

Hydraulic Food-Chain Models

An approach to the study of food-web dynamics in large rivers

Mary E. Power, Adrian Sun, Gary Parker, William E. Dietrich, and J. Timothy Wootton

No habitats on Earth are more dynamic than floodplain rivers. As large rivers flood and ebb, their floodplains and off-river water bodies are alternately connected and disconnected from the main channels. The area of inundated landscape can increase by two to three orders of magnitude from low to high water, and the surface area available for aquatic biological activity increases even more, because when floodplains are inundated, so are their grasses, trees, and the masses of dead organic material stored in these habitats. The enormous fluctuations in resources and habitats that accompany these flood pulses have profound effects on river-floodplain ecosystems (Bayley 1989, Junk et al. 1989, Sparks 1992, Welcomme 1985), whose constituent biota have a variety of feeding and life-history adaptations for sur-

Simulations linking physical and biological processes may guide research on ecological effects of massive changes to rivers and floodplains

viving and exploiting the fluctuations (Adis and Mahnert 1986, Goulding 1980, Junk et al. 1989, Lowe-McConnell 1975).

Floodplain rivers are not only dynamic but also spatially, hydrologically, and biologically complex (Figure 1; Junk et al. 1989, Welcomme 1985). Ecologists have long recognized that spatial heterogeneity and temporal fluctuation can play strong roles in maintaining the richness and complexity of ecological communities. In heterogeneous, fluctuating environments, consumers are less likely to overeat and exterminate their prey (Hastings 1977, Huffaker 1958). Competitors that dominate under particular conditions are likely to lose their performance advantage before they can exclude lesser competitors (Connell 1978, Hutchinson 1961, Tilman 1994). Therefore, the hydrologic fluctuations that impose huge mortality on river biota (Welcomme 1985) may, paradoxically, enhance the persistence of ecological com-

munities by reducing the chances that their constituent populations will go extinct (Sparks 1992, Welcomme 1985).

There is growing appreciation of the need to understand and predict the responses of river ecosystems to their massive rearrangement by humans. Nearly all of the major floodplain rivers in the northern hemisphere, and many in the southern hemisphere, have been leveed and/or impounded for navigation, agricultural development, power generation, or flood control. The 1993 flooding of the Mississippi rekindled the national debate over what is to be gained by increasing the height and extent of levees and what has been lost (Belt 1975, Leopold and Maddock 1954, Mairson 1994). Levees cut off large rivers from their floodplains; dams and diversions artificially stabilize flows, eliminating the natural flood cycles. These changes can be thought of as large-scale experiments that remove spatial and temporal heterogeneity, but they have been underexploited by ecologists, who could use them to study the importance of flood regimes for river and riparian ecosystems (Sparks et al. 1990). Whether rivers are restored by being reconnected to their historic floodplains or continue to be disconnected, tools are needed for predicting the responses of fisheries, nuisance species, and endangered species to hydrologic manipulation. Even when the focus is on target species rather than whole ecosystems, a food-web perspective is necessary, because the

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Figure 1. The Fly River of Papua New Guinea has a turbid (light brown) main channel and numerous, clear (dark) off-river water bodies. The channel is 200 m wide.

population dynamics of any species depends critically on how its resources, prey, and potential predators also respond to environmental change.

river from riparian tropical forests or grassy floodplains and dead aquatic vegetation. *Vegetation* is defined as living aquatic plants or algae. Some of this vegetation floats

(e.g., floating macrophytes, which are abundant in some tropical channels; Junk et al. 1989); some grows on and detaches from river substrates. *Herbivore-detritivores* or grazers feed on both vegetation and detritus and are envisioned in this case as being weak swimming, poorly streamlined organisms like prawns or crayfish (e.g., *Macrobrachium* spp. and *Orconectes* spp.). (Where fishes are dominant grazers, as in many tropical rivers, assumptions about grazer hydrodynamics would clearly change.) *Predators* are considered to be large fish, such as bass or baramundi (*Micropterus* spp., *Lates calcefer*), which are powerful swimmers and voracious consumers of animal prey. While issue can be taken with the simplifications and assumptions underlying our physical and particularly our biological approximations, we view them as examples that should be switched or expanded when the model is tailored to fit a specific river ecosystem. In this article, we use the model to explore how the fundamental temporal and spatial features of flood-

Hydraulic food-chain models

We are developing a modeling approach that links the relatively well-understood responses of river width, depth, and velocity to changes in discharge and the poorly understood responses of river biota to these hydraulic parameters. The food webs are modeled as modified Lotka-Volterra equations for food chains with three trophic levels and two energy sources—detritus and vegetation. We recognize that the strengths of interaction between or among the trophic levels are modulated by the hydrologic changes accompanying the flood pulse. Our purpose in this article is to illustrate a conceptual framework that, when tailored to specific ecosystems, can guide field observations and measurements.

As a first exploratory step, we have aggregated entities in a hypothetical river food web into four functional groups intended to represent the dominant consumers and resources in a river food chain. *Detritus* comprises dead plant material, both litter introduced into the

