (Regal 1977; Wilson 1993).
   B. There is a high degree of specificity and statistical interaction in defense and protection among flowering plant and herbivore taxa (Ehrlich and Raven 1964).
   C. Plants form defense guilds (Atsatt and O'Doud 1976).
II. Other Important Symbioses of Higher Plants in Food Webs (Barbosa et al. 1991; Hunter and Price 1992)
   A. Fungae: plants are rife with fungi, within and outside; symbioses range from mutualisms through pathogenesis (Carroll 1991).
   B. Mycorrhizae: most angiosperms, all gymnosperms, all pteridophytes, and some bryophytes rely on these associations, which involve all major groups of fungi (Trappe and Luoma 1991)
      1. Benefits to plants (Read and Boyd 1986) include the following:
         a) Great increase in surface area of roots (Allen 1991)
         b) Acquisition of water and inorganic nutrients
         c) Amelioration of root bacterial community by modification of carbohydrate environment (Lindermann 1988; Ingam and Molina 1991)
      2. There are several mycorrhizal taxa per plant individual; links exist between plants and even among plant genera (Trappe and Luoma 1991).
      3. Costs to plants include the following:
         a) Loss of fixed carbon to fungus (Harley 1989)
         b) Loss of fixed carbon to linked plants (Read 1984)
   C. Endophytic fungi: nearly ubiquitous in plant kingdom, provide protection against herbivory, and increase competitive ability of host plants (Carroll 1991; Clay 1991); however, they are not just mutualistic (Wilson 1993).
   D. Rhizosphere root and soil bacteria: extremely widespread among plants
      1. Benefits to plants (Shippers et al. 1990) include the following:
         a) Can defend against pathogens (Gilbert et al. 1993)
         b) Supply nutrients to plants
      2. Benefits from nitrogen-fixing bacteria include the following:
         a) Supply plants with nitrogen (Boring and Swank 1984)
         b) Increase competitive ability (Bentley and Johnson 1991)

    c) Modify herbivory by changing noxious phytochemistry

E. Soil microarthropods: voracious and abundant belowground consumers—carnivores, phytophages, fungivores, and detritivores (Walter 1987; Moore et al. 1988).

F. Soil nematodes: the most abundant metazoa in soils—phytophagous, microbiophagous, fungivorous, carnivorous, and omnivorous species (Freckman and Baldwin 1990)

G. Root-grafting plants (Atsatt 1983; Gibson and Watkinson 1992)

H. Epiphytic organisms: complex higher-order interactions among host species, epiphytic organisms (both plant and animal), herbivores, pathogens, predators of herbivores, and abiotic environment (Leber 1985; Ellison and Farnsworth 1990; Coley et al. 1993; Wilson and Ruckleshaus 1993)

I. Reef-building coral and other marine invertebrates are symbiotic with zooxanthellae; such symbiosis is a major reason for the great success of hermatypic corals (Goff 1983).

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