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Floods, Food Chains, and Ecosystem Processes in Rivers

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Note from author: Someone who edited this chapter after the author last saw the galleys added the word "fry" after roach and stickleback in many places where it did not belong. This makes the article incomprehensible, because roach fry (< 20 mm) midges, so are members of the '3rd' trophic level, along with adult and juvenile stickleback and large invertebrate predators (mostly odonates in this system). Adult roach (> 30 mm) feed primarily from the 4th trophic level. They sometimes have algae in their guts, and are considered omnivorous, but in my experiments, adult roach alone did not suppress the standing crops of large Cladophora streamers, the primary macroalgal taxon in this system. I have struck out the word "fry" where it does not belong.

SUMMARY

Disturbance regimens link species and ecosystems. For example, floods that scour channels in river drainage networks can also alter trophic networks that link river biota. The impacts of flood disturbance regimens on trophic structure vary among communities, depending on the attributes of constituent species. In the midwestern United States, where algivorous fish are the principal herbivores, floods may spatially rearrange predators and prey among pool habitats, but larger (reach) scale food chain patterns are not affected, or if altered, are rapidly restored. In California rivers, where fish faunas are relatively depauperate, invertebrates are the chief primary consumers. Here, hydrologic disturbance or its absence does affect food chain length at the reach scale. Scouring floods allow weedy invertebrate species to dominate early successional primary consumer guilds. These species are resilient following physical disturbance but subsequently vulnerable to predation. After prolonged low flow during drought, or in regulated channels with artificially stabilized hydrographs, lower trophic levels become dominated by armored or sessile taxa that are relatively invulnerable to predators. In these late successional communities, the biomass of primary producers is chronically suppressed, and energy flow to higher trophic levels appears to attenuate. In addition, other ecosystem functions may be changed, including nitrogen fixation and river–watershed exchange mediated by floating algal mats

INTRODUCTION

Until relatively recently, succession and food webs have been studied separately. Most studies of disturbance (events that remove large portions of the biota from habitats) and subsequent community recovery, or succession, have focused on species at lower trophic levels that are dominant space holders, typically plants or sessile animals. Succession was assumed to be driven by processes acting within trophic levels, such as competition or facilitation. Studies of multitrophic level interactions, on the other hand, generally ignored the temporal context (e.g., the time since the last environmental disturbance) of the food webs in question.

Only recently has the influence of consumer–resource interactions on the rate of succession gained experimental attention (e.g., Wootton, 1990; Farrell, 1991; and references therein Huntly, 1991 and Ch. 8). The impact of disturbance on trophic structure and dynamics has also received relatively little attention, although two distinct lines of reasoning suggest that disturbance should shorten food chains. Menge (1976; Menge and Sutherland, 1976) observed that mobile intertidal predators, such as whelks and starfish, forage more effectively in the absence of wave shock; disturbance frees sessile prey from mobile predators and shortens functional food chains. Pimm and Lawton (1977) and other theorists have found that model food webs with longer food chains are dynamically more fragile (slower to recover from disturbance). They therefore reason that short food chains should predominate in nature, particularly where environments are frequently disturbed.

In ecosystems where attributes of dominant species change over the course of succession, however, disturbance might lengthen food chains. Early successional species are often more palatable, or susceptible, to consumers than late successional species (Cates and Orians, 1975; Porter, 1977; Lubchenco, 1986). If life history tradeoffs cause species (or vegetative regrowth) that first colonize or recover after disturbance to be more vulnerable to predators, and if mobile predators also arrive during these early stages, the impacts of consumers on resources should be strongest during early phases of succession. Afterwards, the energy flow from prey to predators should wane. Hence, food chain length (in both the functional, top-down, population regulation sense, and the descriptive, bottom-up, energy flow sense) could decrease with time since disturbance.