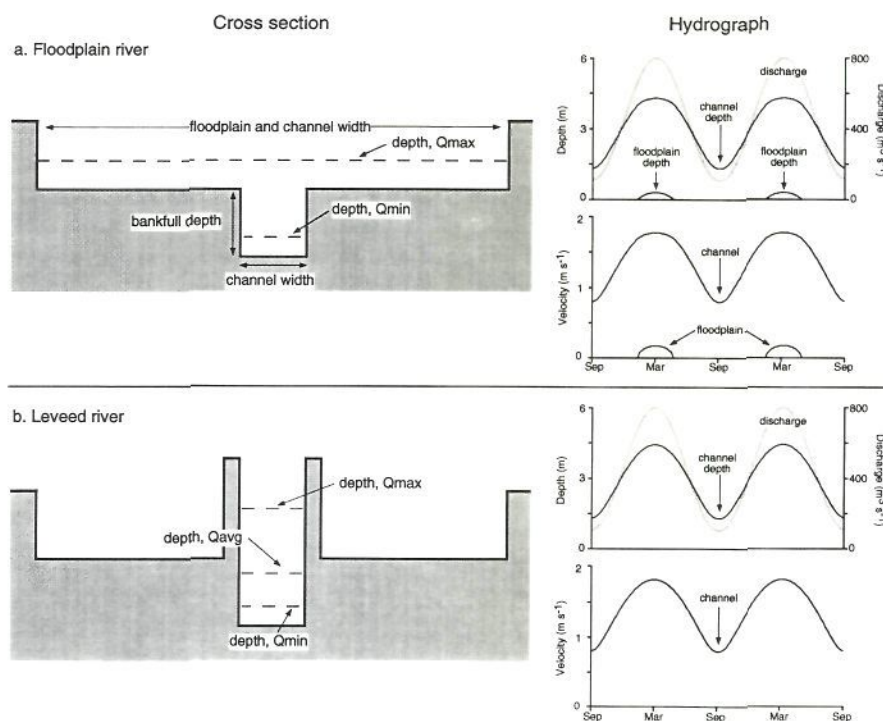


Figure 2. Cross-sections through idealized floodplain (a) and leveed (b) river channels, with corresponding hydrographs for channels with unregulated, sinusoidal flow. Dashed lines indicate channel depth at maximal and minimal discharge in the floodplain river; maximal and minimal discharge in the leveed river with an unregulated hydrograph; and chronic depths with artificially regulated low ($Q_{min} = 100 \text{ m}^3/\text{s}$) and average ($Q_{avg} = 450 \text{ m}^3/\text{s}$) discharge.

plain rivers influence the dynamics of our food chain.

Hydraulic relationships

Although floodplain rivers have complex morphologies, with off-river water bodies that vary in area, depth, shape, elevation, and frequency of connection to the channel, we assume in this article that the single main channel and its floodplain are simple rectangles in cross-section (Figure 2). We consider three cases: a natural river with access to its floodplain; a leveed river cut off from its floodplain by levees that retain high flows; and a river with artificially stabilized flow that never exceeds the tops of its bank, as might occur downstream of a diversion routing water out of the channel or as a regulated release stream from an impoundment. A comparison of the floodplain river and the leveed river with the same hydrograph isolates the effect of habitat expansion and contraction on modeled food-chain dynamics. The influence of temporal hydrologic fluctuation is shown by comparing food chains in the leveed river with a flood cycle and in the same channel with artificially stabilized discharge.

In the model floodplain river, dry-season flow is entirely contained within the main channel. When the depth of rising water in the channel exceeds bank-full depth, the flow spills over and instantly inundates the entire floodplain. Flow is conveyed downstream rapidly through the channel and, after spillover, much more slowly over the floodplain, where it is impeded by roughness from vegetation and organic detritus. The difference in flow rates between channel and floodplain can be calculated from empirical equations relating the roughness of the channel to the flow velocity. Channel and floodplain velocities determine how the total discharge is apportioned between these two habitats (Henderson 1966, Parker 1993).

Total discharge varies seasonally. We use an oscillating sine wave to represent a 12-month cycle with one dry season and one rainy season. In the natural river with access to its floodplain (Figure 2a), most of the



Figure 3. Baramundi (*Lates niloticus*) could be a top predator in the food web modeled in this article. The fish is being displayed by the true top predator in the Fly River food web.

increase in discharge during the rainy season is absorbed by the huge expansion of the river's width. In the leveed channel (Figure 2b), width cannot change, and changes in discharge are apportioned between river depth and flow velocity. Leopold et al. (1964) discuss the hydraulic geometry of rivers (empirical relationships of width, depth, and velocity with discharge).

Trophic relationships

Like their physical setting, trophic networks in rivers are complex and dynamic. Trophic linkages between species form, break, and change in strength as environmental conditions change (Power 1992a, b). Food chains and aggregated functional groups are extremely simplified abstractions that ignore much of the real complexity of food webs. Experimental and comparative studies, however, have suggested that, at least in smaller rivers, there are chains of strong interactions within food webs that dynamically link predators through consumers to plants and detritus (Bowlby and Rolf 1986, Northcote 1988, Perrin et al. 1987, Power 1990, Power et al. 1985, Wootton and Power 1993). Evidence for the importance of strong chains through complex webs

comes from trophic cascades, in which removal or reductions of predators release consumers, which in turn suppress populations of their own resources, producing alternating release and suppression of trophic levels that often reach down to primary producers. Trophic cascades have been documented in lakes (Carpenter et al. 1985), subtidal marine habitats (Estes and Palmisano 1974), and terrestrial communities (Kajak et al. 1968) as well as in rivers.

In developing our hydraulic food-chain model, we initially focus on a three-level food chain with both detrital and producer energy sources, in hopes that interactions of these elements with each other and with their physical environment will capture much of the dynamics to which other components of the river ecosystem are entrained. Equations for biomass dynamics of each of the four trophic elements are tied to channel hydraulics because key parameters in these equations are made functions of width, depth, velocity, or a combination of these variables (see box page 163 and Tables 1 and 2).

