

Disturbance and Food Chain Length in Rivers

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Introduction

"Are trophic cascades all wet?" asks Strong (1992), speculating that trophic cascades (sensu Paine (1980) and Carpenter et al. (1985)) might be exclusive features of aquatic communities because they are simple and poor in species relative to terrestrial communities. River food webs are as complex and speciose as food webs in any other ecosystem (Winemiller, 1990). Nonetheless, field experiments in rivers have documented chains of strong interaction that link predators through consumers to primary producers (e.g., Wootton and Power (1993), Power (1990b), and Power et al. (1985)). In this chapter, we discuss factors that appear to control the length of chains in river food webs. Here, we define the length of functionally significant food chains as the number of feeding guilds (trophic levels) that are alternately released and suppressed following removal of a top predator, with the criterion that changes in biomass at higher trophic levels must affect biomass of primary producers. We will use the impact of higher trophic levels on plants to distinguish threads of weak interactions from chains of strong interactions in food webs. For example, if removing predators increased herbivore biomass, but this herbivore response did not measurably change plant abundance, we would not consider this interaction to be part of a functionally significant food chain. We do not necessarily advocate this as a general definition of food chain length, but use it to explore specific questions in this chapter. In general, it

is important to distinguish when trophic levels are counted by functional (top-down) criteria, which require potential population regulation (Fretwell, 1977; Oksanen et al., 1981), versus descriptive (bottom-up) criteria, based on the number of energy transfers inferred from diet analyses (Cohen, 1978) or isotopic fractionation (Kling et al., 1992). These different criteria are likely to identify chains of different length in the same web.

What determines the length of functionally significant food chains in river food webs? Pimm (1982) has compiled a useful, much cited summary of factors hypothesized to limit food chain length (although he did not distinguish between functionally significant and descriptive food chains). One hypothesis (Elton, 1927) involves design or size constraints: Is a pterodactyl predator mechanically feasible? This hypothesis has not been much studied by community ecologists because of the difficulty of doing evolutionary constraint removal experiments (J. F. Quinn, personal communication). The two most studied hypotheses focus on energy flow and dynamic responses of communities to disturbance. The first predicts that because trophic transfer is inefficient, energy flow could limit the number of trophic levels an ecosystem can support. Therefore, food chains should lengthen with environmental productivity or with the metabolic efficiency of consumers (Elton, 1927; Hutchinson, 1965; Slobodkin, 1961). The second hypothesis, favored by Pimm (1982), predicts that because model communities with long food chains are dynamically fragile and have longer return

times following perturbation, food webs with short chains should predominate in nature, particularly where environments are frequently disturbed. Physical disturbance could also shorten food chains in situations where it has disproportionate impacts on higher trophic levels, as when wave shock inhibits feeding by mobile starfish on sessile intertidal prey (Menge and Sutherland, 1976).

Our studies in northern California rivers suggest that, in contrast to these predictions and observations, the lengths of functionally significant food chains can increase with disturbance, and may shorten with environmental productivity. The mechanisms harken back to Pimm's design constraint hypothesis. Familiar life history trade-offs between resilience following physical disturbance and resistance to predators characterize early versus late successional species at lower trophic levels in marine (Sousa, 1979; Farrell, 1991), terrestrial (Reader and Southwood, 1981; Chapin, 1993; Cates and Orians, 1975), lake (Porter, 1977; Sommer, 1985; Sommer et al., 1986; Vanni and Tenite, 1990), and river (Power and Stewart, 1987; Power 1992a) communities. In systems like rivers, where food web dynamics respond to changes in species dominance during succession, productivity and disturbance may individually and interactively affect food chain length in a manner opposite to that predicted by previous theory.

Effects of Hydrologic Disturbance on River Food Chains: Experiments and Surveys in Northern California Rivers, 1989-1993

Large reaches of rivers can be reset by a single major disturbance, such as a flood that mobilizes and scours the river bed (Fisher et al., 1982). In rivers in regions with Mediterranean-type climates, like those of northern California, floods are most likely to occur during a winter rainy season, followed by a summer dry season marked by gradually decreasing base flow. Year-to-year variation in the severity and timing of floods permits comparisons of trophic structures that develop under different disturbance regimes. In addition, artificially regulated channels can be used as large-scale disturbance removal experiments. Here, we summarize year-to-year contrasts in experimental results from

the South Fork Eel River, an unregulated river in northern California that experienced scouring floods in 1989 and 1993, and drought (with no scouring floods) from 1990 through 1992. In addition, we review results from surveys in four natural and two artificially regulated rivers during 1989, when all unregulated rivers in the region experienced scouring floods.