I will illustrate the interplay of disturbance regimen, species traits, and trophic dynamics with case studies from rivers. In California rivers with seasonal, Mediterranean hydrologic regimens, disturbance susceptible grazers (insects) dominate primary consumer guilds. In a contrasting system, Oklahoma rivers under continental climates, floods can occur during any month, and grazers are herbivorous fish that are resistant to floods, but vulnerable to predators throughout their lives.

CASE STUDIES FROM RIVERS

Algal Food Webs with Insect Herbivores: Northern California

Rivers in Mediterranean climates, such as the Eel of northern California, have winter-flood, summer-drought hydrographs. Under these conditions, dramatic seasonal bloom–detachment–senescence cycles of macroalgae occur. Following scouring winter floods in the South Fork Eel River, macroalgae, dominated by the filamentous green alga, *Cladophora glomerata*, recover before animal densities build up. During this window of time, the food chain has only one functionally significant trophic level, and attached *Cladophora* turfs grow up to 8 m long. Toward mid-summer, these turfs detach to form floating mats that cover large portions of the river surface. Mats disintegrate in late summer, and remnants of turfs and mats take on a knotted, webbed architecture produced by heavy infestations of midge larvae (primarily *Pseudochironomus richardsoni*) that live in the algae and weave it into retreats, or "tufts." Midge populations explode shortly after floating algal mats form, and midges and oligochaetes associated with their tufts become the most numerous macroarthropods in the river (Power, 1990a). They crash as the algae disappear, but whether they contribute to this disintegration or simply track it is not apparent from observation.

Field experiments in the summer of 1989 revealed that higher trophic levels could strongly affect the maintenance and the taxonomic composition of attached algal turfs, as well as the production of floating algal mats. In early June, during the early summer bloom, 6 m^2 pens ("enclosures") built around bedrock or boulders that supported turfs of *Cladophora* were stocked with fish [California roach ~~fry~~ (*Hesperoleucas symmetricus*) and juvenile steelhead (*Oncorhynchus mykiss*)]. In other pens ("exclosures"), all fish were removed. After 5 weeks, algae in enclosures looked very different from algae in exclosures. *Cladophora* turfs in enclosures had collapsed to form a low prostrate mat 1–2 cm high, infested with tuft-weaving midges. In unstocked exclosures, *Cladophora* biomass remained higher, and turfs remained erect and became overgrown with nitrogen (N)-fixing *Nostoc* and an epiphytic diatom (*Epithemia*) that contains N-fixing endosymbiotic cyanobacteria. Kilograms of algae floated to the water surface in exclosures; virtually no floating algae were detected in enclosures (Power, 1990b).

Roach and stickleback fry, and large invertebrate predators (primarily damselfly nymphs) colonized unstocked exclosures, but were virtually absent in stocked enclosures with fish. Separate experiments showed that roach fry, stickleback fry, and lestid damselfly nymphs all had strong effects on midges, producing densities approximately one fourth of the midge densities observed in predator-free controls (Power, 1990b). These experiments, by revealing the importance of small predators in the Eel River food chain, showed that fish exerted indirect negative effects on algae mediated through four trophic levels. By suppressing small predators, fish released algivorous midges, with the predicted impact of greatly reducing standing crops of algae. In exclosures without large fish, three-level food chains maintained higher algal standing crops. The overgrowth of *Cladophora* by N-fixing algal taxa indicated increased N limitation, as predicted by theory (Hairston et al., 1960; Fretwell, 1977).