Detritus standing stocks increase as terrestrial plant litter falls into the channel or inundated floodplain and as vegetation growing within the river dies. Detritus is lost to

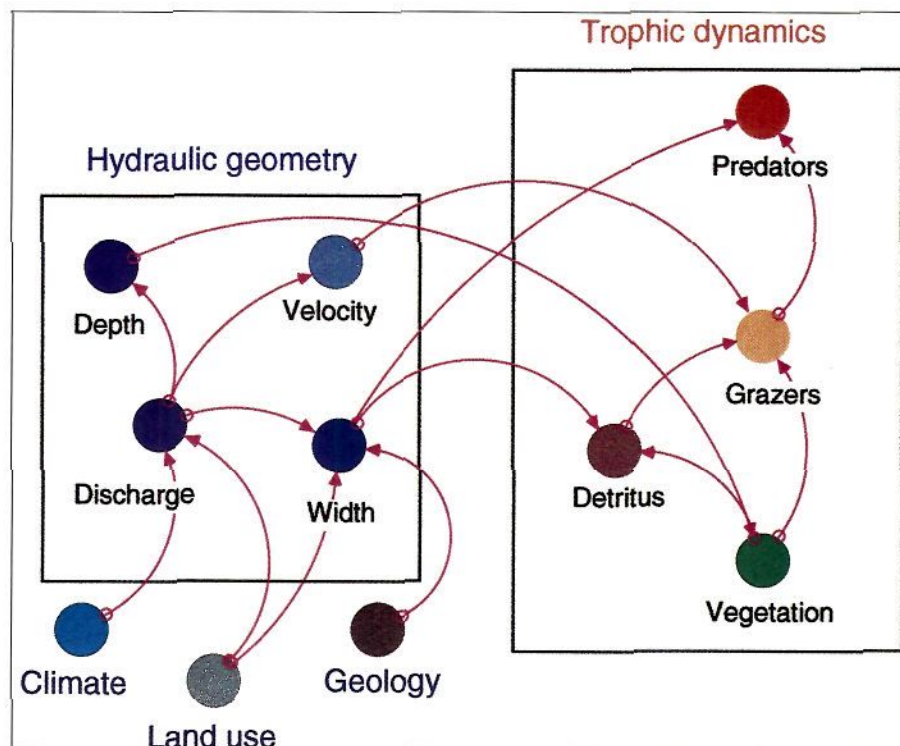


Figure 4. Overview of causal linkages assumed in the hydraulic food-chain model (diagram from Stella simulation software). In natural channels, local geology constrains channel and floodplain width by determining factors like bank cohesiveness or location of mountain ranges or terraces bordering the active floodplain. Alternatively, channel width can be determined by human land use, if levees have been constructed. In natural channels, climate (precipitation) controls discharge. Alternatively, discharge can be artificially regulated by humans by means of upstream diversion or retention structures. Discharge is divided between depth and velocity while flow is confined to the channel and among width, depth, and velocity after spillover in channels with access to their floodplains. Parameters in the trophic equations are functions of hydraulic variables (Table 1). A variety of alternative functional dependencies of trophic parameters on width, depth, velocity, or interactions of these variables could be important in particular food webs.

grazers at a rate determined by their density and that of the detritus, as well as by the grazer's per capita ingestion rate of detritus. For simplicity, we have initially assumed constant per capita ingestion rates by all consumers and predators. Ingestion rates may, however, slow as consumers satiate, particularly if resource availabilities increase abruptly relative to consumer densities. In this case, rates are better modeled with a saturating function such as the Type II functional response of Holling (1959). Detritus is also diminished as carbon is respired to the atmosphere as carbon dioxide. (Losses from the channel reach by downstream flushing of organic matter or living components of the food chain are assumed to be balanced by material washing into

the reach from upstream, so outwash does not change local standing stocks.)

Vegetation renews by logistic growth until it becomes self-limiting, for example, due to self-shading, at a density equal to the environment's carrying capacity. Vegetation that dies without being grazed increases the detritus. (Massive, abrupt die-off of aquatic vegetation may accompany reconfinement of the channel. The amount of vegetation that becomes available as detritus to the river food web depends on factors, such as temperature, that control terrestrial decomposition and export of this material during the low-water period; Bayley page 153 this issue.)

Grazers convert vegetation or detritus to offspring with an effi-

ciency we assume here to be equal, although it could often be lower for detritus, whose food quality depends on the activity and abundance of associated microbial flora (Cummins 1973, Petersen et al. 1989). Grazers are killed by predators or die of other causes. Predators create offspring from their prey and, being at the top of the food chain, suffer only nonpredatory mortality in the model presented here. (Clearly, human fishing adds another functionally significant trophic level in many rivers; Figure 3.)

We assume that plants, but not grazers or predators, have growth rates that are sufficiently rapid, relative to time scales of seasonal environmental change, to attain densities at which competition has dynamic significance. This assumption can be modified to portray ecosystems in which competition occurs within other trophic groups. Details of our equations and parameter values will be presented elsewhere.¹

Linkage of hydraulic and trophic dynamics

In mathematical models, trophic interactions have often been investigated as somewhat disembodied entities, detached from realistic physical or temporal settings (but see Crowley 1978, DeAngelis 1992, Hastings 1977, Holt 1985, Oksanen 1990, Wootton and Power 1993). Most real food webs, however, occur in patchy, gradually changing, or periodically disturbed environments. Our model incorporates both abrupt and gradual changes affecting trophic interactions and biomass dynamics in one (leveed or regulated channel) or two (floodplain and river) habitats. Because we begin here with a one-dimensional model portraying large-river hydraulic and trophic dynamics at a single cross-section, our current model emphasizes temporal dynamics rather than spatial heterogeneity. In the future, it is likely to be important to incorporate more spatial heterogeneity by representing off-river water bodies important in the function of

¹M. E. Power, G. Parker, W. E. Dietrich, and A. Sun, 1995, manuscript in preparation.

river-floodplain ecosystems (Bayley 1989, Junk et al. 1989, Sparks 1992).