Scouring Floods (1989)

Following scouring winter floods, macroalgal recover (by vegetative growth from basal pads) before animal densities build up. Dramatic late spring blooms of *Cladophora glomerata* (a filamentous green macroalga dominant worldwide in temperate freshwaters (Blum, 1956; Whitton, 1970) occur during a window of time when the flood chain has only one functionally significant trophic level. Toward midsummer, *Cladophora* turfs several meters long 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 chironomids, primarily *Pseudochironomus richardsoni*, that live within the algae and weave it into retreats, or turfs. Experimental manipulations of fish in the South Fork Eel during summer low flow in 1989 revealed that they exerted strong impacts on algae that were mediated through four trophic levels (Figure 27.1a). In enclosures with adult California roach (an omnivorous minnow) and juvenile steelhead (a carnivorous salmonid), *Cladophora* was reduced to a low prostrate mat 1-2 cm high, infested with tuft-weaving midges. In unstocked enclosures, *Cladophora* biomass remained higher, turfs remained erect, and became overgrown with nitrogen-fixing *Nostoc* and an epiphytic diatom (*Epihemia*) that contains nitrogen-fixing endosymbiotic cyanobacteria. Kilograms of algae floated to the water surface in enclosures; virtually no floating algae was produced in enclosures (Power, 1990a).

Roach and stickleback fry, and predatory invertebrates (primarily lepid damselfly nymphs) colonized unstocked enclosures, but not enclosures stocked with fish. Separate experiments showed that these small preda-

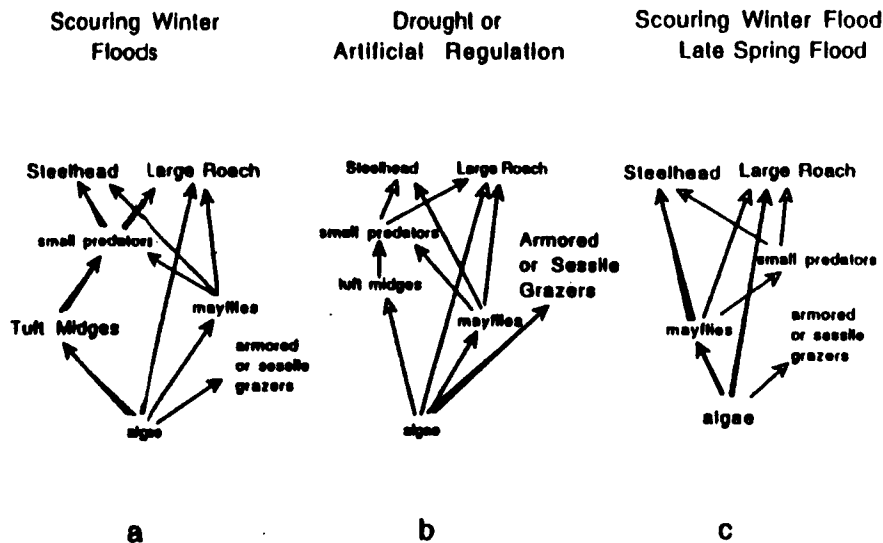


Figure 27.1. Food web modules for the South Fork Eel River, showing functionally significant food chains (black arrows) and other trophic interactions (white arrows). (a) Four-level food chain during the summer low-flow season after scouring winter floods (1989); (b) two-level food chain following flood-free winters (1990–1992) or in regulated channels with artificially stabilized flow; and (c) three-level (to steelhead) or two-level (to large roaches) food chains in the South Fork Eel after scouring winter floods, and a June spate that exported the first growth of algae.

tors could, at natural densities, reduce midge densities to around one-fourth of those of predator free controls. By suppressing small predators, fish released algivorous midges, which suppressed algae. In enclosures, small predators suppressed the midges and permitted higher algal standing crops to persist. The overgrowth of *Cladophora* by nitrogen-fixing algal taxa indicated increased nitrogen limitation in fish enclosures, in accordance with the prediction from food chain theory (Hairston et al., 1960; Fretwell, 1977) that if plants are not limited by grazers, they will become limited by their own resources.