Rampant omnivory was a feature of this food web. For example, large roach [redacted] consume algae and algivorous insects, as well as predatory insects. In 1991, experimental introductions of midge-free *Cladophora* into enclosures showed that the macroalga persisted equally well with roach, with steelhead (pure carnivores), with both, or with neither, supporting the hypothesis that the two-level effects of roach [redacted] as herbivores were less important than their four-level effects as predators of predators. Perhaps more surprising, given the outcome of the experiments, is the observation that roach and steelhead consume many algivores such as mayflies; in fact, algivores make up >60% (by number) of the macroinvertebrates in guts sampled from both fishes. How can trophic cascades showing clear four-level effects be generated in food webs in which omnivory should blur distinctions between trophic levels? A key to this enigma in the Eel River food web is the predator-specific defense of the most abundant algivore, the tuft-weaving midge. Although algal tufts appear to be a completely effective defense for midges against fish, they are only partially effective against predatory invertebrates (Power et al., 1992). Odonates (lestid and aeshnid nymphs) can detect midges within algal tufts, and extract them with "surgical strikes" of their mouthparts. Naucorid bugs detect midges by probing tufts with their beaks. Therefore, when predatory fish eliminate these small predators, they release one guild of algivores that is capable of suppressing algae.

Multi-basin surveys and year-to-year contrasts in food web assembly. Observations of six rivers during 1 year, and of one river over 6 years, provided the opportunity to observe food web changes under contrasting hydrologic regimes. To study the effects of seasonal and hydrologic factors on northern California food webs and algal phenology, I surveyed river biota from 1988 to 1989 in six rivers. Four were unregulated, with a natural winter-flood, summer-drought hydrograph. In these channels, *Cladophora* (the dominant macroalgae in all six rivers) showed its typical bloom–detachment–senescence cycle. In two regulated channels with artificially stable low flow, short viable standing crops of attached *Cladophora* persisted throughout the year. The contrast in *Cladophora* phenology in regulated and unregulated rivers showed that *Cladophora* cycles were extrinsically driven by factors related to the hydrograph.

Survey data on river fauna suggested that flood effects on algae might be mediated through grazers. In regulated rivers, high densities of sessile, cased grazers (e.g., the aquatic moth larva *Petrophila*, the caddisfly *Tinodes*), or mobile grazers with heavy armored cases (e.g., the caddisfly *Glossosoma*), persisted year round. Few predators were observed in these regulated rivers, although the occurrence of isolated individuals indicated that physical-chemical conditions did not preclude them. In unregulated rivers, mobile, nonarmored grazers (e.g., baetid mayflies) initially dominated the fauna in the spring, but their numbers dropped and those of sessile or armored grazers increased later during the low flow season, as predators became more numerous. In a more productive (sunny) river, this transition occurred earlier than in an unproductive (dark) stream (Power 1992).

Further corroboration came during the drought of 1990–1992, when our study site at the South Fork Eel did not experience flooding. Unusually high densities of sessile aquatic moth larvae (*Petrophila confusalis*) and heavy-cased caddis larvae (e.g., *Dicosmoecus gilvipes*) survived through these three winters, and curtailed *Cladophora* blooms the following springs. The summer production of *Cladophora* in 1990, 1991, and 1992 was insufficient to produce the extensive floating mats observed in the South Fork during 1987, 1988, and 1989, when winter floods did occur.

High densities of late-successional grazers and low-standing crops of algae suggest that functionally significant food chains shorten from four to two trophic levels during the prolonged absence of scouring flood disturbance. This interpretation was supported by an experiment conducted during drought in the South Fork Eel, in which exclusion of the large, armored grazer *Dicosmoecus*, a caddisfly, strongly released algae so that floating mats were formed. The impact of steelhead in this experiment was statistically significant (suggesting that steelhead still exerted effects at a fourth trophic level), but was much weaker than the two-level effect of *Dicosmoecus* (J.J. Wootton and M.E. Power, unpublished).

Hydrologic effects on food chains may influence a number of ecosystem-level properties of rivers. If prolonged absence of flood scour leads to a truncated food chain of two functional trophic levels, energy flow to predators should attenuate, and secondary production of fish and other higher trophic levels should diminish. Macroalgae experiencing bloom–detachment–senescence cycles in rivers that periodically scour also provide huge areas of substrate for N-fixing epiphytes, which could significantly enhance fertility in these N-limited waters. Finally, extensive algal mats are food-rich, sun-warmed floating incubators for invertebrates. They increase both the production and the emergence rates of aquatic insects, and are likely to enhance the amount of this production exported from rivers to their watersheds. In the watershed of the South Fork Eel, where the old growth conifer forest vegetation is relatively inedible, this export could be important to terrestrial consumers such as spiders, birds, lizards, and bats.

