Food webs in river networks

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Food webs and river drainages are both hierarchical networks and complex adaptive systems. How does living within the second affect the first? Longitudinal gradients in productivity, disturbance regimes and habitat structure down rivers have long interested ecologists, but their effects on food web structure and dynamics are just beginning to be explored. Even less is known about how network structure per se influences river and riparian food webs and their members. We offer some preliminary observations and hypotheses about these interactions, emphasizing observations on upstream–downstream changes in food web structure and controls, and introducing some ideas and predictions about the unexplored question of food web responses to some of the network properties of river drainages.

Key words: food chain length; food webs; landscape heterogeneity; river networks; stream ecosystems.

INTRODUCTION

Food webs are well described as complex adaptive systems (as lucidly reviewed by Levin (1999)). Like other complex adaptive systems, food webs have diverse components, linked by flows and (often non-linear) interactions, 'which determine and are reinforced by hierarchical organization of these components (Levin 1999; p. 12)'. Paine (1980) pointed out that two distinct flows create different hierarchies in the same food web. Energy flows from more basal resources up to consumers at higher trophic positions, while 'top-down' chains of population control link consumers to the resource populations they regulate or limit, if these consumers are not suppressed by their own predators. Energy flow paths and population control chains are related, but not identical. Organisms should have greater impact in food webs if they have access to better, more productive, or more widely distributed energy sources. Conversely, interactions and impacts of other species may determine the energy source to which a particular

consumer has access. Ecologists have long pondered the historical, environmental and biological controls that determine path and chain lengths and the impacts of particular web members (Hairston *et al.* 1960; Pimm 1979, 1982; Paine 1980, 1988; Power 1992a; Power *et al.* 1996; Post *et al.* 2000). This debate has been somewhat confused when energy flow paths and population control chains were not distinguished. Our present understanding of these relationships is particularly limited by our rudimentary appreciation of the spatial and temporal contexts and scales of food webs. The impacts of web members on each other, and the degree to which energy flow predicts interaction strength, depend largely on which spatial sources of energy and nutrients sustain particular web members, and how resident versus transient these members are in their communities. Synthetic studies that link food web dynamics to spatial fluxes of energy, matter, organisms and information across heterogeneous landscapes (Polis *et al.* 1997; Nakano & Murakami 2001) will contribute much to our understanding of these issues.

In studies of spatial food webs, as of any complex system, trade-offs exist between realism and mechanistic understanding on the one hand, and scope and generality on the other. To explore the effects of landscape heterogeneity on multitrophic level dynamics, ecologists sensibly began with

simplified conceptualizations. These depict fluxes of organisms, energy or materials across habitat boundaries (Holt 1984; Polis *et al.* 1997), over 2-D lattices (Oksanen 1990; de Roos *et al.* 1991), or among islands or patches set in an uninhabitable matrix (chapters in Tilman & Kareiva 1997). Important recent progress towards landscape realism has been made through more explicit, sometimes experimental, studies of the ecological effects of specific landscape features, such as boundary permeability (Cadennaso & Pickett 2000; Laurance *et al.* 2001; Cadennaso *et al.* in press) or geometry (Fagan *et al.* 1999; Anderson & Polis 1999), or seasonal shifts in the relative productivities of habitats coupled by trophic exchange (Nakano & Murakami 2001). However, one general feature of landscapes has so far received very little attention with respect to its influence on spatial food webs. River drainage networks sculpt all terrestrial landscapes, defining their relief, dissection and many other aspects of their heterogeneity. Channel and valley characteristics influence ecologically significant conditions and are partially predictable from landscape position (Montgomery & Buffington 1993; Sklar & Dietrich 1998). Here, we explore how conditions arising from longitudinal and network structure might affect energy flow and species performances in food webs.

A TALE OF TWO NETWORKS

Food web networks are hierarchical. Energy flows up from lower to higher network positions, and consumer control is exerted down some of these paths, but not others. River drainage networks are also hierarchical, with gravity driving water, sediment, solutes and organic matter from ridges dividing watershed down into channels, and from headwaters down mainstems to lowland floodplain rivers and estuaries. With the exception of winds and local back eddies in turbulent water, only biological fluxes (migrations and other movements of individuals) drive materials upstream or upslope. Conditions, resource fluxes and biotic interactions experienced by aquatic, riparian and terrestrial organisms in watersheds vary down longitudinal gradients from headwaters to lowland habitats (Vannote *et al.* 1980; Montgomery & Buffington 1993, 1997). Conditions also vary abruptly, for example, where network confluences inject pulses

of sediment, water, organic matter or organisms from tributaries into mainstems. Longitudinal gradients and their impacts on species distributions have long interested stream ecologists, but upstream–downstream changes in food web interactions are just beginning to be investigated. Even less is known about the network effects per se on organisms and food webs, but these influences may help explain and predict 'cumulative watershed effects', which are of great current concern in watershed management (Li *et al.* 1994; Dunne *et al.* 2001).

In this paper, we discuss classical and more recent ideas for controls on food chain length. We then explore how such controls may vary at different positions in drainage networks where the energy sources, habitat structure and disturbance regimes differ in channels and adjacent watersheds. We draw mainly on our own work with students and colleagues from rivers in north coastal California. A more comprehensive review of the literature relevant to this topic would repay effort, but is beyond the scope of this paper.

CONTROLS ON LENGTHS OF ENERGY FLOW PATHS AND FUNCTIONAL FOOD CHAINS IN FOOD WEBS

There are many interesting questions to ask about the properties of food webs (e.g. Cohen 1977; Paine 1980, 1988; Schoener 1989). Questions about energy path or chain length are particularly informative for guiding investigations of large-scale variation in the distribution of trophic-level biomass (Oksanen *et al.* 1981; Mittelbach *et al.* 1988; Power 1992a), as well as issues of practical interest. If we want to conserve native species, sustainably harvest a resource, or suppress biological pests, we need to know the energy flow paths that support the groups of interest and the top-down controls on their abundance.

Classical hypotheses for environmental controls on the length of food chains (which unfortunately do not distinguish energy flow paths from top-down chains) discuss two environmental variables and one evolutionary factor.

1 *Productivity/efficiency.* Chains should lengthen as fluxes of limiting resources or energy to food webs increase, or as consumers increase their

efficiency of resource capture or conversion (Fretwell 1977; Pimm 1979; Oksanen *et al.* 1981; Fretwell 1987; Pimm & Kitching 1987).

2 *Disturbance/stability*. Chains should be shorter in more frequently disturbed environments (Pimm & Lawton 1977; Pimm & Kitching 1987).

3 *Design constraints*. Pimm (1979) argues that it may be impossible for evolution to build a Pterodactyl predator, for example, because an organism large enough to subdue one could not fly to catch it.