In addition to preying on intermediate predators, roach and steelhead consume many algivores, such as mayflies. This omnivory did not obscure the fourth trophic level effect of fish because of the predator-specific defense of the tuft-weaving midge. While algal tufts appear to be a completely effective defense for midges against fish, they are only partially effective against predatory invertebrates. Odonates (lentic and aeshnid nymphs) can detect midges within algal tufts, and ex-

tract them with surgical strikes of their mouthparts. Therefore, when predatory fish eliminate these small predators, one guild of potentially important algivores is released, and this is sufficient to suppress algae (Power et al., 1992).

Artificial Flow Regulation (1989)

When artificial flow stabilization prevents scouring winter floods, food chains with only two functional trophic levels may develop. In four unregulated rivers (the South Fork Eel and three others), beds were scoured several times over the winter of 1988–1989. During the following summer, *Cladophora* (the dominant macroalga in all rivers surveyed) showed its typical bloom-detachment-senesescence cycle in these four rivers. In two regulated channels where no scouring floods occurred, low but viable standing crops of attached *Cladophora* persisted throughout the year (Power, 1992a).

Visual surveys of fauna in the six channels suggested that hydrologic impacts on algae

were mediated through grazing invertebrates. Following scouring floods, grazer guilds are initially dominated by mobile, nonarmored taxa such as baetid mayflies. Such invertebrates are resilient following physical disturbance. They allocate to growth and reproduction rather than armor or building retreats, and have the short generation times and potentially rapid growth that allow them to quickly exploit resources released by disturbance. Their mobility and lack of armor, however, make them conspicuous and vulnerable to predators. As summer progresses, the grazer guild becomes increasingly dominated by sessile (e.g., the aquatic moth larva, *Petrophila*) or heavily armored (e.g., the large caddis *Dicosmoecus*) taxa that are less vulnerable to predators. In regulated channels, grazer guilds were chronically dominated by predator-resistant armored or sessile taxa (Power, 1992a).

Predators were present in regulated channels, indicating that they were not excluded by physicochemical factors, but they occurred in low numbers, probably because energy flow to their populations was attenuated. With ineffectual predation under prolonged low stable discharge, food chains with only two functional trophic levels appeared to be maintained (Figure 27.1b). The chronically grazed algae never attained biomass levels which became self-limiting in the two regulated channels, explaining why the bloom-detachment-senesescence cycles did not occur (Power, 1992a).

Drought (1990–1992)

More support for the inference that lack of disturbance by flood scour-shortened food chains came from experiments in the South Fork Eel during the summers of 1990, 1991, and 1992. During this drought period, no floods of sufficient magnitude to scour the river's bed occurred. Large numbers of sessile *Petrophila* and armored *Dicosmoecus* overwintered. When *Cladophora* began to grow in May, it was quickly consumed by these grazers. Tuft-weaving midges were rare during these years, limited perhaps by the lack of extensive macroalgal turf and mat habitats which had preceded their population explosions during summers following scouring floods (Power, 1990a).

Fish enclosures and enclosures built around the small remnants of algae in early June (the same start date for 1989 experiments) showed that fish were functionally irrelevant to food chain dynamics in both 1990 and 1991. What algae remained rapidly disappeared in both the presence and the absence of fish. Removal of *Dicosmoecus* in 1992, in contrast, led to a 20-fold increase in floating algae (Wootton and Power, unpublished data), suggesting that the dominant trophic control was exerted by consumers at the second trophic level (Figure 27.1b).

Scouring Floods with a Dry Season Spate (1993)

During the winter of 1992–1993, the drought was broken and the South Fork Eel experienced the first scouring floods in three years. Shortly before the fish manipulation experiment began, an unseasonably late (late May, early June) flood, thought to be associated with an El Niño weather pattern, occurred. Although this spate was too small to move gravels and scour invertebrates, it detached and exported macroalgal growth, which had accrued to lengths of several meters. Fish manipulation experiments were delayed until July, when *Cladophora* turfs had regrown to lengths of 50–150 cm in certain channel reaches.

In the 1993 experiments, three treatments were imposed: steelhead alone, roaches alone, and fish-free enclosures. As in 1989, fish effects on algae were conspicuous five weeks after experiments had started. In the presence of steelhead, *Cladophora* turfs were heavily overgrown by epiphytic diatoms (*Melosira* and *Cymbella*), and standing crops remained about twice as high with steelhead as in the presence of omnivorous roach, or in the fish enclosures. The production of floating algae (mostly diatoms that had sloughed off of *Cladophora*) was 5.5 times higher in steelhead enclosures than in the fish enclosures, and 28 times higher with steelhead than with roaches (Power et al., in preparation).

