

CONTROLS ON FOOD WEBS IN GRAVEL-BEDDED RIVERS: THE IMPORTANCE OF THE GRAVEL-BED HABITAT TO TROPHIC DYNAMICS

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1. INTRODUCTION

Gravel-bedded river habitats are notorious for their spatial heterogeneity and dramatic, rapid fluctuations. This physical environment exerts strong control on river biota, but the effects can be indirect, and mediated through webs of complex interactions. The performances of river organisms under particular environmental conditions, and their consequent impacts on communities or ecosystems, will depend on the evolved characteristics of the biota, the timing of events relative to their life histories and seasonal phenologies, and the states of the physical environments, food webs and ecosystems in which they are embedded. Feedbacks between organisms, environment, and ecosystems occur over a wide range of temporal and spatial scales. Responses of organisms and systems to change are usually non-linear, and often depend on the spatial and temporal context of the interaction. Spatial scales over which dynamically important influences and consequences arise are proving larger than ecologists had previously anticipated (Polis *et al.*, 2000, Chadwick *et al.*, 1999). Finally, many dynamic entities interact. Gravel-bedded river ecosystems include organic detritus, microbes, algae, fungi, vascular and non-vascular plants, invertebrates, and vertebrates comprising a multitude of species, life history stages, and functional groups. Moreover, the physical environment of gravel-bedded rivers is dynamic. Substrate particles, bedforms, channel morphologies, and longitudinal and network linkages in these rivers can change more frequently

and more rapidly than comparable physical features in other (terrestrial, marine, or lentic) habitats.

Food web models provide one conceptual framework for organizing our efforts to understand this complexity. Food webs have been analyzed for their static properties (species richness and trophic connectance as inferred from descriptions in the literature (Cohen *et al.*, 1990; Pimm, 1980, Briand and Cohen, 1989). For predicting population or ecosystem responses to change, however, it is more useful to focus on the dynamic interactions that are likely to affect factors or entities of concern (Paine, 1980). In particular, we want to understand the strong chains of interactions, or “food chains”, that dynamically link predators, primary consumers (herbivores and detritivores), and primary producers and decomposers. Food chains have directionality that matters. “Top down” or “functionally important” food chains link higher to lower trophic positions, connecting species or functional groups of organisms that potentially limit the abundance of their prey or resources, if unchecked themselves by predation or grazing. When such chains of strong interactions link predators through herbivores to plants or algae, they determine much about the physical structure and function of any ecological community. For example, the parity of food chains is argued to determine whether the world looks “green” (chains with odd numbers of trophic levels, e.g. plants alone, or predators protecting plants from herbivores) or “barren” (chains with even numbers, with grazers as top consumers, or with grazers protected by predators of predators) (Fretwell, 1977, Oksanen *et al.*, 1981). “Bottom up” or “energy flow” food chains indicate flow paths of energy or materials (nutrients, contaminants) through food webs. These pathways of trophic transfer reveal sources of the energy and nutrients that sustain organisms. They can differ in length, however, from top-down, population-limiting food chains, even if these involve the same web members (Power, 1990; Power *et al.*, 1996)). Also, as environments change, so can the strength of chains through food webs, even without a change in the web's assemblage of species (Power *et al.*, 1996, Wootton *et al.*, 1996)).

Below, I first describe general constraints on life in water that influence aquatic food webs. Then I review some additional challenges that affect food webs in gravel-bedded rivers. Before exploring the food-web or ecosystem responses to river conditions, however, I will briefly sketch how a sedentary generic population might respond to disturbance regimes characteristic of gravel-bedded rivers. Disturbance regimes, determined by the hydrology and geomorphology of gravel-bedded rivers, and the rate of biotic recovery between episodes of disturbance set by resource supply rates, constrain and shape trophic dynamics in rivers. While physical disturbance in gravel-bedded rivers exerts immediate, first order control on biota, the food webs that re-assemble between episodic disturbances reflect biotic interactions constrained by environmental conditions during stable base flows. These interactions develop over time

intervals set by the disturbance regime, and determine how much of the energy assimilated by the river food web is sequestered at higher, versus lower, trophic positions in food webs.