Despite many food web surveys, particularly across productivity gradients (McQueen *et al.* 1989; Carpenter *et al.* 1991; Power 1992b; Persson *et al.* 1996), and some experimental studies (Carpenter *et al.* 1987; Jenkins *et al.* 1992; Wootton & Power 1993; Wootton *et al.* 1996; Marks *et al.* 2000), little consistent support can be found for predictions of either the classical productivity or the disturbance hypothesis (Hastings & Conrad 1979). However, recent work on this topic has uncovered one factor that does appear to exert a strong, consistent effect: habitat size. Some of the most convincing data ever assembled on this question reveal that in temperate lakes, energy flow paths lengthen with habitat size (volume), but are unrelated to productivity (Post *et al.* 2000). The relationship between food chain length and habitat size may be quite general, and partially driven by design constraints (hypothesis 3). Large habitats support larger taxa, and many food webs are strongly size structured, with larger organisms at higher trophic levels (Menge & Sutherland 1976.; Kerfoot & DeMott 1984; Kerfoot & Sih 1987; Power *et al.* 1997). Size usually matters more than species identity in predator–prey relationships: who eats whom depends on the size (life history stage) of the individuals that encounter each other (Polis *et al.* 1989). Density, however, can sometimes reverse a size-based predator–prey relationship as in pack hunting army ants, dogs or piranhas, or whelks grazing on lobsters (Barkai & McQuaid 1988). Pimm's (1979) pterodactyl populations might similarly have been suppressed by parasites or egg predators. The positive relationship between body size and trophic position is particularly strong in aquatic food webs where most predators are gape-limited because a viscous medium selects against hydrodynamically ineffi-

cient appendages for dismembering prey (Vogel 1981; Power 1987; Power *et al.* 1997). The relationship of food chain length to habitat size may be less clear, however, in habitats such as rivers where cross-habitat exchanges have strong effects (Polis *et al.* 1997; Nakano *et al.* 1999). Analyses of river or adjacent terrestrial food webs may overlook crucial interactions if the boundary of observation or experimentation is drawn at the river surface (Wallace *et al.* 1997; Nakano *et al.* 1999; Power & Rainey 2000; Nakano & Murakami 2001; Sabo & Power in press a, b; Power *et al.* in press).

Post (unpubl. data, 2001) has recently called for an expanded discourse that acknowledges the influence of many factors on food chain length. In general, lengths of food chains are dynamic, responding to a number of non-linear, interacting factors (e.g. Levin 1999; Carpenter 1988). As the abundance of particular web members changes over time, so will the lengths of the chains in the food webs in which they are embedded. For example, Hutchinson (1959) argued that if a secondary top predator depleted its primary carnivore prey over time, it would, of necessity, drop from the fourth to the third trophic level. If predators deplete more edible prey, they enrich primary consumer guilds with inedible taxa, shortening functional food chains that control green biomass in their habitats (e.g. Power *et al.* 1996). Multiple controls on food chain lengths are also likely to interact. Schoener (1989) has proposed a productivity × area hypothesis for food chain length. Disturbance and productivity may also interact to affect food chain length over timescales that encompass species succession (Power *et al.* 1996).

DEMOGRAPHIC AND METAPHYSIOLOGICAL MODELS FOR PREDICTING THE PERSISTENCE AND IMPACTS OF FOOD WEB MEMBERS AT DIFFERENT NETWORK POSITIONS

To think about how complex dynamic controls on food chains might interact over heterogeneous landscapes, we revisit three basic conditions that must be met if increasing the input of a limiting trophic resource to lower trophic levels is to

lengthen food chains or energy-flow paths in a local web. First, a new top 'consumer' must be biogeographically available. Consumer is used here *sensu latu*: this could be a producer or a decomposer, if only non-living resources are available and we are asking whether the local chain will increase from zero to one link. Propagules of the new top consumer must either be able to arrive at the site of the newly enhanced resource or be 'waiting in the wings' as surviving residual biomass, often in resistant life history stages. Environmental heterogeneity in the form of refuges, dispersal barriers or conduits plays an obvious role here. Second, if the flux enters the web several levels below the potential new top consumer, lower trophic levels already present must be able to capture enough of the enhanced flux to augment their own somatic growth or reproduction. Environmental structure and consumer biomass both affect this contingency. For example, if more dissolved nitrogen were added to a smooth channel with fast laminar flow and a thin film of periphyton, little of this nitrogen would be assimilated locally, even if the periphyton were nitrogen limited. Third, lower trophic levels already present must use the augmented resource to produce new tissue that the new potential top consumer can ingest and assimilate. Enhancing ecosystem productivity will not increase lengths of energy flow paths or top-down food chains if it is sequestered in defended tissues or individuals. Only if these three conditions are met can enhanced productivity lengthen food chains (Fig. 26.3 in Persson *et al.* 1996).

Timescales are implicit in the verbal arguments above. Before discussing spatial heterogeneity, let us scale these arguments to what are perhaps the most fundamental temporal scales affecting food webs: (i) time since disturbance (defined *sensu* Sousa (1984): a discrete event that kills or removes local biota, freeing space and other resources); and (ii) recovery times following resets for key populations. To maintain itself in a periodically disturbed habitat, a population, such as a new apex member of a food web path or chain, needs a positive per capita realized rate of natural increase, R, high enough so that:

$$dN(t)/dt = R(N, t) N(t) > 0 \text{ when } N(t) = N(0) \tag{1}$$

where $N(t)$ is the number of individuals or biomass [i] in the population at time t; $N(0)$ is the number of individuals or residual biomass (survivors or recolonists) present soon after disturbance resets the environment and t is the time since disturbance. The severity of a local disturbance, as well as spatial heterogeneity in the form of refuges from disturbance, both affect $N(0)$.

The influence of spatial heterogeneity also unfolds as we consider R, the function describing the population growth rate. R [individuals produced per individual per time, ($i\ i^{-1}\ t^{-1}$)] here can be any suitable function describing positive population growth (e.g. exponential, linear or sigmoidal). To investigate the role of environmental conditions (as well as natural history traits), we can unpack the parameter R following Schoener (1973):

$$R = f[(c \times p) - m] \tag{2}$$

where p is the proportion time (t) spent foraging [$t\ t^{-1}$], c is per capita rate of energy (e) harvest [$e\ i^{-1}\ t^{-1}$], f is conversion efficiency [$i\ e^{-1}$] and m is the per capita energetic cost of maintenance [$e\ i^{-1}\ t^{-1}$]. We can use equations 1 and 2 to ask whether a key population in a functional group can re-establish after disturbance, so that it could persist under a given environmental regime, assuming no losses to biotic enemies. In other words, this analysis would address the question of whether conditions and local resources satisfy requirements that determine a species' fundamental niche (Hutchinson 1959). For example, is there sufficient productivity area (Schoener 1989) to support such a population? Habitat productivity [energy area^{-1} time^{-1}] × foraging area [area] are positively related to c, per capita rate of energy harvest, but increasing foraging area may also increase m, energetic costs, if travel is expensive. Equation 2 must be parameterized to reflect a particular natural history because the costs of travel relative to exhaustive local grazing on depleted resource patches vary greatly among taxa and habitats.

This demographic analysis establishes criteria for the persistence of a single population under a given environmental regime at a particular drainage network position. While these criteria are necessary, they would not necessarily be sufficient for persistence, as they do not take interactions among web members into account. For such a food web

analysis, we turn to the metaphysiological models of Getz (1991, 1993, 1994), which portray trophically stacked populations with elegant conciseness. Getz calls his models metaphysiological because they describe the biomass dynamics of populations in terms of collective intake and metabolism, instead of the birth and death rates of individuals (although equivalent terms for intrinsic rate of increase, r, and carrying capacity, K, in traditional logistic equations can be derived from his formulations [Getz 1993; p. 290: eqs (7) and (8)]. The per biomass growth rate for a population is:

$$\mathrm{d}x_i / \mathrm{d}t = x_i \, f_i \, (g_i) - x_{i+1} \, g_{i+1} \qquad (3)$$

where $f(g)$ describes a population's per biomass growth rate for a given collective rate of resource uptake $g\,(x_i, x_{i+1})$. Equation 3 holds for all populations or functional groups in a food chain with n levels, with $g_{n+1} = 0$ for the top predator, n. For the lowest level, the resource flux for x_0 might also be modified to describe a constant or environmentally determined input rate of photons or dissolved nutrients.

A simple formation for per biomass growth used by Getz (1993) to produce the hyperbolic relationship commonly expected between resource uptake and population growth rates is:

$$f_i \, (g_i) = \rho_i (1 - \kappa / g_i) \qquad (4)$$

where ρ is the maximum growth rate that can be sustained on $\delta > 0$, the maximum per biomass rate of resource extraction achievable at high resource fluxes, and κ is the minimum resource uptake rate needed for positive population growth (a compensation point).