An overview of causal linkages assumed in our model is depicted in Figure 4. Local geomorphology (e.g., where terraces or mountains confine the floodplain) and land use (e.g., whether or not levees have been constructed) determine floodplain width. Climate (e.g., precipitation) and land use (e.g., water storage or diversion) govern discharge. Width, depth, and velocity vary with discharge. How these variables adjust to discharge depends on the cross-sectional dimensions of the channel and floodplain (Figure 2). Width, depth, and velocity influence trophic dynamics by affecting key parameters in the biomass balance equations (see box this page and Table 1) and by affecting the seasonal access of biota to the floodplain in unveeved channels.

Floodplain and channel habitats in unveeved rivers are connected and disconnected abruptly when flow depth spills overbank or ebbs below bank-full depth and is reconfined in the channel. At spillover, the large standing stock of dead plant material on the floodplain becomes available to river grazers. After spillover, these grazers, as well as their predators, distribute themselves evenly over all inundated habitat (so their densities in channels temporarily drop). Here, we assume that mobile grazers and predators occupy the floodplain only when water is deeper than 0.2 m because this depth has been found to be a critical threshold below which larger prey are vulnerable to fishing birds. Armored catfish (family loricariidae) in Panama and grazing minnows (*Camptostoma*) in Oklahoma avoid water shallower than 0.2 m, even when their food is abundant there and scant in deeper habitats (Power 1984, 1987). Similarly, crayfish (*Orconectes propinquus*) in Michigan may avoid shallow water because of risk from wading and diving birds, as well as terrestrial predators like raccoons (Creed 1990, 1994).

Some vegetation in the channel is attached to the substrate and some floats freely. At spillover, the free-floating fraction is distributed over the floodplain, where it grows rapidly because of the enormous in-

Biomass balance equations for trophic dynamics subject to hydraulic constraints

$$\begin{aligned} \text{Detritus:} \quad & \frac{dD}{dt} = I + m_v V - c_h HD - m_d D \\ \text{Vegetation:} \quad & \frac{dV}{dt} = rV \left(\frac{K-V}{K} \right) - c_h HV - m_v V \\ \text{Herbivore-detritivores (grazers):} \quad & \frac{dH}{dt} = b_h c_h HV + b_h c_h HD - c_p HP - m_h H \\ \text{Predators:} \quad & \frac{dP}{dt} = b_p c_p HP - m_p P \end{aligned}$$

Table 1. Symbols used in biomass balance equations.

Symbol	Meaning	Units
D	Detritus standing stock	g/m ²
V	Vegetation biomass	g/m ²
H	Grazer biomass	g/m ²
P	Predator biomass	g/m ²
b _h	Conversion efficiency for grazers eating vegetation or detritus	g/g
b _p	Conversion efficiency for predators eating grazers	g/g
c _h	Per capita grazing rate on detritus or vegetation	m ² ·g ⁻¹ ·d ⁻¹
c _p	Per capita predation rate on grazers	m ² ·g ⁻¹ ·d ⁻¹
r	Maximal intrinsic rate of increase for vegetation	d ⁻¹
I	Input of allochthonous detritus	g·m ⁻² ·d ⁻¹
K	Carrying capacity (asymptotic biomass) for vegetation	g/m ²
m _d	Loss rate of detritus	d ⁻¹
m _v	Nongrazing mortality of channel vegetation	d ⁻¹
m _h	Mortality of grazers not due to predation	d ⁻¹
m _p	Mortality of predators	d ⁻¹

crease in habitat surface area. On the falling limb of the hydrograph, when flow drops to bank-full depth, the water is reconfined in the channel, drying up the floodplain. Standing stocks of detritus and vegetation available to the river consumers drop to zero on the floodplain, while standing stocks within the channel do not change. In contrast, mobile grazers and predators return to the channel, except for that fraction left stranded on the floodplain. Mortality from stranding can be high. Bonnetto et al. (1969, cited in Welcomme 1985, p. 170) estimated that in the Paraná River, Argentina, the biomass of fish that die annually by stranding is four times that caught by the fishery.

Between the threshold transitions of spillover and reconfinement, gradual changes in width, depth, and velocity also affect the performance, gains, and losses of food-chain constituents. There are few

data quantifying how hydraulic parameters affect the performance of organisms likely to be dominant interactors in river food webs, so our discussion here is largely speculative. The elucidation of mechanistic linkages between physical environmental variables and species' performance and impacts is one of the most crucial areas of research for the eventual application of models to actual problems.

Trophic parameters in each of the biomass balance equations (in box) can be linked to hydraulic variables. For example, we might expect the loss rate of detritus as respired carbon dioxide to decrease with increasing depth, because water temperature and microbial concentrations would both be likely to decrease as depth increases. Vegetation carrying capacity (K) should decrease with depth if vegetation is light-limited. If plants are nutrient-limited, their growth rate (r) might

Table 2. Hydraulic influences.

Symbol	Response	Used in simulations
c_h	Decreases linearly with velocity after a certain threshold, and ramps down to zero at the slip speed	Yes
c_p	Decreases with width, due to higher proportion of refuge area on floodplain. In channel, increases above a threshold velocity at which flow dislodges and washes away refuges	Yes
l	Increases with width, due to higher litter input over floodplain	Yes
K	Decreases with depth due to light limitation	No
r	Increases with velocity due to increases in nutrient flux	No
m_d	Decreases with depth due to temperature or oxygen stratification	No

increase up to a point with velocity, which would increase the flux of nutrients available to attached vegetation (Whitford and Schumaker 1964). Above a certain velocity, however, local growth might be reduced by sloughing, or by light limitation if high flows become more turbid. Arthropod grazers like crayfish or prawns that are not particularly streamlined might use fewer of their appendages for food gathering and more for holding on to the substrate as flow velocity increased.