These results suggest that steelhead exerted strong effects on algae from the third, rather than the fourth trophic level in 1993 (Figure 27.1c). The slip in trophic position of steelhead in enclosure food chains supports

the inference that tuft-weaving midges, the herbivore susceptible to small predators but not to fish, were crucial to their fourth-level effects in 1989. Tuft-weaving midges were rare during the 1993 experiments. Afterward, by late August, midges increased to densities at which they eventually reduced *Cladophora* turfs and mats to the same knotted, webbed remnants that had been conspicuous by July in the 1989 postflood season. The midge was late in recruiting to the Eel in 1993, probably because of the loss of its macroalgal turf and mat habitat in the early summer flood. The remaining functionally significant herbivores, dominated by mayflies, were vulnerable to fish. Steelhead reduced densities of small predators in their enclosures, but they also suppressed herbivores enough to release epiphytic diatoms. These diatoms, in turn, came to dominate the producer assemblage as they overgrew and sloughed from their macroalgal hosts.

Roach, whose enclosures had the least algae, also played a different trophic role in 1993 than in 1989. Roach are omnivores whose guts can be filled with diatoms, or invertebrates, or both. During the drought year of 1991, bundles of *Cladophora* from a tributary of the South Fork Eel were placed in enclosures. This manipulation was intended to address the question of whether algae declined with roach in 1989 because of their direct impacts as grazers (second-level effects), or their indirect impacts as predators of predators (fourth-level effects). In that experiment, *Cladophora* standing crops persisted equally in the presence and the absence of roach (Power, unpublished data). This result, and the architecture of the collapsed *Cladophora*, which indicated heavy infestation by midges in fish enclosures, suggested that in 1989, fourth-level effects of roach outweighed their impacts as grazers. *Cladophora* in the 1991 introduction was relatively free of epiphytic diatoms. In 1993, roach herbivory on the epiphytic diatoms was conspicuous, both from their control of epiphyte standing crops in their enclosures, and from the gut contents. Roach also eliminated predatory insects (e.g., lestickids) and larger insect grazers (e.g., mayflies). Unlike steelhead, however, roach are not piscivorous, so the young of the year of roach and stickleback recruited heavily to their enclosures.

As in 1989, lestickids and fish fry (the small-predator guil) were extremely abundant in the fish enclosures. The intermediate standing crops of floating algae in enclosures (five times higher than in roach enclosures, but only 18% as high as in steelhead enclosures) could be due to the fact that invertebrate and small fish impacts were weaker than those of either large fish. Predatory lestickids and fish fry could have suppressed herbivory, but not as strongly as did predatory steelhead. Invertebrate herbivores and roach fry (which eat diatoms as well as small invertebrates like midges (Power, 1990a)) could have suppressed algal accrual, but not as strongly as diatom grazing by adult roach. Further work is needed to evaluate the strengths of these various direct and indirect trophic linkages. At this point, however, it is clear that functional food chain length and the trophic positions of particular taxa in the Eel River are not fixed, but change in response to temporal (and spatial (Power, 1992b)) variation in the environment. In both flood years, but in neither drought year, steelhead had strong effects that cascaded down to algae (from the fourth and third trophic levels in 1989 and 1993, respectively). Succession at lower trophic levels appears to be the mechanism by which lack of disturbance shortens functional food chains in these river communities.

Discussion

While predictions about the effect of disturbance on food chain structure are largely derived from computer models (e.g., Gardner and Ashby (1970) and Pimm and Lawton (1977)), insights from the natural history of constituents of real food webs are needed to interpret patterns in the real world. In a study attempting to distinguish productivity from disturbance as factors constraining food chain length, Pimm and Kitching (1987) set up artificial pots to simulate phytotelmata in a Queensland rain forest. Setting out a new pot was considered a disturbance. Pimm and Kitching introduced leaf litter into these pots at ambient, half-ambient, and twice ambient rates, a fourfold range in productivity. Their system appeared to have two top predators, leptoactylid frog tadpoles, which ate mos-

quito larvae, and predatory chironomids, which ate saprophagous chironomids.