2. LIFE IN WATER: AQUATIC PRODUCERS, CONSUMERS, AND INVERTED PYRAMIDS OF TROPHIC LEVEL BIOMASS

Water is more viscous than air, so aquatic primary producers float, or if attached, are buoyed by the water column. Unlike terrestrial plants, they do not need rigid, cellulose or lignin-rich stems to reach the light. Aquatic producers also benefit from high surface to volume ratios, which facilitate absorption of dissolved nutrients, as well as inorganic carbon, which diffuses more slowly through water than air. Consequently, primary producers at the base of aquatic food webs (which are predominantly algae and cyanobacteria) tend to be small (10-100 μm in diameter). Water viscosity constrains mobile aquatic predators in the opposite way. Most aquatic predators lack hydrodynamically cumbersome grasping appendages with which to dismember prey, so they are gape-limited, consuming only prey that fit into their mouths. Therefore, aquatic food webs are more hierarchically size-structured than terrestrial webs, with larger organisms at higher trophic positions (with the exception of parasites and pathogens).

Longevity and generation time increase with body size, and therefore, in aquatic food webs, with trophic position. At the base of the food chain, actively growing algae have extremely short generation times, on the order of days. Algorous midges and mayflies, with generation times of weeks to months, are eaten by predatory prawns, crayfish, or nymphal predatory insects (e.g., stoneflies, dragonflies, damselflies), with generation times of months to years. These small predators are in turn consumed by fishes and other vertebrates, with generation times of years to decades. These patterns can lead to inverted pyramids of trophic level biomass rarely seen in terrestrial food webs (Elton, 1927), in which a small, sometimes nearly unobservable biomass of algae and microbes with rapid turnover rates supports a moderate biomass of invertebrates, which supports an equal or even larger biomass of longer-lived vertebrate predators. In general, aquatic ecosystems with strongly inverted trophic level biomass and long functional food chains have characteristics appealing to humans: clear water, inconspicuous algal growths, and abundant large fish, bird, and mammal predators, including human fishers. Food webs with inverted pyramids of trophic level biomass perform two "ecosystem services" (*sensu* Dailey, 1994). They sustain the production of desirable high trophic level vertebrates (salmon, eels, eagles). These in turn may suppress organisms at

lower trophic levels which, if left unchecked, can produce nuisance or even health-jeopardizing conditions (eutrophication, insect pest outbreaks).

The distribution of trophic level biomass in aquatic food webs does not always remain satisfactorily inverted, however. If water bodies receive more nutrients than their food webs can assimilate, or if they lack conditions or habitat structures required by key consumers or predators, these habitats can develop “bottom heavy” food webs characterized by blooms of undesirable algae and invertebrates tolerant of eutrophic conditions. Such webs support few or no top predators.

Natural disturbance regimes can contribute to the maintenance of inverted trophic pyramids. Disturbance (defined by ecologists as a discrete event that kills or removes organisms, freeing resources and space (Sousa, 1984)) can foster predator-dominated food webs for two reasons. First, organisms at lower trophic levels are less mobile, and hence more vulnerable than top predators to mortality during disturbance. Second, the plants and herbivores that first recolonize emptied habitats tend to be fast-dispersing, fast-growing species that are more vulnerable to predators, and of higher food quality, than the organisms that tend to dominate food webs later, after long disturbance-free periods (Power *et al.*, 1996; Wootton *et al.*, 1996). In rivers, the disturbances that reset and rejuvenate food webs are typically related to large changes in discharge.

3. LIFE IN RUNNING WATER: DISCHARGE FLUCTUATION AND SCOURING FLOODS

Periodically, most rivers experience rapidly fluctuating discharge. Increasing river discharge expands the habitat, connects formerly isolated sub-habitats (e.g. off-river water bodies, channel reaches isolated by subgravel flow), and abruptly alters physical gradients and resource availability. When discharge rises above a certain threshold (typically bankfull in gravel-bedded rivers (Henderson, 1966)), sediment transport is initiated. Life in gravel-bedded rivers is severely disrupted by episodic bed-mobilizing floods that dislodge, crush, bury or export organisms, causing huge mortality. After flood waters subside and the bed comes to rest, surviving organisms and recolonists build back their populations during a period of biotic recovery called succession. The duration of stable low flow periods between floods and the productivity of biota during these inter-flood intervals affect both the amount of biomass that accrues (Figure 1) and the trophic structures that develop.