In our model, we assume such grazers feed at a maximal rate until currents reach a threshold velocity, above which their per capita ingestion rates decline linearly, until they lose their grip on the substrate and stop grazing altogether. We call that velocity the slip speed. For eight crayfish species, slip speeds in plexiglass flumes ranged between 26 and 50 cm/s (Maude and Williams 1983). Hart (1992) found that at near-bed velocities of more than 50 cm/s in a cobble-bedded Michigan stream, a dominant attached macroalga, *Cladophora*, escaped grazing from crayfish, which were able to suppress the alga at lower current velocities. (Hart attributed the higher apparent slip speed for crayfish in the field to the rough streambed.) Predator attack rates on grazers might also decline with current velocity because of constraints on prey encounter or handling (Hansen et al. 1991). How-

ever, we visualize the top predators as powerful, streamlined swimmers like predatory fish (Figure 4). Swimming power may compromise maneuverability, however, so we have made predator attack rates reflect limited ability to search in structural refuges for prey.

Prey refuges in the main channel are envisioned as log jams that, like grazers, can be dislodged by high flows. In model simulations, refuges cover a maximal proportion of the channel bed (5%) at low flow, but they begin to be dislodged at flow velocities of 1 m/s and are washed away when flows exceed 2 m/s. Refuges for prey from predators are assumed to cover 20% of the floodplain, where current velocities never get high enough to dislodge them. As a consequence, predator attack rates are even lower after spillover than would be expected from prey dilution over the floodplain.

Results from preliminary simulations

Examples of simulation output for a floodplain river with one high and one low water period per year simulated by sinusoidal discharge, a leveed river with the same sinusoidal discharge, and a regulated river with artificially stabilized low (100 m³/s) and artificially stabilized average (450 m³/s) flow are shown in Figure 5. The floodplain river with both temporal and spatial seasonal dy-

namics (Figure 5a) maintains, over the long term, the most stable populations at higher trophic levels (grazers and predators). In the leveed channel with sinusoidal discharge, predators initially increase as they benefit from prey concentrated in channels with little refuge. This initial advantage, however, allows predators to harvest their prey at an unsustainable rate, so prey are eventually driven to low levels at which predators starve.

In channels in which constant low discharge is maintained, grazers show damped oscillations but persist. Grazer oscillations are coupled with damping oscillations in their detrital and plant foods, as in many other trophic models that, like ours, are derived from classical Lotka-Volterra models of consumer-resource dynamics. The grazer densities that are eventually sustained in the low, constant discharge channel are not sufficient, however, to maintain a viable predator population. Predators decline asymptotically to zero in this simulation (Figure 5c). In the channel with constant average discharge, flows are chronically too high for the nonhydrodynamic grazers to feed effectively, and they starve, followed by the crash of their predator's population.

Although these simulation results are consistent with some predictions about the influence of spatial heterogeneity and temporal fluctuation on population and food-web persistence (Huffaker 1958, Hutchinson 1961), they are at odds with others. In mathematical models of food webs that lack explicit temporal or spatial contexts, longer food chains were found to be more dynamically fragile with longer return times to equilibria following perturbations (Pimm 1982). Therefore, food webs with short chains were predicted to predominate in nature, particularly where environments are perturbed (Pimm 1982, Pimm et al. 1991). Our simulations, in contrast, suggest that the longest (three-level) food chains are maintained only when the environment fluctuates. Predator populations persist longer in channels subject to discharge fluctuation than in channels with stabilized flow (Figure 5b versus Figures 5c and 5d), and they persist over the

long term only when biota have periodic access to inundated floodplains (Figure 5a).

These results are congruent with current understanding of the importance of the flood pulse in floodplain rivers (Bayley 1989, Junk et al. 1989, Sparks et al. 1990). A somewhat more unexpected outcome of these simulations is that biota do not simply track hydrologic changes. Longer biotically driven cycles can be superimposed on the hydrologic cycles (e.g., Figure 5b). In other simulations, predators, grazers, and vegetation showed damped oscillations with wavelengths much longer than the annual hydrologic cycles, which were closely tracked only by detritus. These cycles damped as the modeled food web adjusted to a perturbation caused by setting initial densities at levels away from the system's equilibrium. While aspects of this behavior depend on arbitrary initial conditions, transient dynamics following perturbations may be quite important in real rivers, which can experience striking year-to-year, as well as within-year, variation in discharge.

In the simulations reported here, the hydrograph had seasonal, but no year-to-year, variation. Few river hydrographs are this regular, but some, for example, that of the Orinoco River at Ciudad Bolivar (Figure 21.5 in Vasquez and Wilbert 1993), are close. In future studies, we plan to use hydraulic food-chain models to explore the effects of runs of unusually dry or wet years on food webs.

Future needs and directions

To advance modeling efforts to the point where they might eventually address real ecological and management issues, we need better information on two aspects of river food webs. First, which are the key taxa or functional groups that are linked in the chains of strong interactions? Second, how do their performances and impacts in food webs vary under changing environmental conditions, such as the dramatic fluctuations in area, depth, and velocities of river habitats?

These questions are interrelated.