The rate of resource uptake for level i is modelled as a functional response with consumer saturation and interference (DeAngelis *et al.* 1975):

$$g_i \, (x_{i-1}, x_i) = (\delta_i \, x_{i-1}) / (\beta_i + x_{i-1} + \gamma_i \, x_i) \qquad (5)$$

where β_i is the half saturation resource level for an isolated biomass unit that experiences no conspecific influence on its intake, and γ_i is a dimensionless self interaction scaling parameter ($\gamma_i > 0$ for interference, $\gamma_i < 0$ for social facilitation of feeding).

The dynamics of each population in a trophic stack are governed by the five parameters ρ, κ, β, γ and δ. Values of these parameters (as well as

values of parameters in equations 1 and 2) would themselves be determined by evolved traits and the environmental context. Drawing from our river and watershed research, we explore how these parameters might vary among different functional groups in food webs and how the values for a given functional group may change down drainage networks. We next consider aggregated functional groups in a food web fragment that seems sufficient to explain much of the spatio-temporal variation in trophic level biomass, particularly of algae, in the rivers we have studied. First, we will compare the constraints and adaptations of different groups that might affect their parameter values in the different environmental contexts that occur at different landscape positions. Then we will summarize geomorphic studies of longitudinal changes in channel environments and offer some ideas for the influences of network properties of rivers that are largely unstudied to date. Finally, we will explore, in a preliminary fashion, how environmentally mediated shifts in metaphysiological or behavioral and demographic parameters in a population might influence its impact on food webs at different channel network positions.

FUNCTIONAL GROUPS IN A FOOD WEB FRAGMENT

Consider simplified food web fragments (sensu Holt 2002) such as those presented in Fig. 1, with highly aggregated functional groups. Two basal energy sources fuel most river food webs: terrestrial plant detritus (leaves, fruits, flowers, stems, or soil carbon and associated fungi and bacteria) and attached algae. This energy flows either to vulnerable primary consumers that support predators or to invulnerable primary consumers that sequester energy without passing it up the food web. Vulnerable primary consumers in rivers include thin soft fish and naked, mobile invertebrates (e.g. mayflies and free-living midges). In contrast, other aquatic primary consumers are protected with heavy armor or sessile life styles and are rarely eaten by gape-limited aquatic predators (Hershey 1987; Power 1987, 1992b). Armored loricariid catfish are the top consumers in two-level food chains in Panamanian streams. They effectively suppress algae across a wide range of
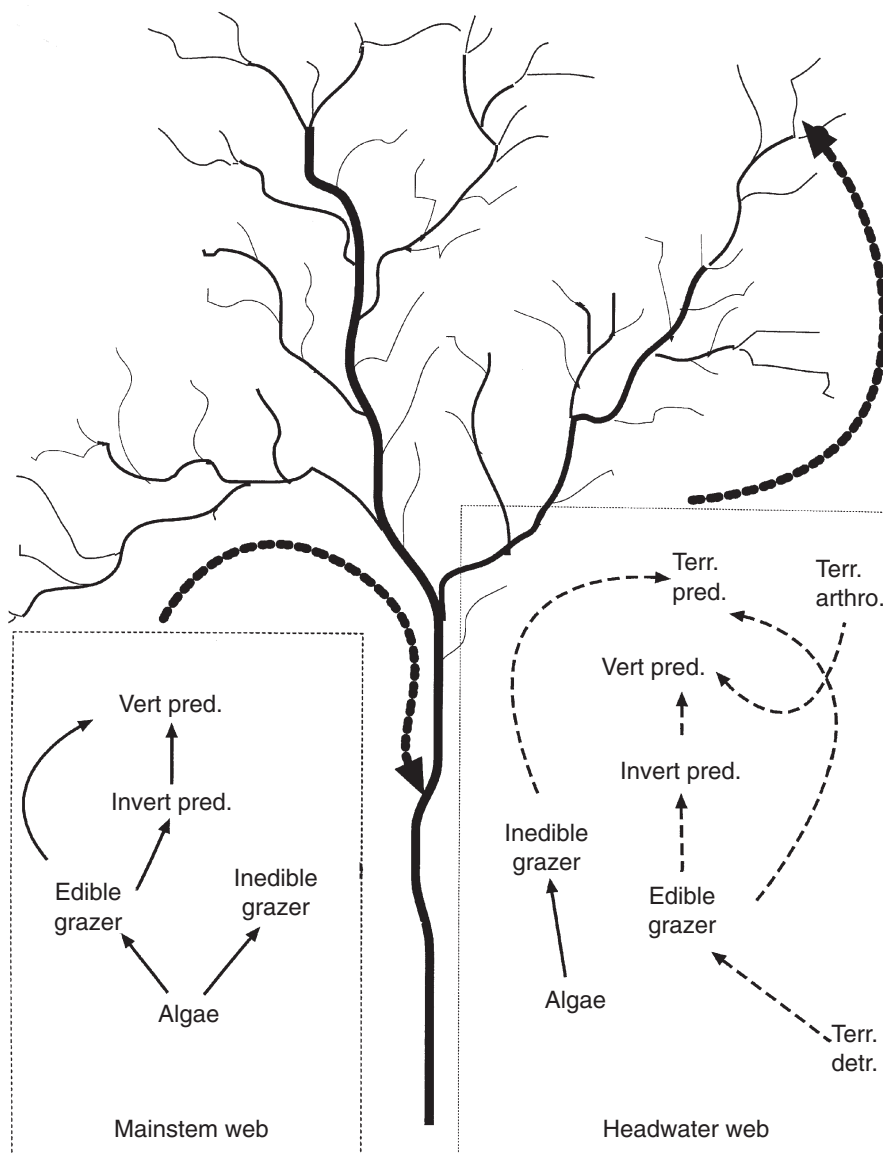
Fig. 1. Food web fragments depicting aggregated functional groups that influence the South Fork Eel food web in headwater (right) and mainstem (left) channels. Solid lines in web diagrams depict linkages that have been demonstrated to limit resource populations under certain environmental conditions. For the mainstem food web, the longer chains dominate after flood disturbance, and the short, two level chain dominates during drought years and during prolonged absence of scouring floods. Dotted lines for the headwater web depict energy flow linkages for which the top-down impacts are still unknown.

primary productivities and seasonal conditions (Power 1983, 1984b, a). In temperate streams, stone cased caddisflies, sessile midges and aquatic lepidopterans that live under silk cases attached to rocks are similarly invulnerable to most predators (Hershey 1987) and also suppress algae, unimpeded by predators (Feminella *et al.* 1989; Power *et al.* 1996). For example, large, armored caddisflies (*Dicosmoecus gilvipes*) are invulnerable to most fish in the upper portions of river networks in the Pacific Northwestern USA (Johansson 1991; Tait *et al.* 1994; Rader 1997). Defended and vulnerable taxa may be functionally distinct at other trophic positions [e.g. edible and inedible algae (Leibold 1989; Carpenter *et al.* 1993; Romo *et al.* 1996)]. It

is in primary consumers, however, that these differences have affected the river food webs that we have studied in temperate and tropical rivers (Power 1983, 1984b; Power 1987; Power *et al.* 1996; Wootton *et al.* 1996; Marks *et al.* 2000). There is increasing general recognition that attributes of intermediate consumers (herbivores and detritivores) may affect energy flow and population regulation in food webs as much as top predators or basal resources (Sinclair & Arcese 1995; Duffy & Hay 1991; Schlapfer & Schmid 1999).