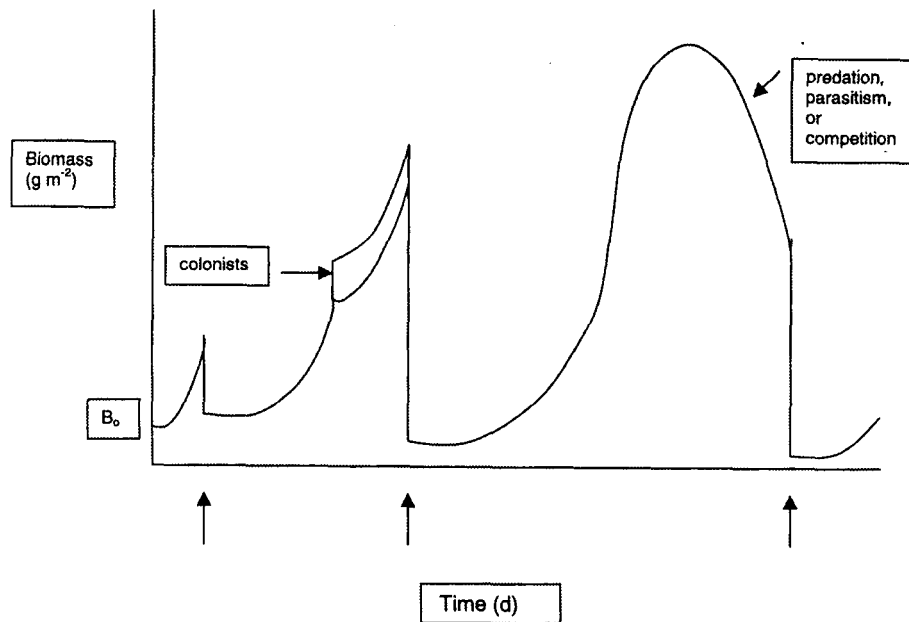


Figure 1. Biomass changes of a population of small, relatively immobile stream organisms following floods (indicated by arrows). Different severities of floods reset biomass to different levels ($B_{0,s}$). The biomass of the population recovering from this residue is augmented by colonists following the second flood. Following the third flood, recovery proceeds to the point at which biological interactions (either intraspecific competition, or interspecific competition, predation, or parasitism) start to limit the population.

The microbes, fungi, algae, plants, invertebrates and vertebrates that make up river food webs have widely different life histories, hence vulnerabilities and responses to flood scour. Evolved traits affect their resistance to disturbance and their resilience and interactions during succession during intervening periods of stable low flow. Because organisms at different trophic positions are reset to different degrees by floods, and recover at different rates, food web control shifts over the course of succession, so that a given population may be primarily resource-limited early in succession, and predator-limited later, or vice versa. Biotic interactions, adverse or beneficial, direct or indirect, can be crucial even (perhaps especially) when recovering populations are initially sparse. The

physical structure of the gravel-bedded river has a huge effect in mediating these interactions. To set the stage, let us first imagine how the gravel-bedded habitat should influence dynamics of individual populations of stream organisms, if these were supported by resource fluxes but otherwise untrammelled by biotic interactions.

3.1 Recovery of river populations following bed scouring floods

Consider first the basic biomass dynamics of a population of small, relatively immobile organisms in a gravel-bedded river subject to periodic flooding (Figure 1). We will scale time with respect to the last bed scouring flood (similar arguments would apply to de-watering episodes), and envision the spatial domain as a small point area (a few cm^2) on the bed surface. Biomass at time t (B_t) increases (initially assume exponentially) until it is reset by flood scour, which kills or removes individuals and exports biomass. The peak amount of biomass accrued before the next disturbance depends on B_0 , the residual biomass remaining immediately after the last scouring flood; t , the time elapsed since this disturbance; and r , the rate of exponential recovery. B_0 can serve to define the severity of the disturbance (from the point of view of this population). For a given bed-mobilizing discharge, habitat features such as channel morphology and sediment size distribution on the bed and in transport would affect scour intensity. Attributes of the biota (resistance to abrasion, dislodgement, or crushing) would also influence B_0 . The time since the last scouring flood, t , would depend on extrinsic factors affecting discharge (timing of precipitation, snow melt, dam releases, etc.), subject to some internal feedbacks (e.g., accrual of riparian trees or sedges that reduce channel conveyance and alter the critical shear stress necessary to move bed particles). During the post-flood recovery, the exponential rate of biomass accrual, r , would depend on the flux of nutrients and photons available to plants or algae, or the food flux available to consumers, and the proportion of these resources converted to production (the elaboration of new biomass). Conversion efficiency (grams consumer biomass produced per gram food ingested) increases with food quality (e.g., the stoichiometric correspondence of food C:N:P ratios to those of consumers) and also under benign environmental conditions that allow organisms to spend less energy on repair or homeostasis, and more on somatic growth or reproduction.