Floating algal mats, insects, fish, and terrestrial consumers. Algal dynamics in river channels may affect terrestrial consumers by mediating both the rate of aquatic insect production and the amount that is exported from rivers to their watersheds. Algal mat formation coincides with order-of-magnitude increases in the densities of aquatic insects in the Eel River. Rates of emergence of adult insects were three to six times higher from floating mats than from benthic algal turfs (Power, 1990b). Floating mats may serve as refuges for insects from fish predation. In short-term experiments, rates of fish predation were 16 times higher in benthic algal turfs than in floating algal mats (Power, 1990b). As mentioned above, insect growth and development are probably accelerated in floating mats.

Floating algal mats not only increase production of certain insect taxa, but may also route this production from the channel to the land. The function of floating mats as potential valves diverting secondary production between adjacent ecosystem compartments depends on when mats form and how long they last. If algal mats disintegrate and sink before insect larvae emerge, they may serve as time-release capsules of food for fish. If mats last until insects complete their life cycles and emerge as winged adults, they can divert insect production from aquatic to terrestrial consumers. The second function is probably important, because the generation times of mat-dwelling insects such as chironomids are short. We are monitoring lateral penetration by aquatic insects from the river bank to sites up to 200 m back into the forest (M.S. Parker and M.E. Power, unpublished). The ratio of aquatic insects to total insect biomass on both sticky traps and spider webs is predicted to increase in "big algae years" relative to drought years during which floating mat formation is curtailed. The effects of aquatic and terrestrial insect availability on the growth and reproductive success of the spiders (M.S. Parker and M.E. Power 1993 and unpublished) will reveal how algal dynamics in the river affect the fitness of numerous consumers in its watershed. Future collaborations with bat biologists will examine ecological linkages of rivers and their watersheds over larger spatial scales.

Algal Food Webs with Herbivorous Fish: Midwestern Rivers

Grazing minnows, piscivorous bass, and stream algae. Prairie streams of Oklahoma can flood during any month of the year. The dominant herbivores in many of these streams are grazing minnows: *Campostoma anomalum*. In one such stream, Brier Creek of south-central Oklahoma, enormous pool-to-pool variation in algal standing crops occurs. Some pools are filled with filamentous green algae (*Rhizoclonium*, closely related to and to some phycologists, synonymous with *Cladophora*). Other pools appear nearly barren. The barren pools contained schools of *Campostoma* and the green pools lacked these grazers, and contained their bass predators (*Micropterus salmoides*, *M. punctulatus*). During periods of low flow, pools in Brier Creek were well isolated by long shallow riffles, but during floods, these riffles became corridors rather than barriers. Floods redistributed minnows or bass among stream pools, but complementary distributions of bass with minnows, and of minnows with algae, were maintained or reestablished within weeks in new locations. Similarly, when bass were experimentally removed from a green (three-level) pool and minnows were added, pool substrates were grazed to a barren (two-level) state within weeks. Where bass were added to a naturally barren minnow pool, minnows emigrated or were eaten, and algae built up to "green" levels, again within weeks (Power et al., 1985).

Campostoma are thin, soft fish, vulnerable to swimming predators throughout their lives. In contrast, neither adult *Campostoma* nor bass are vulnerable to floods (although their fry can be obliterated), and there is no disturbance-related switch in taxa dominating primary consumer guilds. The relative resilience of food chains following floods in these systems, in contrast to the changes seen in northern California rivers, illustrates that species attributes strongly affect the consequence of disturbance regimens for food chain length.