They found that both predators colonized new pots several weeks after they had been colonized by primary consumer prey, and took this as evidence that disturbance could shorten food chains. (Their criterion for food chain length was descriptive (are predators present or absent?), not functional (do predators suppress consumer densities?).) The predatory chironomid's density was significantly positively correlated with leaf litter input rate, while tadpole density was negatively correlated (possibly because females avoided ovipositing in containers made cloudy by decomposing leaves). Pimm and Kitching (1987) interpreted these results as refuting the hypothesis that productivity lengthens food chains. A subsequent study in which productivity was varied 100-fold rather than fourfold did, however, firmly document that the longest food chains assembled in containers with the highest rates of resource input (Jenkins et al., 1992).

Pimm and Kitching's (1987) inference that disturbance shortens food chains is based on the observation that the predators colonized new habitats more slowly than their prey did.

Whether this occurs depends on two natural history features of predators relative to their prey: (1) How rapidly they can find and exploit new habitats or feeding opportunities; and (2) how susceptible they are to the physical disturbance that empties habitats in the first place. Predators are often larger and/or more mobile than lower trophic levels, but they may also be rarer. It is difficult, therefore, to generalize about how quickly organisms at higher vs. lower trophic levels will discover empty habitats and new, underexploited resources. In addition, a new or emptied habitat may need to accrue a certain prey density before it supports predators (e.g., MacArthur and Wilson (1967), and Holt (Chapter 29)). As we argue below, however, early successional patches or habitats may often be more profitable as foraging arenas.

When new experimental containers were set out to simulate disturbance, all trophic levels were similarly affected (absent at the onset). What happens when disturbance has unequal impacts at different trophic levels (Figure 27.2)? Their greater mobility may save predators from disturbances that annihilate herbivores or plants. Wolves and hawks may elude forest fires or landslides that kill

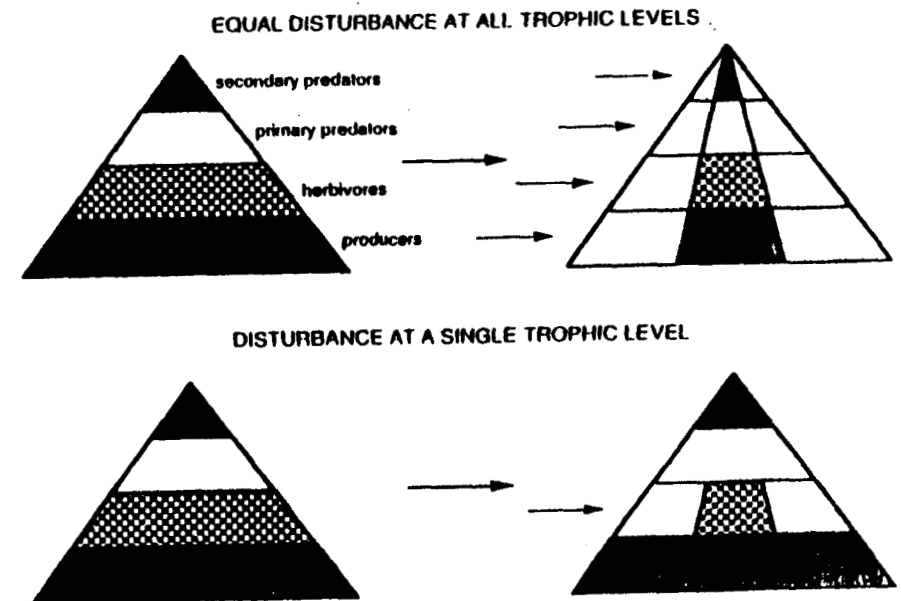


Figure 27.2. Different possible effects of disturbance in food chains. (a) Disturbance reduces all trophic levels proportionately; and (b) disturbance has large effects only at one trophic level

less mobile voles, insects, herbs, and trees. In rivers, large fish swim above the mobilized bed during floods, while rockbound invertebrates and attached algae are scoured and crushed. In these, probably common, cases, food-chain dynamics are altered primarily by succession at lower trophic levels (Figure 27.2h).