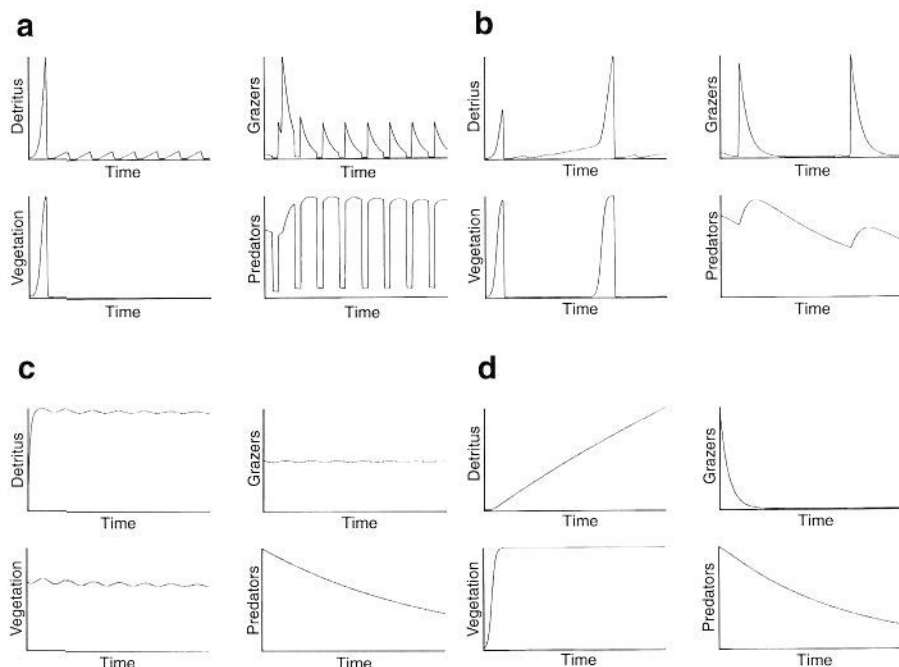


Figure 5. Simulation results for four cases: (a) a river with access to its floodplain and sinusoidal discharge (only channel shown); (b) a leveed river with sinusoidal discharge retained entirely within the channel; and regulated rivers with low (c) and average (d) flow that does not exceed bank-full depth.

Properties of organisms, for example their size, are likely to affect their performance under certain environmental conditions, and environmental conditions are likely in large part to determine which types of organisms can be "strong interactors" (Paine 1980) at a given place and time. Slip speeds for grazers, for example, are likely to depend on whether large prawns or minuscule mayflies (order Ephemeroptera) are the dominant consumers of vegetation and detritus in the food web. Which grazers dominate, in turn, is likely to be strongly influenced by which prove hydrodynamically competent under particular flow regimes (Hart 1992).

Size structure and life-history stage structure are important features of biological populations (Ebenman and Persson 1988, Mittelbach et al. 1988) not yet accounted for in our model. Welcomme and Hagborg (1977) modeled growth, mortality, and recruitment for a river-floodplain fish population with four discrete age classes, exploring the impacts on fish production of minimal dry season area and maximal area inundated during floods. One promising area for future de-

velopment would be to combine models of age- or size-structured populations, like theirs, with models of multitrophic level interactions, like ours, in an exploration of how population and community dynamics interact in fluctuating environments. A particularly crucial feature to study would be seasonal life-history bottlenecks for key populations.

Different life-history stages of river organisms typically occupy different habitats. For example, off-river water bodies (e.g., oxbow lakes, billabongs, or varzea lakes) serve as rearing habitats for juveniles of species that occupy the main river channels after reaching maturity (Welcomme 1985). In addition, different fish species may segregate between off-river lakes and the main channel during low flow and then interact as both enter the floodplain after its inundation (Welcomme 1985). Our model does not represent off-river water bodies, but the consequences for food webs of the spatial heterogeneity and potential refuges from predators and competitors that they contribute are important to explore in future modeling efforts.

In addition to the general compli-

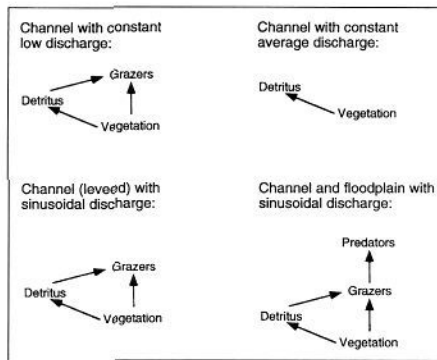


Figure 6. In these simulation results, food chains are shortened to one or two levels in channels without access to their floodplains, and the predator level persists only when floodplains are periodically inundated.

cations introduced by size and habitat structure, site-specific natural history information is necessary to tailor models to specific ecosystems. We have attempted to model the habitat and trophic dynamics related to spillover, reconfinement, and hydraulic changes driven by seasonal discharge fluctuations, which are macroscale attributes of all large rivers. It is harder to generalize the postulated trophic interactions among large rivers.

We expect that some behaviors of our model are general, such as seasonal dynamics of the food web due to the tendency of grazers to profit from access to the inundated floodplain and the tendency of predators to benefit when prey are concentrated with them in channels. These dynamics underlie the tendency of temporal and spatial variation to promote the persistence of longer food chains (Figure 6), as Huffaker's (1958) experiments demonstrated. Other results are clearly sensitive to the natural history features postulated for specific strong interactors, such as the grazer slip speeds. Modeling efforts are useful if they focus attention on those natural history attributes of biota and ecosystems that warrant further study because of their potential importance to dynamics.

Conclusions

Large rivers have been defined as "those large enough to intimidate research workers" (D. P. Dodge, cited by Hynes 1989). Modeling ef-

forts are particularly important to guide field studies in these large, dynamic systems, where sampling and experimental manipulations are difficult. We see the interplay of modeling and field investigation as the best approach to understanding the complex environmental problems such as those that arise when levees eliminate the floodplain and the flood pulse, or regulation eliminates, alters, or dampens seasonal changes in discharge—the master variable that limits and resets river populations throughout entire drainage networks. We expect that future research is likely to support the basic ecological paradox of rivers: that large, frequent hydrologic perturbations are crucial for long-term maintenance of their biodiversity, their enormous productivity, and the higher trophic levels, which include the biological populations most prized by humans.

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References cited

Adis, J. and V. Mahnert. 1986. On the natural history and ecology of *Pseudoscorpiones* (Arachnidae) from an Amazonian blackwater inundation forest. *Amazoniana* 9: 297–314.