Fish, snails, and cyanobacteria. In Ozark rivers, *Campostoma* in the deeper channel and snails along shallow river margins both have strong effects on taxonomic composition of producer assemblages. Rock substrates are covered with dense cyanobacterial black felts <1 mm high, which, as our field experiments demonstrated, were maintained by intense grazing. When felt-covered rocks in the Baron Fork of the Illinois River were protected from grazers in in-stream flowing channels, they were overgrown within weeks by turfs of diatoms 8–10 cm high. When transferred to the open stream, these turfs were stripped off by grazing minnows within minutes, and after 11 days of chronic grazing, black felts reappeared. Cyanobacterial felts also developed under chronic grazing on unglazed tiles that had not previously been colonized by river flora. *Calothrix*, a dominant cyanobacterium in the natural stream flora, resists grazing by virtue of its basal growth. Cell division in *Calothrix* is restricted to five to six cells above the basal heterocyst. Grazers therefore

remove the distal portions of trichomes and seston, including diatoms capable of overgrowing colonies, but leave behind both the basal regenerative portion of the cyanobacteria and the N-fixing heterocyst. This interaction, which appears analogous with maintenance by grazers of grasslands (e.g., McNaughton, 1984) in some terrestrial ecosystems, has ecosystem-level implications for N loading and fertility of rivers in this region (Power et al., 1988). During floods, *Calothrix* is scoured from rocks. It is not clear that it could reestablish as a dominant unless chronic herbivory favored it over attached green algae and diatoms. Because of the different species traits of both the N fixers and the grazers, flood disturbance may reduce N fixation in Ozark rivers, and enhance it in rivers of northern California. These ideas remain to be tested.

DISCUSSION

These and other experimental studies of river food chains suggest that trophic interactions make a profound difference to the function of river ecosystems. Simple theory (Hairston et al., 1960; Fretwell, 1977) can guide us, via "postdiction" from field experiments, in assessing how many functionally important trophic levels underly the patterns of distribution and abundance of river biota that recur between floods. We still need the much-sought "Field Guide to Strong Interactors" (S. Carpenter, pers. comm.) to predict, from the properties of species making up communities, which will be the strong threads through food webs that link predators or consumers to plants.

Such a guide may prove elusive, because interaction strengths, or impacts in general, of particular species are contingent on their temporal and spatial contexts (Mills et al., 1993). As a consequence, the length of functional food chains can vary in changing or heterogeneous environments, sometimes abruptly. For example, in Panamanian rivers, one can put one's finger on the point at which a two-level food chain dominated by grazing fishes becomes a three-level chain topped by fishing birds. This point occurs as one moves up from deeper heavily grazed substrates to shallow river margins rimmed with "bathtub rings" of algae (Power, 1984; Power et al., 1989). In rivers where lower trophic levels exhibit tradeoffs between resistance to scour and resistance to predation, interaction strengths and food chain lengths change more gradually, as months pass after scouring floods. As argued in the preceding sections, this apparent succession of grazers in northern California rivers allows functional food chains to shorten from four to two levels during drought or in regulated channels. After years of diverted and regulated flow, heavy growths of willow and alder tend to encroach into channels. This could be interpreted as further truncation of the food chain toward one trophic level (woody plants, whose spread and accrual are not suppressed by herbivores). The longer the period of artificial low flow, the larger are the plants in the deactivated channel, and the larger are the flood releases that would be required to restore the natural river system, along with favorable spawning and rearing habitats for top predators such as salmonids.

Better understanding of the consequences of flushing flows for river food chains and river–watershed linkages is crucial for river management and restoration, particularly in massively rearranged water systems such as those of California. In periodically scoured channels, food webs are reset to trophic configurations that divert more energy to higher trophic levels. Flushing flows are a key to geomorphic and food web restoration in rivers, when used with knowledge of how local key species interact with each other and with their physical environment.

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