Population recovery may be more complex, for example if populations of local survivors are boosted by colonists (Figure 1, second inter-flood interval). Mobile taxa seek refuge during bed mobilization in stable subsurface layers, if they can burrow vertically into hyporheic gravels with water-filled, oxygenated pore spaces (e.g., Holomuzki and Biggs, 2000). Laterally, off-channel water bodies or tributaries, as well as patches of substrate or bankside habitats immobilized by boulders or bedrock, large woody debris, or living vegetation,

may also provide refuges. Refuges also preserve relatively immobile organisms, which subsequently can drift to recolonize disturbed sites. Diatom accrual after floods may accelerate downstream as local recovery is augmented by colonists from upstream (Peterson, 1996). Aquatic insects also recover from floods in desert streams via “air force reserves” of winged adults that oviposit into denuded habitats (Gray and Fisher, 1981). Exponential growth rates, r_c , of such immigrants may differ from those of the local survivors, if, for example, they are less damaged, or in different life history stages.

Population recovery may not be a simple exponential function of time if some organisms grow linearly (e.g. chains of filamentous algae), or if population density affects the efficiency of acquisition and use of resources supplied in rivers. For example, a taller mesh of attached algae projecting high into the flow would intercept and retain more of the nutrients in the river water column than would a thin skin within the substrate boundary layer. Per biomass growth could therefore accelerate initially, but after a certain biomass, this algal assemblage could start to self-shade, or develop enough form drag to slough (Pringle *et al.*, 1988, Biggs, 1996, Power and Stewart, 1987). Therefore, per biomass growth rates might commonly accelerate as sparse populations build up initially, then decelerate as densities reach self-limiting levels (“carrying capacities”).

Populations may be regulated or limited not only by competition with conspecifics, but also by other species limited by space or other shared resources. In addition, as populations become dense, they tend to attract and support predators, parasites, or pathogens. Possible effects of adverse biotic interactions on our focal population are depicted in Figure 1 during third inter-flood interval. How does the gravel-bedded habitat affect when, over the course of succession, these inter-specific interactions start to influence food webs?

4. FOOD WEB INTERACTIONS BETWEEN FLOODS

4.1 Early succession: one functional trophic level

As previously described, organisms at lower trophic levels suffer more mortality during disturbance because they are more immobile and less able to seek refuge than predators. Nonetheless, basal organisms (e.g. primary producers) enjoy a window of time after floods in which they are released from predation, because surviving predators are displaced and diluted at higher river discharges. If the basal taxa are largely primary producers, the food chain can be said to have only one functional trophic level. Of the basal taxa, primary producers typically recover from disturbance first, because 1) they fix their own carbon and don't have to wait for a prey base to develop (Holt, 1996); 2) they have shorter generation times; and 3) they include scour-resistant taxa like certain adnate

(low profile) algae (Biggs, 1995; Biggs, 1996), which persist after floods, particularly where sheltered by small surface irregularities or micro-fissures on surfaces of rocks. Sand stored in gravel-bedded rivers strongly reduces algal survival during floods, as it scours cells out of these small refuges during transport (Power and Stewart, 1987). Some algae may survive even this, however, as do partially endolithic cyanobacteria (Oscillatoriales) in a south-central Oklahoma stream, which color the limestone bedrock blue-green within a few days following scouring floods (Power and Stewart, 1987). Recently scoured bedrock, boulder, and larger cobbles may not be even slippery to the touch, but adnate diatoms, bluegreen algae, and adhesive basal cells of green filamentous algae persist to regrow vegetatively. (Smaller cobble, pebble, and gravel substrates typically lack algal residues after transport, and must be reseeded by propagules (spores or fragments capable of attachment and growth) (Biggs, 1996; Stevenson, 1990; Power and Stewart, 1987; Power, 1990, 1992), which are only available intermittently.) Following scouring winter floods in the Eel River of north coastal California, algal turfs several meters long regrow by late spring on boulders and bedrock substrates. Cobble, pebble and gravel substrates remain relatively barren, however, until seeded by late summer reproduction of the dominant green macroalga, *Cladophora glomerata* (Power, 1992).