Because of their importance to channel food web structure and dynamics, we focus on grazers, both edible (e.g. naked or mobile) and inedible

(armored or sessile), as we hypothesize about how the key metaphysiological parameters in the Getz (1994) models (Fig. 2) might influence landscape patterns in food webs. We would predict that inedible grazers would be more adept at extracting scant resources (e.g. a sessile or armored scraper would probably leave less residue after grazing a small site than a mobile 'skimmer') and so would have lower half saturation constants, β. The maximum rate of resource uptake at high resource densities, δ, would probably be larger for mobile, edible grazers, by virtue of their better resource tracking [faster conversion of resource pulses to production instead of defense (Fig. 2a)]. The same constraints would make the compensation point κ (uptake rates needed for positive growth) higher for inedible grazers that must allocate to defense in addition to growth and offspring (Fig. 2b). Mobile grazers would have higher population growth at a given uptake rate because of more efficient conversion of intake to production, and also greater absolute potential uptake rates (Fig. 2a).

Aquatic carnivores eat vulnerable aquatic primary consumers, each other and also terrestrial invertebrates that fall into streams. By feeding on vulnerable grazers, aquatic predators may indirectly release algae from herbivory (in a chain with three functional trophic levels), or they may prey on key primary aquatic carnivores, releasing certain herbivores, which then suppress algae, [creating a four level top-down chain (Power 1990b)]. Whether predators are at the third or fourth trophic level positions in the chain that supports them depends on the abundance and activity of primary consumers with predator-specific defenses effective against secondary, but not primary, carnivores (Power 1990a). Completely invulnerable grazers, if abundant, reduce the access of vulnerable prey and, therefore, predators to algal carbon. Such invulnerable grazers are trophic cul de sacs in food webs, reducing energy flow to fishes and other aquatic predators (Tait *et al*. 1994; Parker & Power 1997), and diminishing the top-down control that predators exert in food chains (Power 1995; Wootton *et al*. 1996).

After aquatic insects emerge as flying adults, however, they become potentially vulnerable to terrestrial predators, such as spiders, adult odonates, lizards, birds and bats. Rates of emergence
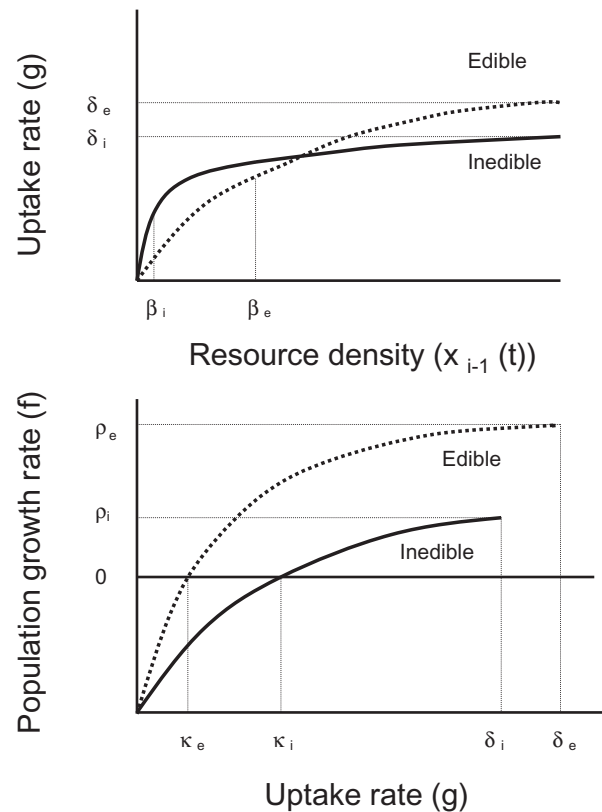

Fig. 2. Possible contrasts in Getzian relationships between resource density, population uptake rate (a) and population growth (b) for edible, 'e' (e.g. naked, mobile) grazers and inedible, 'i' (e.g. sessile or armored) grazers. Less mobile, inedible grazers often scrub local substrates more thoroughly, leaving less residue, so may have lower half saturation constants, β, than mobile edible grazers that may 'skim the cream' when harvesting resources. Because of better resource tracking, edible grazers may have higher maximum rates of resource uptake, δ. Because of allocations to defense, the resource uptake necessary for inedible grazers to achieve positive population growth, K, may be higher (but this would depend on how the costs of defense and costs of locomotion compare in particular systems). Production efficiency δ/K (Getz 1993) should, therefore, be higher for edible grazers, which is frequently observed. The maximum rate of population growth at high resource intake should, therefore, be higher for edible grazers. These trait-based performances may explain, among other things, why armored grazers are (as observed by McNeely, unpubl. data, 2001) abundant in headwater streams of extremely low primary productivity (a potential consequence of their putative low half-saturation constants, β) (modified from Getz 1993).

and lateral diffusion into the watershed of aquatic insects, as well as the ability of various terrestrial predators to track this prey flux, are strongly influenced by the position within drainage networks. Network position affects not only channel habitats, but also geomorphic and vegetative structure and environmental conditions in the riparian zones and upland valley slopes adjacent to the channel (Power & Rainey 2000; Power *et al*. in press). Down drainage networks, disturbance regimes, habitat productivity, habitat structure and size, and edge to area ratios all vary in ways that are partially predictable from general geomorphic relationships (Vannote *et al*. 1980; Montgomery & Buffington 1997; Montgomery 1999). Next we present a very brief overview of what is known about downstream changes in channel environments.

CHANNEL AND WATERSHED ENVIRONMENTS DOWN DRAINAGE NETWORKS

Geomorphologists have made considerable recent progress in explaining and predicting systematic downstream changes in river and watershed environments. Some site-specific features can be predicted at real landscape positions from physical first principles; others must be empirically predicted, and still others simply mapped. Large-scale mapping is more feasible now than it was in the past because of newly available high resolution digital elevation data and the computational power necessary to process these data (Dietrich *et al*. 1993). Discharge, slope, channel hydraulic geometry (Leopold *et al*. 1964), sediment size and transport processes all change systematically downstream. The environmental conditions and habitat structures that they establish depend, as a first approximation, on local channel slope (e.g. Montgomery & Buffington 1997) or on drainage area and local channel slope (Sklar & Dietrich 1998).

Stream drainage networks begin some distance down from the watershed divide, where the downslope flux of water and sediment first cuts a distinct channel head into the hillside. The channel head tends to persist at a given location unless environmental changes in runoff or vegetative cover cause the hillslope position where conditions

cross the threshold for channel initiation to move up or down slope (Dietrich & Dunne 1978; Montgomery & Dietrich 1988). Downstream from the channel head, the upstream limit for production of aquatic organisms begins where surface water is retained long enough for individuals to complete their aquatic life stages. Clearly, this boundary will also change with the precipitation regime and the permeability of the bed and the surrounding watershed (Hynes 1975). As channels collect discharge with downstream increases in their drainage areas, their slopes decrease. These channels widen, deepen and flow faster according to empirical rules of hydraulic geometry that relate channel width, depth and velocity to discharge that scales with drainage area (Leopold *et al*. 1964). As one moves from headwaters through upstream tributaries to mainstems downstream, wider channels and increasing setback of the bordering forest from active channel margins increase sunlight to the streambed. As a result, both stream temperature and algal primary productivity increase. Carbon inputs to rivers shift from allochthonous terrestrial detritus to algal production along this gradient (Vannote *et al*. 1980; Davis-Colley & Quinn 1998). As width : depth ratios increase and slopes decrease, channel habitats change from cascades and stepped pools constrained by coarse bedrock and boulder substrates, to plane bed glides and meandering pools and riffles in middle reach mainstems, to broad channels with floodplains and off-channel water bodies in the lowlands (Montgomery & Buffington 1997). Corresponding to these slope and drainage area-driven changes, bed materials change from boulders and bedrock in headwaters, to cobbles, pebbles and gravel in mid-reaches, to sand and silt near river mouths (Leopold *et al*. 1964; Montgomery & Buffington 1997). Increasingly downstream, the path and form of a river becomes less constrained by resistant rock or vegetation, and more 'the author of its own geometry' (Leopold *et al*. 1964), except where it is engineered (dammed, diked or diverted) by humans.