Species which first colonize disturbed habitats have proven more vulnerable to predation than late successional species in terrestrial (Cates and Orians, 1975; Reader and Southwood, 1981), marine (Sousa, 1980; Latchenco, 1986), and freshwater (Porter, 1977; Sommer, 1985; Sommer et al., 1986; Vanni and Temte, 1990; Power, 1992a) communities. Life history trade-offs between resilience to physical disturbance and resistance to predation occur because of design constraints: adaptations and life styles which protect consumers from predators tend to slow the recovery of their populations from indiscriminate mortality imposed by physical disturbances. Consider, for example, the aquatic moth larva, *Petrophila*. This insect, once established, is invulnerable to most predators in the Eel River because of its inconspicuous, sessile life beneath a silken tent attached to rock substrate. It can graze only the area under its tent, unlike mobile mayflies which forage widely and opportunistically on richer algal patches (Kohler, 1984). This restricted energetic intake, along with the allocation of time and energy to construction of the silken retreat rather than to protoplasm and gametes, slows the ability of such a species to rebuild its population after scouring floods. As time goes on, however, *Petrophila* and other sessile, case-dwelling grazers increasingly dominate consumer guilds from which the faster-growing, mobile, naked grazers (e.g., baetid mayflies) have been gleaned by predators. If defended primary consumers eventually sequester most of the habitat space and primary production, energy flow to predators, and the ability of predators to suppress primary consumers, should wane. By periodically reducing densities of defended taxa at lower trophic levels, disturbance could lengthen food chains.

Disturbance and productivity may interact to influence food chain length, sometimes also in a direction opposite to that previously predicted (Figure 27.3a). If sessile or ar-

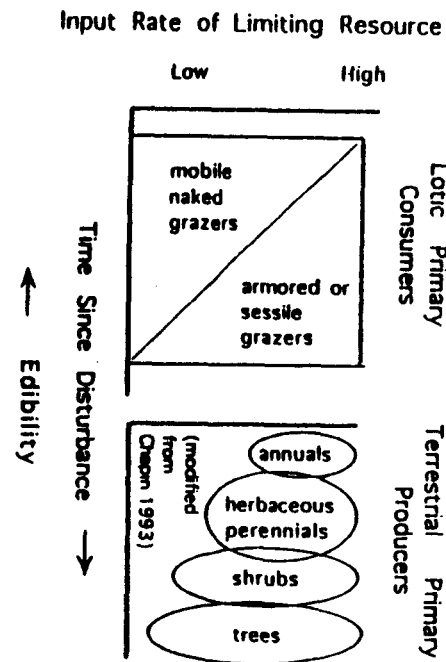


Figure 27.3. Types of taxa that dominate terrestrial primary producer assemblages (a) (modified from Chapin (1993)) and some lotic primary consumer assemblages (b) as a function of resource level and time since disturbance.

mored grazers grow and take over space and resources earlier in productive than in unproductive habitats, they might exclude vulnerable grazers sooner. Preliminary support comes from comparisons of invertebrate surveys in the sunny, productive South Fork Eel, and its dark, unproductive tributary, Elder Creek. In both channels, mobile grazers initially dominated in the spring, after scouring floods had subsided. Over the summer, as predator densities built up, sessile grazers increased until they were more abundant than declining mobile grazers. This switch in dominance within the primary consumer guild occurred one month later in dark Elder Creek than in the sunny South Fork Eel (Power, 1992b). (Further study is needed to assess, among other things, whether defended grazers competitively exclude vulnerable grazers when both experience increased resource inputs.)

In contrast, terrestrial plant responses to

productivity might lengthen food chains (Figure 27.3b). Plants endemic to nutrient-poor soils tend to have low relative growth rates (even when transferred to richer soils) and are less palatable to herbivores than plants from rich environments (e.g., Coley et al. (1985)). Intrinsic feedbacks reinforce the relationship between low productivity and attenuation of potential energy transfer. Herbivores may amplify initial differences in soil fertility by consuming high quality vegetation before plants resorb nutrients. If these herbivores are homeotherms, they burn off carbon and return proportionately more nitrogen to the soil, amplifying initial spatial variation in primary productivity (Chapin, 1993). When productivity is contingent on soil fertility, plant allocation and decomposition mechanisms, in addition to the original energetic arguments, could allow richer habitats to support longer food chains.

Intermediate Disturbance and Food Chain Length

If the switch at lower trophic levels from edible early successional species to less edible later successional species depicted for California rivers (Figure 27.4a) occurs in other systems, an intermediate frequency of disturbance should often maximize functional food chain length. It may be difficult to predict which trophic level will change most during succession because of idiosyncratic local natural histories, but taxa that trade off predator resistance against resilience to physical disturbance are likely to occupy lower trophic levels. Top predators which pursue mobile prey have to be highly mobile themselves (Oksanen, 1991), and this may preclude defenses like armor or refuging behavior. In addition, the need of top predators to locate and exploit recently disturbed patches where prey are more edible may be as important as energetic considerations in accounting for the larger foraging areas of higher trophic levels in both aquatic and terrestrial environments.