4.2 Middle succession: maximal food chain length

The adnate algae that survive scour are susceptible to shading or nutrient limitation as taller algae accrue. As competition intensifies, some diatoms grow up into the water column, on gelatinous stalks (*Gomphonema*) or as tall upright cells (*Synedra*) or colonial chains (*Melosira*). As they grow up above the substrate, these highly palatable and nutritious cells become increasingly vulnerable to grazers. Grazing intensity increases as flood waters recede and animal populations recover and concentrate.

As flows clear and the water warms up, algal growth may still outstrip losses to grazers, so that large biomasses of macroalgae accrue in sunlit rivers with sufficient nutrients. *Cladophora glomerata* is a dominant filamentous green macroalga common worldwide in sunny, clear-flowing gravel-bedded temperate rivers (Whitton, 1970). Its rough walls provide good attachment sites for epiphytic diatoms (e.g. *Cocconeis*, *Epithemia*, *Gomphonema*), which can grow so thickly that their biomass exceeds that of the host alga. Epiphytic diatoms block access of their hosts to light and nutrients, they may puncture cell walls exposing hosts to fungal or bacterial infection (Stevenson and Stoermer, 1982), and they greatly increase the palatability of host algae to grazers. If grazers are delicate (e.g. mayfly nymphs), they may benefit host algae by cleaning them of epiphytes (Dudley, 1992, Bronmark, 1989). Larger grazers like tadpoles or

algivorous minnows consume hosts along with their epiphytes (Kupferberg, Marks *et al.*, 1994, Power and Matthews, 1983). For either type of grazer, the proliferation of epiphyte-hosting macrophytic algae increases the energy-producing surface area in rivers by many orders of magnitude (Stevenson and Stoermer, 1982).

With the exception of adult algivorous fish, most primary consumers (of algae and detritus) in streams are larval aquatic insects, crustacea, molluscs, and anuran tadpoles that are susceptible to scour mortality. Some of these organisms can survive scouring floods in protected microhabitats, but they require larger refuges than the micro-fissures or surface irregularities of rocks that can protect adnate algal cells 2-3 orders of magnitude smaller. Invertebrates find some refuge from scour (as well as de-watering (Boulton, 1989) and predation (Brusven and Rose, 1981) in water-filled pores in the stable hyporheos below the layers of gravel that move during transport. Infilling of these pore spaces by fine sediments therefore greatly increases invertebrate mortality during and between floods. Scour-resistant vegetation (e.g. sedge tussocks, well-anchored riparian trees), large woody debris, or protective channel features such as bedrock formations also offer refuge either directly or by securing stable patches of surface substrates.

Despite some survival in high flow refuges, flood-induced mortality and export of invertebrates (as well as young, weakly swimming life stages of fish (Harvey, 1987)) can be enormous. Much insect recovery in rivers following floods occurs through recolonization by dispersing, reproductive adults (Gray and Fisher, 1981). In Mediterranean streams in which seasonality of bed scour, or de-watering, is relatively predictable, life histories of animals may be timed adaptively (Gasith and Resh, 1999) to minimize exposure of the more vulnerable life stages to stress. In rivers where flood timing is less predictable, asynchronous generations of species ensure a more constant "air force reserve" of winged adults to repopulate streams after scour or de-watering (Gray and Fisher, 1981; Fisher, 1983).

As animal densities increase following floods (because of both population recovery and habitat contraction), the early successional life stages and taxa of insects are often more vulnerable to predation than those that predominate later, after prolonged stable low flow. This is because the early successional invertebrate assemblages are dominated by fast growing, rapidly dispersing taxa that tend to be mobile and naked, or only lightly armoured with chitin. There is also an ontogenetic factor: young instar larvae and juvenile vertebrates are often more vulnerable than older, larger, harder individuals to predators. In river systems in which insects dominate the primary consumer guild, it can be argued that food chain length (in the top down sense) changes from one trophic level (as algae recover from floods before animal densities build up) to longer food chains in which predators can suppress primary consumers which, if left

unchecked, could suppress algae. These food chains can have three or four trophic levels, depending on whether they include potentially important primary consumers that have defenses effective against top, but not intermediate predators (Power, 1990; Power *et al.*, 1996). As the low flow period continues, however, food chains can shorten again, due to the waxing prominence of defended taxa at lower trophic levels.