In headwaters, disturbances related to sediment transport are rare (few or none per millenium), but catastrophic, deriving from debris flow into channels. In upstream tributaries (drainage area $A < 10 \, km^2$), rare superfloods (recurrence intervals >30 years) may transport the boulders making up

most of the bed materials. Transport of finer (sand, gravel, pebble-sized) sediments through these reaches is much more frequent, but because these fine sediments make up a relatively small proportion of the river bed in unimpaired headwaters, fines may not have strong impacts on local biota. In middle reach mainstems, most of the bed materials are smaller cobbles, pebbles and gravels, and floods typically move them several times per year. Here, fine sediments are retained longer and have more devastating effects as disturbance agents (Power & Stewart 1987; Waters 1995; K. B. Suttle et al. unpubl. data, 2001). In lowland floodplain rivers, transport of the fine bed materials (sand and silt) is chronic (Dietrich & Dunne 1978).

Environmental controls on food webs down drainage networks

How do downstream changes in habitat size and structure, disturbance, productivity and temperature affect functional groups and food webs? Superimposing a food web network over a drainage network and predicting its response is a challenging task. As a first step, we will explore three downstream gradients that influence particular trophic linkages in webs: (i) changes in habitat geometry that affect aquatic-terrestrial exchange; (ii) changes in productivity that affect terrestrial and algal carbon sources to different consumers; and (iii) differences in disturbance regimes that mediate the relative dominance of vulnerable and invulnerable primary consumers and, therefore, web connections of predators.

We use field observations and a limited literature review to suggest how selected parameters in equations 1 and 2 may change for key functional groups at different landscape positions, and how these changes affect their influence in food webs. This is a preliminary exploration intended to introduce hypotheses that might be studied more thoroughly and systematically in the future.

Habitat size and river-to-forest export

Obviously, channel habitat size (volume or area) increases downstream. Wide, sunny mainstem channels (A > 100 km²) contain more aquatic predators (e.g. large fish, otters, wading and diving birds and snakes) due, in part, to larger habitat volume. Fish and other large fully aquatic taxa do not usually occur in the steepest headwater reaches with slopes >10%, where habitats are small (A < 1 km²) and sometimes ephemeral. However, food webs in these small headwaters are not predator-free. Salamanders are highly carnivorous (Parker 1991, 1993) and some cannot withstand fish predation; thus, they are restricted to fishless headwaters (Petranka 1983). In general, because edge : area ratios increase upstream, small headwater channels are believed to be more influenced by terrestrial ecosystems. This influence has been considered largely in terms of allocthonous energy inputs into streams from terrestrial detritus (Vannote 1980) or insects (Nakano et al. 1999), but may also pertain to the influence of terrestrial predators on stream prey (Jackson & Fisher 1986; Power & Rainey 2000; Nakano & Murakami 2001; Power et al. in press).

Habitat characteristics of watersheds surrounding steeper tributaries may facilitate some terrestrial predators and impede others. Smyth (cited in Power et al. in press) observed that a dominant riparian spider along the South Fork Eel (S. Fk Eel) and its tributaries, Tetragnatha versicolor, was much denser along the productive mainstem S. Fk Eel. However, spiders had longer diel foraging periods in upstream, darker tributaries [i.e. upstream increases in its parameter p (the proportion of time spent foraging in equation 2)]. Spiders in Elder Creek (A 17 km²) foraged 24 h day⁻¹, while along the S. Fk Eel (A 80–130 km²), they foraged only after dark. Smyth advanced two non-exclusive hypotheses for this shift across habitats during the foraging period. Tetragnathids are particularly vulnerable to desiccation and may have been precluded from foraging along mainstems by day because of wind or heat. Alternatively, they may have been obliged to forage longer to meet their energy requirements in the less productive upstream tributaries. In either case, the behavioral change increases the probability that energy captured by these spiders (which feed almost exclusively on emergent aquatic insects) is transferred up food chains to day-foraging terrestrial birds, reptiles or parasitic flies (A. Smyth in Power et al. in press).

Other predators are constrained by upstream conditions. Sceloporine lizards, which are important predators on spiders and other terrestrial, as

well as aquatic, arthropod prey in sunny downstream cobble bar habitats (Sabo 2000), drop out of headwater tributaries when solar radiation becomes insufficient to support the long activity periods necessary to maintain their growth. Parameter p in equation 2 for these lizards decreases upstream. Declining arthropod abundance and activity upstream (by lowering parameter c) may also affect the position of this distribution threshold in drainage networks. Some insectivorous bats are deterred from headwater hunting because splashing water in these steep reaches interferes with their ultrasonic foraging calls. Bat species that forage primarily over quiet water, lower in the drainage network, move many kilometers downstream for hunting, even if their day roosts are located near headwaters (W. E. Rainey, pers. comm., 2000).

Seasonality may influence the strengths of these cross-habitat trophic linkages. If insects emerge late in the season they may avoid population control from predation by bats, birds, lizards or spiders that have become seasonally inactive or, in the case of some bats and birds have migrated to other habitats. A similar situation may hold for insects in which development is slowed in cool, unproductive portions, high in the drainage networks. Life history differences among functional groups may interact with landscape impacts on development rates to influence taxon- and landscape-specific strengths of cross–habitat food web interactions. Seasonal influences on these cross-habitat trophic fluxes may also differ between the eastern and western coasts of continents. East coast and central continental temperate watersheds experience terrestrial productivity peaks during the late spring and summer, while productivity in small streams in upper watershed positions peaks during early spring and autumn, when leaves have fallen from the trees. Seasonal, reciprocal complementary stream and watershed production coupled with cross-habitat trophic exchange can support higher densities of fish and birds than could be maintained by either habitat alone (Nakano & Murakami 2001). On the western edges of continents under Mediterranean climates, terrestrial and aquatic productivity are seasonally reversed and are less offset than under continental regimes. River productivity is minimal during the scouring, turbid, winter floods and peaks during the summer when the terrestrial productivity is starting to decline due to drying. W. E. Rainey (pers. comm., 2001) has hypothesized that certain Northern California bats, whose October to March hibernation is fuelled by aquatic insect prey captured during the previous summer, may exert time-lagged subsidized predation on terrestrial insect prey when bats emerge in the spring, before river insect populations recover from the scouring, turbid winter floods. Considerable year-to-year variation in rainfall occurs in California and in other Mediterranean regions (Gasith & Resh 1999), however, and multiyear droughts (with no scouring winter floods) can alter the hydrologic regimes experienced by river life and, consequently, food web structure.

The importance of terrestrial predation to the dynamics of aquatic populations has not been well quantified, but may decrease downstream for a number of reasons. Increasing setback of terrestrial vegetation from the stream reduces perches, web sites or cover for terrestrial predators. The aquatic habitat gains volume and structural complexity, offering prey refuges from wading and diving predators. In addition, more aquatic insects should be harvested before they emerge by aquatic predators as these become more abundant, diverse and larger downstream. An exception to this trend may occur when and where channel productivity downstream becomes high enough to support floating mats of aquatic algae or emergent or floating macrophytes. These interfaces serve as food-rich thermal incubators for certain insect taxa and also as partial refuges from fish predation (Power 1990b). They act as 'valves' for river food webs, increasing the rate of aquatic insect production and diverting it from aquatic predators to consumers in terrestrial food webs (Power *et al.* in press).

Productivity and carbon sources

As one moves from headwaters through upstream tributaries to mainstems downstream, more sunlight hits the streambed and stream temperature and algal productivity increase. Carbon sources to river food webs shift from allochthonous detritus to algal production along this gradient (Vannote *et al.* 1980; Davis-Colley & Quinn 1998), but carbon sources to all members of food webs do not change in lockstep.