Several examples of succession from more edible to less edible taxa occur in primary producers. In midwestern (Power and Stewart, 1987) and California (Power, 1992b) rivers, filamentous green algae of the order Cladophorales, which become covered with

epiphytic diatoms, are replaced during succession by Zygnematales, which slough epiphytes with mucus secretions, and are less nutritious for grazers (Kupferberg et al., 1994). Following disturbance by boulder rolling, intertidal seaweeds undergo succession in which less edible *Gigartina* spp. replace more edible *Ulva* spp. (Sousa, 1979). Another intertidal sequence (Figure 27.4b) illustrates successional changes in food chain length. Wave bashing bares rock, which is initially colonized by algae that support grazers which can be suppressed by birds (Wootton, 1993; Frank, 1992; Lindberg et al., 1987). Over time, blue mussels and acorn barnacles replace seaweeds as dominant space holders. (These sessile invertebrates are often considered basal species, like primary producers. They hold space, and filter allochthonous plankton rather than allochthonous photons.) Mussels and acorn barnacles support predatory snails, which are eaten but not suppressed by birds (Wootton, 1990). Over time, however, goose barnacles become the dominant, space-holding basal species, and only one trophic level (birds) is supported (Wootton, 1993). Eventually, California mussels replace the goose barnacles, and are not effectively suppressed by any consumer in the upper intertidal (above the foraging range of the starfish *Pisaster*).

After disturbance lays bare dry land, highly edible weedy annuals colonize first, if resources suffice (Figure 27.4c) (Chapin, 1993). Annuals support small herbivores, such as insects, which are also weedy or fugitive (less-defended) species. Small invertebrate herbivores are often held in check by predators, parasites, or pathogens, so that they do not attain densities that measurably suppress plant biomass (e.g., De Bach (1974)). Over time, annuals are replaced by perennials (e.g., grasses) which can sustain heavy grazing by ungulates, which are often not predator-limited (McNaughton et al., 1989). Grasses are often succeeded by woody shrubs, which may be damaged by browsers, but are less likely to be kept at chronic low-standing crops by herbivory. Trees can make up the last stage in terrestrial plant succession, as when forests encroach upon old fields. Large trees store much of their aboveground carbon in refractory wood, and are unlikely to be demolished by herbivores.