Bayley, P. B. 1989. Aquatic environments in the Amazon Basin, with an analysis of carbon sources, fish production, and yield. *Can. Spec. Publ. Fish. Aquat. Sci.* 106: 399–408.

—. 1995. Understanding large river-floodplain ecosystems. *BioScience* 45: 153–158.

Belt, C. B. Jr. 1975. The 1973 flood and man's constriction of the Mississippi River. *Science* 189: 681–684.

Bonetto, A. A., W. Dioni, and C. Pignatelli. 1969. Limnological investigations on biotic communities in the middle Parana river valley. *Int. Ver. Theor. Angew.*

Limnol. Verh. 17: 1035–1050.

Bowlby, J. N. and J. C. Roff. 1986. Trophic structure in southern Ontario streams. *Ecology* 67: 1670–1679.

Carpenter, S. R., J. F. Kitchell and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35: 634–639.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310.

Creed, R. P. Jr. 1990. The direct and indirect effects of omnivorous crayfish on stream benthic communities. Ph.D. dissertation, Michigan State University, East Lansing, MI.

Creed, R. P. Jr. 1994. Direct and indirect effects of crayfish grazing in a stream community. *Ecology* 75: 2091–2103.

Crowley, P. H. 1978. Effective size and the persistence of ecosystems. *Oecologia* 35: 185–195.

Cummins, K. W. 1973. Trophic relations of aquatic insects. *Annu. Rev. Entomol.* 18: 183–206.

DeAngelis, D. L. 1992. *Dynamics of Nutrient Cycling and Food Webs*. Chapman and Hall, London, UK.

Ebenman, B. and L. Persson. 1988. *Size-structured Populations*. Springer-Verlag, Berlin, Germany.

Estes, J. A. and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. *Science* 185: 1058–1060.

Goulding, M. 1980. *The Fishes and the Forest: Explorations in Amazonia Natural History*. California University Press, Berkeley, CA.

Hansen, R. A., D. D. Hart, and R. A. Merz. 1991. Flow mediates predator-prey interactions between triclad flatworms and larval black flies. *Oikos* 60: 187–196.

Hart, D. D. 1992. Community organization in streams: the importance of species interactions, physical factors, and chance. *Oecologia* 91: 220–228.

Hastings, A. 1977. Spatial heterogeneity and the stability of predator-prey systems. *Theor. Popul. Biol.* 12: 37–48.

Henderson, F. M. 1966. *Open Channel Flow*. MacMillan Publishing Co., New York.

Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European Pine Sawfly. *Can. Entomol.* 91: 293–320.

Holt, R. D. 1985. Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution. *Theor. Popul. Biol.* 28: 181–208.

Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* 27: 343–383.

Hutchinson, G. E. 1961. The paradox of the plankton. *Am. Nat.* 95: 137–146.

Hynes, H. B. N. 1989. Keynote address. *Can. Spec. Publ. Fish. Aquat. Sci.* 106: 5–10.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. *Can. Spec. Publ. Fish. Aquat. Sci.* 106: 110–127.

Kajak, A., L. Andrzejewska, and Z. Wojcik. 1968. The role of spiders in the decrease of damages caused by Acridoidea on

- meadows—experimental investigations. *Ecol. Pol.* 16: 755–764.
- Leopold, L. B., and T. Maddock. 1954. *The Flood Control Controversy*. Ronald Press, New York.
- Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. *Fluvial Processes in Geomorphology*. Freeman, San Francisco, CA.
- Lowe-McConnell, R. H. 1975. *Fish Communities in Tropical Freshwaters*. Longman, London, UK.
- Mairson, A. 1994. Great flood of '93. *Nat. Geogr. Mag.* 185: 42–81.
- Maude, S. H., and D. D. Williams. 1983. Behavior of crayfish in water currents: hydrodynamics of eight species with reference to their distribution patterns in southern Ontario. *Can. J. Fish. Aquat. Sci.* 40: 68–77.
- Mittelbach, G. G., C. W. Osenberg, and M. A. Leibold. 1988. Trophic relations and ontogenetic niche shifts in aquatic ecosystems. Pages 219–235 in B. Ebenman and L. Persson, eds. *Size-Structured Populations*. Springer-Verlag, Berlin, Germany.
- Northcote, T. G. 1988. Fish in the structure and function of freshwater ecosystems: a "top down" view. *Can. J. Fish. Aquat. Sci.* 45: 361–379.
- Oksanen, T. 1990. Exploitation ecosystems in heterogeneous habitat complexes. *Evol. Ecol.* 4: 220–234.
- Paine, R. T. 1980. Food webs: linkage, interaction strength, and community infrastructure. *J. Anim. Ecol.* 49: 667–685.
- Parker, G. 1993. Howard Creek Diagnostic Study, White Sulphur Springs, West Virginia. Report prepared for the Soil Conservation Service, US Department of Agriculture, Morgantown, WV.
- Perrin, C. J., J. L. Bothwell, and P. A. Slaney. 1987. Experimental enrichment of a coastal stream in British Columbia: effects of organic and inorganic additions on autotrophic periphyton production. *Can. J. Fish. Aquat. Sci.* 44: 1247–1256.
- Petersen, R. C. Jr., K. W. Cummins, and G. M. Ward. 1989. Microbial and animal processing of detritus in a woodland stream. *Ecol. Monogr.* 59: 21–39.
- Pimm, S. L. 1982. *Food Webs*. Chapman and Hall, London, UK.
- Pimm, S. L., J. H. Lawton, and J. E. Cohen. 1991. Food web patterns and their consequences. *Nature* 350: 669–674.
- Power, M. E. 1984. Depth distributions of armored catfish: predator-induced resource avoidance? *Ecology* 65: 523–528.
- _____. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. Pages 333–352 in W. C. Kerfoot and A. Sih, eds. *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England, Hanover, NH.
- _____. 1990. Effects of fish in river food webs. *Science* 250: 411–415.
- _____. 1992a. Top-down and bottom-up forces in food webs: Do plants have primacy? *Ecology* 73: 733–746.
- _____. 1992b. Habitat heterogeneity and the functional significance of fish in river food webs. *Ecology* 73: 1675–1688.
- Power, M. E., W. J. Matthews, and A. J. Stewart. 1985. Grazing minnows, piscivorous bass and stream algae: dynamics of a strong interaction. *Ecology* 66: 1448–1456.
- Sparks, R. E. 1992. Risks of altering the hydrologic regime of large rivers. Pages 119–152 in J. Cairns Jr., B. R. Niederlehner, and D. R. Orvos, eds. *Predicting Ecosystem Risk*. Advances in Modern Environmental Toxicology—Vol. 20. Princeton Scientific Publishing Co., Princeton, NJ.
- Sparks, R. E., P. B. Bayley, S. L. Kohler, and L. L. Osborne. 1990. Disturbance and recovery of large floodplain rivers. *Environ. Manage.* 14: 699–709.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2–16.
- Vasquez, E., and W. Wilbert. 1993. The Orinoco: physical, biological and cultural diversity of a major tropical alluvial river. Pages 448–471 in P. Calow and G. E. Petts, eds. *The Rivers Handbook*. Blackwell Scientific Publications, London, UK.
- Welcomme, R. L. 1985. River fisheries. Fisheries Technical Paper 252. UN Food and Agricultural Organization, Rome, Italy.
- Welcomme, R. L., and D. Hagborg. 1977. Towards a model of a floodplain fish population and its fishery. *Environ. Biol. Fishes* 2: 7–24.
- Whitford, L. A., and G. J. Schumacher. 1964. Effect of a current on respiration and mineral uptake in *Spirogyra* and *Oeclogonium*. *Ecology* 45: 168–170.
- Wootton, J. T., and M. E. Power. 1993. Productivity, consumers, and the structure of a river food chain. *Proc. Natl. Acad. Sci. USA* 90: 1384–1387.
- Zaret, T. M., and R. T. Paine. 1973. Species introduction in a tropical lake. *Science* 182: 449–455.