In a survey of 70 studies of temperate and boreal river food webs, which included his own data from the South Fork Eel and its tributaries, Finlay found that algal carbon signatures became more ^{13}C enriched downstream, while signatures of terrestrial vegetation, detritus and dissolved organic carbon derived from terrestrial sources remained constant (Finlay 2001, p. 1057, Figs 1 and 2). Shredders (primary consumers known to ingest terrestrial leaves) maintained a terrestrial carbon signal over the entire range of the drainage areas (<1–2060 km²). Downstream of small (<10 km²) drainages, all other consumers, scrapers, filter-gatherers, collectors, and invertebrate and vertebrate predators, tended to become isotopically heavier downstream, suggesting that they derived much of their carbon from algae. In small headwaters with drainage areas <10 km², all consumers except scrapers had terrestrial carbon signals. Scrapers, however, had an algal signal as far up into the watershed as they were collected (Finlay 2001, p. 1058, Fig. 4 and pers. comm., 2000). For example, in the S. Fk Eel watershed, Sugar, McKinley and Fox Creeks (drainage areas of 0.6, 1.0 and 2.5 km², respectively), armored scrapers (*Glossosoma penitum*) had an algal carbon signal that was lighter than terrestrial carbon signatures at these headwater sites (Finlay 2001; Finlay *et al*. in press). Predators (steelhead or rainbow trout *Oncorhynchus mykiss* or Pacific giant salamanders *Dicamptodon ensatus*) had terrestrial carbon signatures, as did their prey (vulnerable mayflies, midges, stoneflies, and for the fish, terrestrial invertebrates). These results led McNeely and Finlay (pers. comm., 2000) to hypothesize that depletion of sparse algae by invulnerable *Glossosoma* at these sites reduced access to algal carbon for vulnerable grazers (e.g. heptageniid mayflies, chironomids) and aquatic predators. In Getz's models, lower half saturation coefficients, β, of the *Glossosoma* could allow them to persist at lower resource productivity and deplete algal standing crops below the levels needed to sustain populations of edible grazers. Although inedible grazers are postulated (Fig. 2) to need higher uptake rates to maintain positive population growth, their severe grazing may deplete resources below levels that are mechanically harvestable by edible grazers. Experimental removal of invulnerable grazers might shift upstream the productivity threshold at which algal carbon begins to support both vulnerable primary consumers and predators. Alternatively, if fish were more dependent on terrestrial invertebrates in headwaters than lower in the watershed, removing inedible grazers would have less effect.

McNeely removed all *Glossosoma* (up to several thousand individuals per m²) from replicated whole pool habitats in Fox Creek. Despite the closed forest canopy (<5% open) over this headwater stream, she observed a conspicuous release of algal standing crops dominated by the highly edible diatoms *Melosira* and *Cymbella* following her removal of *Glossosoma* (F. C. McNeely, unpubl. data, 2001). Her experiment suggests that food web interactions may influence energy sources to web members in these upstream habitats. While energy sources influence interaction strength in food webs (Elton 1927; Polis *et al*. 1997), these results remind us that the converse is also true. In general, we need more information on how changing conditions across landscapes differentially influence functionally significant groups in food webs (e.g. vulnerable *vs* invulnerable grazers). Some important differential responses involve the resistance or resilience of such taxa following disturbance.

Disturbance regimes

Disturbance often acts most severely on basal taxa in food webs (e.g. rock bound algae and small invertebrates in rivers) because they are usually less mobile than predators. Organisms at lower trophic levels, while generally more susceptible to disturbance, vary in resilience. Early successional primary consumers are commonly soft-bodied, small and vulnerable to predators, with short generation times and rapid growth rates when the environment is favorable. In rivers, they may be more likely to survive scour than invulnerable prey or producer taxa because they are small enough to seek refuge in pore spaces below or lateral to mobilized layers of the river bed. Small prey species may also survive dewatering in pockets of residual lateral or subsurface water. Such refuges would increase $N(0)$ in equation 1. In addition to this resistance to disturbance, early successional taxa may exhibit greater resilience (greater R in equation 1). Insects with short generation times may be flying above rivers during these disturbances in

'air force reserves' of winged adults (Gray & Fisher 1981), able to recolonize rapidly following the disturbance. In their aquatic larval stages, however, primary consumers with heavy armor or sessile life styles are less mobile and, hence, less able to escape disturbance [lower $N(0)$]. They are also slower to recover afterwards (lower R) because of their allocation to defense rather than to growth or progeny. As time since disturbance passes, however, these invulnerable grazers may increasingly dominate late successional primary consumer guilds because they do not suffer losses to predators and they may also be superior competitors for space and primary production (McAuliffe 1983, 1984; Li & Gregory 1989). For some taxa, traits influencing roles in successional food webs may differ in different life stages. For example, limnephilid caddisflies (which include *Dicosmoecus*) are strong fliers as adults (F.C. McNeely, pers. comm., 2001), but as larvae they grow and develop relatively slowly. In various mainstems of the Eel River (drainage areas from 114 km^2 to 1929 km^2), we have found that invulnerable invertebrate grazers are less resilient to flood scour than vulnerable grazers. During drought years that lack scouring winter floods, or in regulated channels where flood scour is artificially eliminated, densities of armored or sessile grazers increase by up to two orders of magnitude (Power 1992b; Wootton *et al*. 1996). At these densities, invulnerable grazers sequester algal productivity (in Fig. 2a, this would mean that they lower resource density to the point where uptake rates by edible taxa are less than those by inedible taxa). As a consequence, top-down and bottom-up food chains shorten to two trophic levels (Power 1992a, 1995; Power *et al*. 1996; Wootton *et al*. 1996; Parker & Power 1997).

Secondary productivity (co-influenced down river networks by both primary productivity and temperature) may interact with disturbance regimes to strike different balances between vulnerable and invulnerable primary consumers at different network positions. For example, if disturbance regimes are similar in unproductive tributaries and more productive mainstems, recovery of late successional, inedible taxa should be more rapid in productive mainstems where these taxa can garner energy more rapidly. Surveys of food web recovery in the sunny South Fork Eel (A 100–130 km^2) and its less productive tributary, Elder Creek (A 17 km^2) offer preliminary support for this prediction. Following floods that scoured both channels, invulnerable grazers replaced vulnerable taxa as dominants in the primary consumer guild several weeks later in Elder Creek than in the South Fork Eel. This interaction of productivity and disturbance reverses the predictions of the classical single factor hypotheses for productivity and disturbance effects on food chain length, and may be general when food webs reassemble over timescales that permit species succession (Power *et al*. 1996).

Frequency of bed mobilizations typically increases down drainage networks. In larger tributaries and middle reach mainstems, bed scouring floods may move cobbles and gravel substrates several times per year, although flood frequencies drop during natural droughts or because of human regulation of stream flow (Stanford & Ward 1989; Power 1992b). Headwaters (A < 10 km^2), if not dewatered, provide the most stable environments available in river drainages. Sands and gravels are transported through these boulder and bedrock dominated reaches, but affect a relatively small area of the bed. In the Eel River drainage, McNeely has found very high densities (>1000 small individuals per m^2) of the invulnerable armored caddisfly *Glossosoma* in dark headwater channels. This inedible grazer occurs even in the smallest headwaters sampled (e.g. Sugar Creek, drainage area <1 km^2 (Finlay 2000; F.C. McNeely, unpubl. data, 2001). Whether *Glossosoma* populations are maintained in headwaters by adult dispersal, or because local populations are not frequently obliterated by disturbance, remains to be determined.