4.3 Late succession: shortened food chains

The absence of winter floods in northern California rivers (during drought or in artificially regulated channels), can shorten food chains by allowing the second trophic level to become dominated by predator-resistant grazers. Large armored caddisflies (*Dicosmoecus gilvipes*) have summer densities of ca. 1 individual m⁻² following flood years, but increase to ca. 90 individuals m⁻² during drought (Wootton *et al.*, 1996). At these higher densities, the predator-resistant caddisflies dominate two-level algal based food chains in the rivers, rendering fish predation functionally irrelevant with respect to trophic limitation of algal biomass. In other streams outside the biogeographic range of *Dicosmoecus*, sessile grazers like *Petrophila* can dominate the grazer guild of regulated rivers. Because these late successional organisms allocate to defense against predators (carrying around heavy armor, or adopting a sessile life under a silken retreat attached to the substrate), they are slower to build up biomass after a physical disturbance like flood scour. Once they do, however, they seem relatively resistant to biotic pressures of competition or predation (Power *et al.*, unpublished data).

Similar successional changes can occur at the first trophic level. If grazing invertebrates, tadpoles, or fish selectively deplete higher profile diatoms, or green algae that are covered with diatoms (Power, 1983; Kupferberg *et al.*, 1994), less palatable or vulnerable algal taxa will start to predominate. The types of grazer resistant algae will depend importantly on light, thermal and nutrient regimes (Biggs *et al.*, 1998), and on whether the dominant grazers are small (invertebrates), or large (algivorous fishes). Under intense, chronic fish grazing, adnate diatoms on rock surfaces persist (on Central or South American streams (Power and Matthews, 1983; Flecker, 1992, 1996), or are replaced by felts of adnate cyanobacteria. In Ozark streams in the Central USA, for example, chronically grazed gravel substrates are covered with black, adnate felts of the cyanobacterium *Calothrix*. This alga, like others in the order Rivulariales, has basal growth (only 5-6 cells extending only 10s of μm above a basal nitrogen-fixing cell (heterocyst) divide (B.A. Whitton, pers. comm.). With this functional morphology, *Calothrix* can withstand heavy chronic grazing in a manner analogous to grass (Power *et al.*, 1988). When experimentally released from grazing, these cyanobacterial felts became overgrown within weeks by thick

turfs of the filamentous colonial diatom, *Melosira*, which in turn were stripped bare within minutes of exposure to schools of the grazing minnow *Campostoma*.

In other systems, algal succession without grazer gleanings can drive food chain collapse. Heavy epiphyte burdens can, after months of stable flow, cause macroalgae like *Cladophora* to senesce, detach from the substrate, and float as mats that accumulate in slack-water areas of rivers, or hang up around emergent boulders. At this point, senescent attached and floating *Cladophora* become additionally overgrown by loosely attached or floating mats of cyanobacteria (*Nostoc*, *Anabaena*) and green algae (Zygnematales). Warm water Zygnematales produce copious extracellular mucous, which protects them against the diatom epiphytes. Mucous production allocates resources from growth, so may account for the delay, following flood scour in sunny northern California rivers and prairie margin streams of the US mid-west, in the appearance of these taxa (*Mougeotia*, *Spirogyra*) (Power, personal observations, Power and Stewart, 1987). Such an allocation would illustrate the often inferred life history trade-off of slower growth for less vulnerability to consumers in later successional species (as contrasted with fast growth but vulnerability to consumers in early successional species). Such trade-offs among producers, and in some gravel-bedded rivers, among primary consumers, would cause periodic flood disturbances to rejuvenate food webs supporting predators. This is a third argument (in addition to cleaning and replenishing spawning gravels, and flushing non-native species downstream) for managing North American salmon-bearing streams with periodic flushing flows.