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Currently, there are only about 1,800 manatees left.

Need for Ecosystem Management of Large Rivers and Their Floodplains

These phenomenally productive ecosystems produce fish and wildlife and preserve species

Richard E. Sparks

Most of the 79 large river-floodplain ecosystems in the world have been altered by human activities; the rest are likely to be altered soon (Welcomme 1985). These complex ecosystems are composed of the flowing channels that most people associate with rivers, together with the floodplain lakes, backwaters, forests, and wetlands that harbor much of Earth's terrestrial and freshwater biodiversity (Figures 1-3). River-floodplain ecosystems, unlike most lakes, are characterized by seasonal floods that promote the exchange of nutrients and organisms among a mosaic of habitats and thus enhance biological productivity (Bayley page 153 this issue, Junk et al. 1989).

Annual flood pulses are so predictable and long-lasting that plants, animals, and even human societies have adapted to take advantage of them. In ancient Egypt and Mesopotamia, the fertility of the soils was renewed each year by the annual overflow of the rivers, thereby sustaining large populations in one place for millennia and permitting the development of great civilizations. Outside these floodplains, the fertility was exhausted by a few years of steady cultivation, so people had to move on.

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Ecosystem management works to guide, rather than thwart, natural processes

Despite centuries of alteration in the developed world, remnant river-floodplain ecosystems still exist. Central Europe's largest river, the Danube, retains 650 km² of its former floodplain in Slovakia and Hungary despite changes caused by dredging, channelization, and dam-building (Bacalbasa-Dobrovici 1989, Pearce 1994).

In the United States, most of the 98,000-square-kilometer floodplain along the Mississippi downstream from the mouth of the Ohio has been leveed and drained for agriculture, but sizable floodplains have been preserved along the upper Mississippi north of St. Louis as part of the National Fish and Wildlife Refuge System (NRC 1992). Two large tributaries of the Mississippi—the Illinois River, and the lower portion of the Missouri River—retain flood pulses and floodplains, and a major distributary (branch) of the Mississippi—the Atchafalaya—is building new deltaic floodplain in the Gulf of Mexico, thereby increasing what is already North America's largest remaining (5700 km²) river overflow swamp (Hesse et al. 1989, 1993, NRC 1992).

In the developing world, exten-

sive river-floodplain ecosystems remain, but they are diminishing at increasing rates as land use intensifies and as many countries attempt to follow the western model of economic development through the use of massive water resource projects (Sparks 1992). There now are dams on virtually all the large rivers in Africa (Obeng 1981). In South America, the upper Paraná is dammed, but the middle and lower reaches still retain natural floodplains, and the Paraná's largest tributary, the Paraguay, remains free-flowing.¹ Earth's largest river (in terms of flow), the Amazon, remains undammed, but it has been affected by clearing of the upland and floodplain forests. Also, 100 planned tributary dams may block or impede fish migrations (Fearnside 1989, Junk and de Mello 1987).

In 1993 and 1994, international attention was focused on large rivers and their floodplains when disastrous floods occurred in Bangladesh, western Europe, and the United States. Now questions are being asked about the effectiveness and cost of current flood and floodplain management policies and about the potential for reducing future flood damage by preserving and restoring large river-floodplain ecosystems and their tributary watersheds and wetlands (Sklar 1993, Sparks and Sparks 1994).

This focus on flood-damage re-

¹Edmundo Drago, 1994, personal communication. Instituto Nacional de Limnología, Santa Fe, Argentina.