RIVER DISCONTINUUA AND NETWORK EFFECTS

For 20 years, the river continuum concept (Vannote *et al*. 1980) has been our dominant conceptual framework for river ecosystem structure. This model emphasizes downstream gradients in energy inputs and other variables. Many key habitat features in drainage networks, however, are patchy and abruptly discontinuous, on large (Stanford *et al*. 1988; Stanford & Ward 1989; Montgomery 1999) or small (Townsend 1989; Pringle

et al. 1988) scales. In some cases, structures that retain fine sediments or water translocate downstream conditions to upstream positions. Log jams retain pockets of fine gravels high in tributaries that would otherwise be too steep to retain them and, consequently, extend upstream spawning habitat for salmonids (Abbe & Montgomery 1996). Woody debris dams also provide low flow refuges during high flows for young salmonids and other weakly swimming organisms, allowing them to persist in steeper regions of the network during spates. Pools scoured downstream from large logs can reach the water table after more aggraded channel reaches have dried up. Log jams are less abundant and more ephemeral downstream after mainstem channels become wider than the tallest trees and can no longer retain them. Dams, engineered by humans (Stanford *et al.* 1988) or beavers (Naiman *et al.* 1988), or imposed by landslides also transplant downstream conditions (finer sediments, shallower channel slopes, deep lentic habitats) upstream in drainage networks. The importance of natural and human-engineered 'serial discontinuities' has been pointed out by several authors (Stanford *et al.* 1988; Stanford & Ward 1989; Montgomery 1999), but their general effects on food webs remain poorly known.

Network effects are another source of longitudinal discontinuities. We describe three effects that the hierarchical network structure of river drainages impose on organisms and food webs, which to our knowledge have received little or no attention from stream ecologists. First, the network structure of river drainages creates distinct nodes where tributaries join mainstems and inject pulses of extra water, sediment, organisms or organic matter, ranging from fine particulate matter to large logs. These local loads may create particularly rich environments near the nodal points in mainstems before flows disperse these materials downstream. In the South Fork Eel, there are conspicuous loadings of caddisfly larvae at tributary junctions, where they probably accumulate after drifting down tributaries. Lamprey larvae (*Lampetra tridentata*) aggregate at these junctions, probably tracking enrichments of fine particulate organic matter in the sediments. The foothills yellow legged frog, *Rana boylii*, which is in decline throughout much of its range, maintains traditional oviposition sites at tributary confluences.

Two hypotheses were proposed by Kupferberg (1996) for this pattern. First, adult frogs that overwinter in the tributaries may simply move to the closest mainstem reach to breed. Alternatively, the small deltas that form at these sites from cobble and boulder accumulations are sought out by frogs because they provide areas where changes in mainstem discharge impose less risk of detachment or desiccation to frog egg masses. Deposits of cobbles and boulders from tributaries also accumulate along mainstem shorelines to form cobble-bar habitats providing important cover and thermal environments for riparian lizards (Sabo 2000). *Rana boylii* tadpoles and caddis larvae are important primary consumers in the river food web. Lizards prey on and are subsidized by aquatic insect emergence (Sabo & Power in press a, b). Food web linkages of larval lampreys are still poorly known, but possibly important because of the high abundance of these interstitial detritivores.

A second effect of network structure is to repeatedly juxtapose very different habitats, where small tributaries enter mainstems. At these confluences, the adjacency of habitats with contrasting environmental conditions makes it possible for mobile organisms to exploit widely varying environments. Juxtaposition of productive mainstems and unproductive tributary habitats in river networks sets the stage for 'spillover predation' (Holt 1985; Oksanen 1990), in which predators from the more productive habitat opportunistically take prey from adjacent habitats that would be too unproductive, if isolated, to maintain predator populations (Fig. 3). Spillover predation at confluences might be intensified by the extra enrichment of resources described above. Therefore, being near confluences might lengthen and strengthen top-down food chains in the darker tributaries, with severe adverse impacts on tributary prey that would not be resilient to losses to subsidized mainstem predators. This prediction remains, to our knowledge, untested.

Similar effects can arise when predators (or other web members) need two habitats that provide different essential requirements. For example, where small, dark, steep, narrow tributaries join low gradient, wide, sunny, productive mainstems, foragers such as riparian spiders or salamanders may have access within their foraging ranges to productive
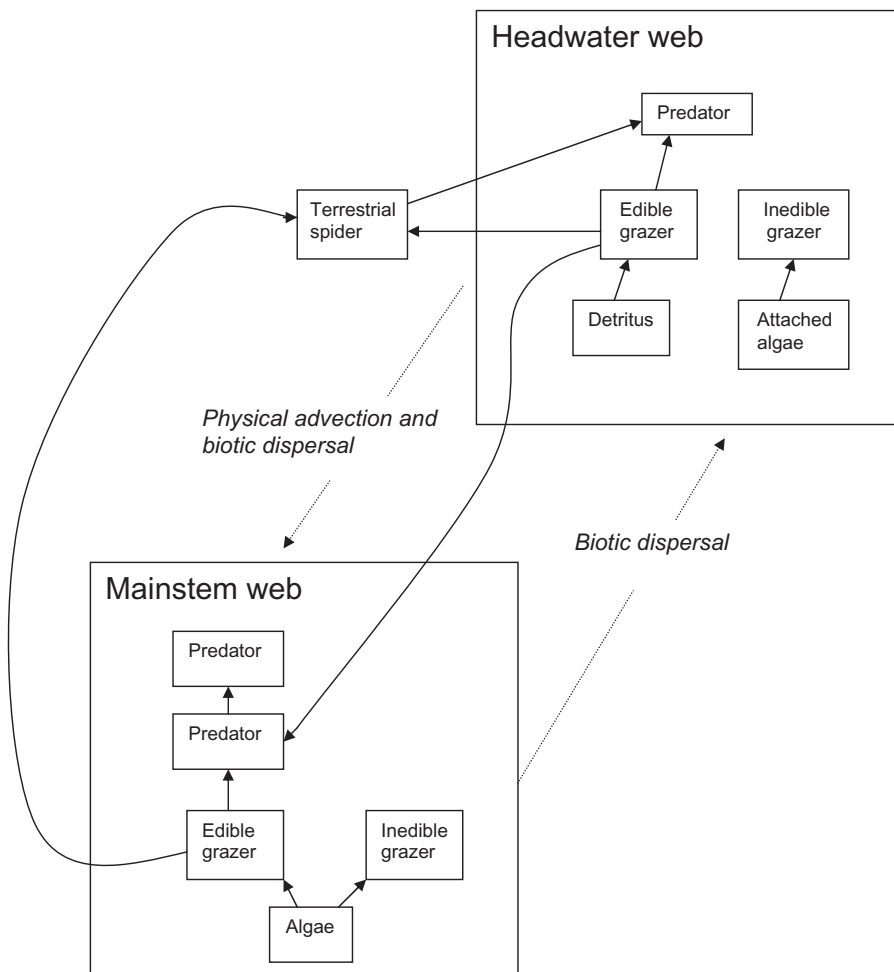
Fig. 3. Simulation models for interactions of, and fluxes between, webs and organisms at network nodes. These models can be parameterized based on trait-based and site-based performances of organisms and on disturbance/recovery regimes representative of the local environments (e.g. unproductive, but less frequently disturbed headwaters, linked to productive, more frequently scoured mainstems). Solid arrows show the direction of energy transfer, dotted arrows depict movements between headwater and mainstem habitats.

habitats where food abounds and to cool unproductive habitats where they can escape desiccating heat and wind. In terms of Getz's metaphysiological parameters, such a population could lower its compensation point κ as individuals take refuge from harsh conditions while resting in headwaters, while raising its resource uptake rate g as individuals foray into more productive mainstem habitats, possibly during times of the day or night when that habitat is more benign. These adjacent conditions may allow a number of organisms to persist and influence food webs in habitats that could not, if isolated, support their populations.