Examples of Possible Successional Changes in Functional Food Chain Length

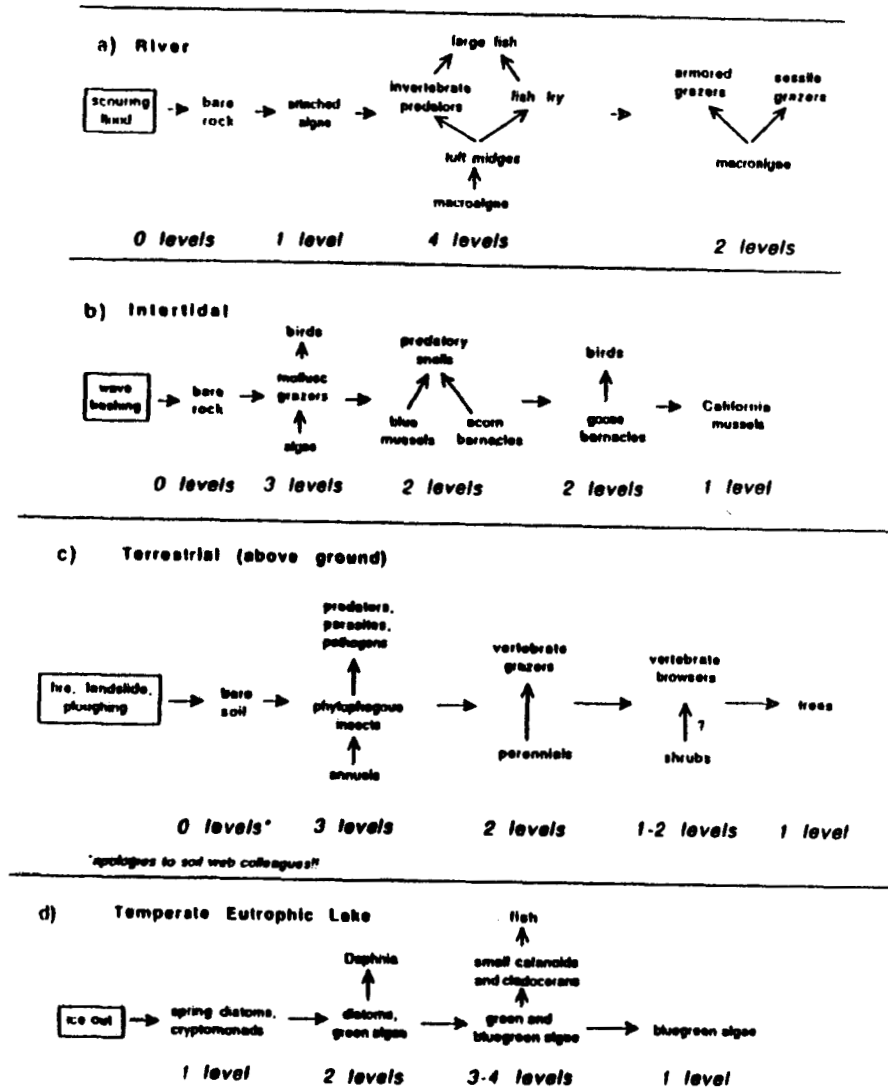


Figure 27.4. Examples of possible successional changes in functional food chain length in (a) A river under a Mediterranean hydrologic regime; (b) the upper rocky intertidal of the Pacific Northwest; (c) a terrestrial aboveground setting; and (d) a temperate eutrophic lake. Boxes surround the initial disturbance event which resets the community by imposing mortality and lowering densities of some organisms.

H Hairston et al. (1960) reasoned that mature terrestrial forests were three-level systems (maintained because predators checked herbivores). On the other hand, forests might be, at least periodically, one-trophic-level systems, dominated by large plants whose own structure and defense thwart damaging herbivory (Ehrlich and Raven, 1965; Murdoch, 1966). Clearly, trees are periodically vulnerable, as when bark beetles kill large tracts of drought-stressed pines, or when seedlings experience recruitment bottlenecks due to rodent grazers (Ostfeld and Canham, 1993). But large trees withstand herbivory and other stresses (e.g. floods, fires (Stone and Vascey, 1968)) that kill producers in more vulnerable life history or successional stages. Within the lifespan of adult trees, other factors that influence the intensity and functional importance of herbivory are likely to change (Ostfeld and Canham, 1993).

In contrast, algal life spans are brief compared to those of consumers in lakes. In temperate eutrophic lakes, both phytoplankton and zooplankton show pronounced seasonal succession (Vanni and Temte, 1990; Sommer, 1985). After ice-out, highly edible diatoms and cryptomonads bloom (Figure 27.4d). By summer, less edible cyanophytes dominate the phytoplankton. Large zooplankters like *Daphnia* dominate the zooplankton early on, but are replaced over time by smaller calanoid copepods and cladocerans, which are less conspicuous and profitable as prey for planktivorous fish. In Vanni and Temte's (1990) experiments in Lake Mendota, Wisc., zooplankton grazers suppressed spring phytoplankton, but not late-summer, cyanobacteria-dominated phytoplankton. These and other experiments suggest that during spring-summer lake succession, food chain lengths can increase (from one to two, three, or four functional trophic levels, depending on the impacts of planktivorous and piscivorous fish (Carpenter et al., 1987)), but may (by the criterion we use here) decline back to one functional trophic level after grazer-resistant algae come to dominate.

Scenarios depicted in Figure 27.4 might not occur if prey have sufficiently high rates of intrinsic increase that they need not invest in defense (Holt, 1977; Jeffries and Lawton, 1984), or if systems with invulnerable plants or prey are later invaded by such taxa (Til-

man, 1982). Other changes, driven by extrinsic factors like weather (Carpenter, 1988) or intrinsic changes such as the modification of predator-prey interactions by refuge provided by accruing plant biomass, will complicate successional trends predicted for food chain length. Rather than argue that intermediate disturbance should always lengthen food chains, we offer this idea as one hypothesis for probing the spatial and temporal changes in interaction strengths, trophic positions of taxa, and functional food chain lengths that complicate food webs in the real world.

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