4.4 River morphology and spatial controls on river food chains

Spatial heterogeneity, as well as temporal fluctuations, determine the ability of consumers to track and suppress algae, or of predators to track and suppress grazers. In gravel-bedded streams of central Panama, armoured catfish (Loricariidae) are the dominant algae grazers. With their dermal plates, formidable spines, and large body size, these grazers can outgrow gape-limited swimming predators in these relatively small ($DA = < 200 \text{ km}^2$) streams. Loricariids consequently could track algal productivity extremely closely on a pool-to-pool scale over tens of kilometres, despite enormous variation in the local growth rates of algae due to heterogeneous shading by forest canopy. Where algae grew 16x faster in sunnier pools, these grazers were ca. 16 x denser, both in numbers and in biomass, because on average the species and size class composition of loricariids were similar in sunny, dark, and half-shaded pools. Consequently, algal standing crops were indistinguishable over this light gradient, until substrates were experimentally placed in positions unavailable to grazers (Power, 1984). Within pools, however, catfish could not track algal productivity over the entire depth gradient, because they were vulnerable to

fishing birds (and other raptorial predators that are not gape limited) in areas less than 20 cm deep (Power *et al.*, 1989). Birds fish most frequently and effectively in water < 20 cm deep (Power, 1984), where there is insufficient warning between the bird's surface splash and its strike for fish to escape (Kramer *et al.*, 1983). In Panama (and in prairie rivers where grazing minnows are important algivores), "bath tub rings" of higher algal standing crops appear from the water's edge down to approximately the 20 cm depth contour (Power, 1984). Channel cross-sections during base flow discharges will determine how much substrate area will be protected from these grazers, and where higher algal standing crops will accrue to enhance annual energy budgets of the stream food web, and to provide food and cover useful for smaller organisms, including young-of-the-year fishes, larval amphibians and invertebrates, which are less vulnerable to birds than to predatory fishes in deeper water (Power, 1987).

The pool-to-pool tracking of algae by armoured catfish in Panama was not achieved by *Campostoma anomalum*, algivorous minnows that are the predominant grazers in prairie streams of Oklahoma. *Campostoma* are thin, soft fish that remain vulnerable to predatory fish (e.g., bass) throughout their lives. Where schools of these grazing minnows occur, stream substrates are denuded of algae, and harbour very scant adnate diatoms and bluegreen algae, many of these regenerating from *Campostoma* feces (Power and Matthews, 1983). Other, often adjacent pools lack *Campostoma* and contain bass, and luxuriant standing crops of attached algae (dominated by *Rhizoclonium*, a close relative of *Cladophora*). Experimental transfers of bass into *Campostoma* pools, and of *Campostoma* into bass pools after predator removal, changed the algal standing crops from barren to luxuriant and vice versa within five weeks (Power *et al.*, 1985). Natural floods that rearranged bass and minnows among pools were followed by the predicted changes in algal biomass.

River morphology that influences riffle depth or pool-riffle differentiation during base flow will determine the degree to which prey and larger predatory fish are periodically isolated by long shallow riffles. One might predict that in larger gravel-bedded rivers with deeper riffles, bass (or other large predators) would have more chronic access to *Campostoma*, and three-level trophic configurations (with released algae) would prevail. In fact, we saw the opposite pattern in the Baron Fork of the Illinois River. In this Ozark stream, *Campostoma* was again the dominant herbivore grazing deeper substrates. (Here the shallow margins of the creek had bathtub rings not of algae, but of grazing snails, which were restricted to depths shallower than those occupied by *Nocomis*, a minnow genus specialized as a snail predator). Schools of thousands of *Campostoma* swam throughout the Baron Fork, and the gravel substrates were covered with adnate felts of *Calothrix*, the grazer-resistant cyanobacteria, as described above. Our ad hoc explanation for this clear "two level" control is that the bass species in the Baron Fork was not the more piscivorous large

mouthed and spotted bass (*Micropterus salmoides*, *M. punctulatus*) of Brier Creek, but the more invertivorous small mouthed bass (*M. dolomieu*). The preferred prey of small mouthed bass are crayfish, and night snorkeling showed that crayfish were extremely abundant in the habitat. One reasonable interpretation, which remains untested, is that Baron Fork was in fact a four-level functional food chain, in which human anglers suppressed small mouthed bass populations, releasing both the preferred prey (crayfish) and less preferred prey (*Camptostoma*), with the latter applying chronic heavy grazing to the algae. This grazing pressure undoubtedly had ecosystem level effects, by maintaining dominance of nitrogen fixing, tightly adhering cyanobacterial felts. Our short-term grazer-exclusion experiments showed that in the absence of grazing, these felts were overgrown (within weeks) by the loosely attached *Melosira*, a diatom well-represented in plankton. If these changes in abundance and taxonomic composition of the algal assemblages persisted, nitrogen loading and the extreme water clarity of these Ozark streams might both be reduced, affecting both aesthetic values and insect and fish production.