Third, the hierarchical structure of river networks sets up a system of spatially separated, repeating environments that are rarely directly linked. To a mobile organism, the channel network presents a decision tree. Upstream movement will be dispersive, while downstream transport and migration will be concentrative. Individuals or

propagules are diluted among many alternative channels if they move upstream, while they become concentrated if they move downstream. For organisms, this means that within-channel species and genetic diversity may decline upstream (Horwitz 1978; Hughes *et al.* 1995; Schmidt *et al.* 1995), while beta-diversity (variation among channels) increases. These effects probably exert more influence on the population genetics and micro-evolution of fully aquatic organisms such as fish (Turner & Grosse 1980; Turner *et al.* 1984) than on amphibians or aquatic insects in which the adults sometimes disperse over drainage divides (Jackson & Resh 1989; Jackson & Resh 1991). What might this hierarchical structure mean for food web interactions? Headwater channels that subsample mainstem species assemblages should have lower species diversity than mainstems, offset to some degree if habitat specialists occur there and not at lower network positions. Headwater

webs may include populations that are released from competitors, predators or from the parasites that limit them at lower network positions. This release might occur either stochastically because of the upstream dispersive effects of networks or deterministically because the enemy in question cannot tolerate conditions imposed upstream by the longitudinal environmental gradient. These alternatives could be distinguished by transplant experiments, as well as by extensive sampling to compare the composition of assemblages at equivalent headwater positions in the networks. If headwater channel food webs were self-contained compartments, we might expect shorter food chains with stronger top-down effects of taxa at lower trophic levels. As discussed, however, these impacts might be offset by more intimate links with terrestrial ecosystems in headwaters. If terrestrial consumers limit aquatic prey or if terrestrial detritus subsidizes aquatic predators so that they can persist despite inadequate aquatic productivity, food chains would be less likely to shorten upstream.

CONCLUSIONS

We introduced this review by emphasizing that population control chains and energy flow paths are distinct in food webs. We close by revisiting these distinctions in headwaters and lower mainstem channels. Disparities between energy flow paths and population control paths are revealed when the experimental removal of organisms releases 'hidden trophic levels' (Paine 1980). Manipulations in the South Fork Eel watershed have revealed hidden trophic levels in both mainstems and headwaters. In lower mainstems, removal of top predators (larger fish) released guilds of smaller predators (e.g. odonate larvae, fish fry) that had previously been rare and inconspicuous (Power 1990a). In the headwaters, removal of glossosomatid caddisflies from a reach with <5% open canopy released previously inconspicuous colonial diatoms, which grew to substantial biomass (F.C. McNeely, unpubl. data, 2001). Careful observational studies can also detect cases in which biomass does not correspond to potential functional importance in food webs. In a New Hampshire headwater stream, where up to 99% of

the standing crop of organic matter in the channel was terrestrial detritus, a common local caddisfly was inferred, on the basis of gut contents and relative assimilation rates, to be built primarily of algae (Mayer & Likens 1987). Isotopic patterns suggest that scrapers are built of algae as far up in the drainage networks as they can be collected, and even where algal accrual on rocks is undetectable (Finlay 2000, 2001). Clearly, standing crops of this rapidly growing, rapidly depleted resource do not reveal its importance as an energy base in some headwater streams.

We speculate, however, that the relationship between biomass and food web impact may be stronger in headwaters than in lower channels for animals, particularly for mobile taxa. This may be true for at least four reasons:

1 *Space*. First and simplest, habitat volumes are smaller, so the same biomass of organisms represents a higher density in headwaters than in lower reaches. At the same absolute biomass, interactions among mobile individuals in headwaters should be more frequent on a per capita basis, unless cooler temperatures or different habitat structure greatly reduce their activity or encounters.
2 *Time*. Residence times of individuals in a given reach are likely to be longer in headwaters, where upstream dispersal is curtailed and downstream washout during bed scour is rare. If organisms in lower mainstems are more transient, they would be more likely to derive their sustenance and translocate nutrients outside the local habitat, weakening their local impacts. In contrast, nutrient translocation or subsidized predation impacts could be locally strong where topography (deep pools, waterfalls etc.) creates temporary holding areas or barriers for migrant fishes or other dispersing organisms.
3 *Energy*. Because headwater habitats are less productive, food extraction and nutrient excretion by individual organisms should have greater per biomass effects on local energy flow and material cycling. These effects would be enhanced in headwater channels with vegetative or geomorphic structures that increased retention of materials or organisms (Meyer *et al*. 1988; Palmer *et al*. 1996). In productive downstream habitats, where biomass turnover could be faster,

organisms with low biomass may play stronger dynamic roles in food webs than in less productive headwaters.

4 *Chance assembly and shorter food chains*. Because upstream movements disperse and separate organisms, headwaters may contain subsets of mainstem species assemblages in which certain populations are released from competitors, predators or parasites that limit them at lower network positions. These releases would be more likely for taxa at low or intermediate trophic levels (e.g. primary consumers) because predators require their prey for persistence (Holt 1996), and in size structured aquatic food webs they are less likely to be physically accommodated as habitat volumes shrink upstream. Therefore, relatively high primary consumer densities in headwaters probably indicate two-level, rather than four-level food chains, with these grazers exerting top-down control on their preferred resources.

These observations together suggest that energy flow, biomass and interaction strength might be more directly related in headwater food webs than in lower watershed positions, at least for consumer populations. This prediction might be tested initially by staging population or guild removal experiments at upstream and downstream watershed positions, to compare per capita or per biomass impacts on other web members, or other ecosystem properties of interest. To explore the topic more deeply, we would have to learn more than we currently know about the dispersal and foraging ranges of organisms in rivers and watersheds, as well as the spatial and temporal scales of fluxes of their resources. Tracers (stable isotopes, trace elements, exotic contaminants or genetic markers) coupled with experiments will increasingly reveal the spatial scales of food webs that influence energy pathways, population limiting chains and their relationship in food webs (e.g. Finlay *et al*. 1999; Power & Rainey 2000; Finlay *et al*. in press).

Habitat structure and environmental conditions in drainage networks are partially predictable from controls on geomorphic processes by local gradient and drainage areas, as well as aspect, climate, land use and geologic parent material. These general landscape relationships could be used in compara-

tive studies to reveal the general effects of spatial heterogeneity on food web interactions and the resource flow paths affecting them. Mensurative and manipulative experiments that examine species performances and interactions at different drainage network positions, and relate these to habitat structure, disturbance, productivity or other systematically varying conditions, should provide general insights into the relationships between biomass and energy flow and interaction strengths. What are the potential intrinsic growth rates of organisms if they are not resource limited at various landscape positions? Will *in situ* food webs change when basal resources are experimentally augmented? Where will consumer manipulations have strong effects? How are species interactions influenced by resource fluxes and, conversely, where, when and how do species interactions affect the flow paths of resources and their capture by particular web members? Certain mobile organisms with wide environmental tolerances (or life history stages that use different habitats) may experience river food webs as network based. These organisms could sample the range of resources and conditions offered throughout much of the system, choosing the best available at any given time. By behavioral 'ideal free' responses (Fretwell & Lucas 1970; Power 1984b; Oksanen *et al*. 1995), they could track and damp out local resource pulses as these arose. Other less mobile or tolerant organisms could be thought of as network-controlled. Their distributions or the source areas of their resources might be locally restricted because of drainage network features that restrict their percolation through the system (e.g. waterfalls that block fish movements or predator or warm water barriers in mainstems that preclude the dispersal of headwater species from one tributary to another). More tracking and tracer studies are necessary to ascertain where along this continuum particular taxa fall. We suggest that synthesizing LaGrangian tracer studies with Eulerian manipulative experiments in comparative studies of food webs at different drainage network positions and at similar network positions across landscapes will add useful realism to our understanding of the links between energy flow and interactions in food webs and landscape heterogeneity. Progress along these lines should reveal new principles linking food web energetics and

dynamics to the nested scales of heterogeneity in landscapes that constrain both.

ACKNOWLEDGEMENTS

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