4.5 The importance of the gravel-bed habitat to trophic dynamics

Food web ecologists would obviously like to be able to predict (and sometimes control) food chain length in rivers. As mentioned above, people worldwide often prefer more production of predators (salmonids, eels, bass, eagles) and less accumulation of algae or certain insects. General theory that relates food chain length to environmental conditions is not yet particularly helpful. Chains in food webs have been predicted to lengthen with productivity, because trophic transfers are inefficient, so longer chains can be supported by more energy flow into the base (Lindeman, 1942; Pimm, 1982). They are predicted to shorten with disturbance, because long food chains have shown less resilience than short chains in computer models that lack spatial or temporal contexts (Pimm, 1982; Pimm and Lawton, 1977). We have seen that in gravel-bedded rivers, where species succession influences the recovery of food webs between scouring floods (and after episodes of de-watering), food chains may be initially shortened by disturbance (if algae recover first), but are subsequently lengthened by the early prominence of more edible taxa at lower trophic levels. The subsequent shortening of functional food chains, as assemblages of basal prey taxa become more inedible, might actually be accelerated by productivity. Following disturbance, taxa that allocate to defenses at the expense of growth or reproduction can build up their populations more rapidly in productive environments. Where disturbance and species succession afterwards is an important determinant of the taxonomic composition of web members at lower trophic levels, as in gravel-bedded rivers, the effects of disturbance and productivity on food chain length are likely to be the reverse of those predicted by previous theory (Power *et al.*, 1996).

To relate food chain dynamics to the physical dynamics of gravel-bedded rivers, we must understand how disturbance, productivity, and habitat structure constrain energy flow and biomass accrual by potentially significant species in local assemblages. During initial stages of recovery from disturbance, who persists? Where, and at what densities? What controls rates of recolonization from refuges? How do rates of resource capture and conversion at various trophic levels change over time, with changes in physical conditions and densities of biota? Where and when will interactions between organisms at different trophic levels become dynamically significant? How will grazing, or predation alter the species composition of webs, and change the strength of food web interactions? What will be the important feedbacks by which biota influence physical conditions (e.g., creation of egg and larval incubators for insects by algal mats that trap sun-warmed surface waters; creation of hypoxic conditions, if algae start competing with animals for oxygen)?

I have touched on a few of the physical aspects of gravel-bedded rivers that influence the initial conditions and the subsequent trajectories of biotic recovery following episodic disturbance. Factors like channel morphology, bed texture, and the amount of sand in storage will affect the severity of scour, for example. Recovery rates will depend on watershed scale controls and discharge-driven changes in water clarity, irradiation, temperature regimes, nutrient fluxes, velocity gradients, wetted habitat area, and linkages with lateral habitats. The intensity and outcomes of interactions of biota will depend on factors like the availability of refuges offered by depth, turbidity or structural cover from predators. Organisms at different trophic levels, and vulnerable versus invulnerable organisms within trophic levels, will respond differently to changes in resources, temperature, disturbance regimes, and physical structure, so food chains with different levels of top-down control will assemble under different conditions (Marks *et al.*, 2000; Wootton *et al.*, 1996). Predicting how food web configurations should change over time with changes in flow, sediment, solar irradiation, chemical fluxes, or species composition is clearly an enormous challenge. It might be more feasible to do this in rivers than in other habitats, however, for two reasons. First, the pronounced size structure of river food webs (larger, longer-lived, more mobile, but more slowly reproducing organisms at higher trophic positions) gives us some ability to predict the relative responses by various trophic levels to environmental change. Second, rivers scientists have many opportunities to observe pronounced physical changes and the ecological responses that follow them, because rivers are so dynamic over time scales that are short relative to the time scales of our research. This dynamism does not always seem convenient to experimentalists who find their enclosures stranded in trees twenty feet above the benthic habitat they thought they were studying. Nonetheless, this is a feature that favours “adaptive management” approaches (Walters, 1986), and can be turned to our advantage in longer-term, larger scale river research.

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