



# How does floodplain width affect floodplain river ecology?

## A preliminary exploration using simulations

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### Abstract

Hydraulic food chain models allow us to explore the linkages of river discharge regimes and river-floodplain morphology to the structure and dynamics of modeled food webs. Physical conditions (e.g. depth, width, velocity) that vary with river discharge affect the performance (birth, growth, feeding, movement, or death rates) of organisms or trophic groups. Their performances in turn affect their impacts on food webs and ecosystems in channel and floodplain habitats. Here we explore the impact of floodplain width (modeled as  $1\times$ ,  $10\times$  and  $40\times$  the channel width) on a food web with two energy sources (detritus and vegetation), invertebrates that consume these, a size structured fish population which consumes invertebrates and in which larger fish cannibalize small fish, and birds which feed on large fish. Hydraulic linkages to trophic dynamics are assumed to be mediated in three ways: birds feed efficiently only in shallow water; plant carrying capacity varies non-linearly with water velocity, and mobile and drifting organisms are diluted and concentrated with spillover of river discharge to the floodplain, and its reconfinement to the channel. Aspects of this model are based on field observations of Junk and Bailey from the Amazon, of Sparks from the Mississippi, and on our observations of the Fly River in Papua New Guinea.

The model produced several counter-intuitive results. Biomass of invertebrates and fish increased with floodplain width, but much more rapidly from  $1\times$  to  $10\times$  floodplains than from  $10\times$  to  $40\times$  floodplains. For birds, maximum biomass occurred on the  $10\times$  floodplain. Initially high bird biomass on the  $40\times$  floodplain declined to extinction over time, because although favorable fishing conditions (shallow water) were most prolonged on the widest floodplain, this advantage was more than offset by the greater dilution of prey after spillover. Bird predation on large fish sometimes increased their biomass, by reducing cannibalism and thereby increasing the abundance of small fish available to grow into the larger size class. Sensitivity analyses indicated that model results were relatively robust to variation in parameter values that we chose, but much more exploration and calibration with field data are needed before we know how specific our results are to the structure and other assumptions of this model. We share with others the opinion that progress towards understanding complex dynamic systems like floodplain river ecosystems requires frequent feedback between modeling and field observations and experimentation. This understanding is crucial for river management and restoration. Organisms in real rivers have adapted to track and quickly exploit favorable conditions, and to avoid or endure adverse conditions. It is when we engineer away this environmental variability that we threaten the long term persistence of river-adapted biota.

### 1. Introduction

Floodplains sustain much of the biodiversity and

productivity of river ecosystems. Large rivers of similar discharge have floodplains that range from one to over

forty times the widths of their channels. If the same discharge flows through floodplains of different widths, flow depth and velocity in channels and floodplains will differ, as will the duration of floodplain inundation and the complexity and extent of floodplain habitats that develop. These factors will affect detritus, microbes, plants, invertebrates, fish, reptiles and amphibians, mammals, and fishing birds that make up river and floodplain food webs. How might variation in floodplain width (and consequently in the depth and duration of inundation) affect floodplain river ecology?

Here, we explore this question with a simple simulation model of the dynamics of a food web in a river with seasonally fluctuating discharge. Components of this river food web spread across a floodplain when it is inundated at high water, and the mobile organisms concentrate back into the channel during reconfinement. We explore the consequences of floodplain width for this model food web by comparing trophic structures that develop when the floodplain is one, ten, and forty times the width of the channel.

Our model assumes extremely simplified spatial and dynamic properties of both physical and biological components of the ecosystem, and ignores most of the local and regional variations in climate, hydrology, geology, land use, and biota that characterize real floodplain ecosystems (Welcomme, 1985; Junk et al., 1989; Sparks et al., 1990). Such simplistic simulations can serve as reference states (Paine, 1994) against which to evaluate the more complex dynamics of real ecosystems. Field studies of real systems, including studies in which effects of floodplain width can be inferred from experimental or comparative methods (e.g. Sparks, 1992) are critical, however, for real scientific understanding. Modeling efforts like ours should be viewed as guides that may be useful in the design of these field measurement programs. Interplay between modeling and field studies is particularly important in studies of large rivers, where the difficulties of sampling and experimental manipulations require that studies be designed with much foresight.

## 2. Determinants of floodplain width

No general geomorphic theory is available that predicts floodplain width in natural rivers, but it is clear that erodibility of valley walls, the history of base level

controls (due to sea level fluctuations) and the size of the river are controlling factors. The width of a floodplain and its elevation relative to the channel bed are not static features of fluvial landscapes. Instead, rivers may adjust in many ways to changes in sediment load, river discharge, and base level, which is altered by tectonics or sea level oscillation. All large rivers that empty into the sea have undergone dramatic changes due to sea level fluctuations.

The evolution of floodplains in response to changing boundary conditions and water and sediment loads must force a corresponding change in river ecosystems. This change has, through time, influenced the evolution of endemic species, and affected geographic distributions of river biota. The model we present here explores a small piece of this larger evolutionary issue by examining how floodplain dynamics might affect biota with particular attributes that determine their performances under various hydrologic conditions. Organism responses to environmental changes in turn affect the dynamics and structures of their food webs.

In addition to variation and change through time in floodplains of natural rivers, modern river floodplains have experienced abrupt and widespread alteration because of human activities. Rivers are dismembered from their floodplains when humans construct levees. Gravel mining, as well soil compaction due to development or grazing in watersheds, can cause channels to incise below their former floodplains, also severely curtailing the relative width of active floodplain habitat available to river biota. Therefore, effects of changes in floodplain width on ecosystem functions are of management interest.

## 3. Modeling approach

Our model links food web dynamics to river hydraulics by simulating the impacts of changing habitat availability and physical factors on web members. Performances of food web members (e.g., growth, reproduction, consumption, movement, and mortality rates), and consequently their impacts on each other and their 'interaction strength' (*sensu* Paine, 1980), are modeled as functions of dynamic physical factors in their environment (see also Power et al., 1995). Below, we outline the basic hydrologic changes that

occur in model rivers with identical channels but floodplains of three different widths (Fig. 1). All three rivers are subject to the same regular seasonal discharge regime (one low flow and one high flow period per year). Next, we identify how width, depth, and flow velocity might affect the performances of detritus or organisms which we have aggregated into five functional groups: detritus (and associated microbes); aquatic vegetation (attached and floating algae and macrophytes); grazing invertebrates that eat both detritus and vegetation; small (juvenile) invertebrate-eating fish that grow into big fish; big fish that eat small fish and invertebrates and give birth to the small fish; and fishing birds that eat only big fish (Fig. 2). We then explore the consequences of floodplain width for the structure and dynamics of the model food web made up of these groups. Next we evaluate the sensitivity of

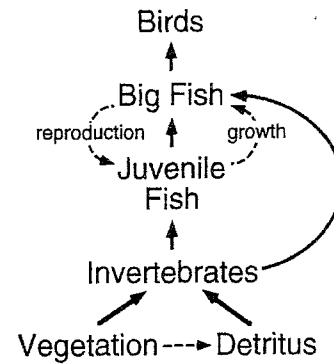
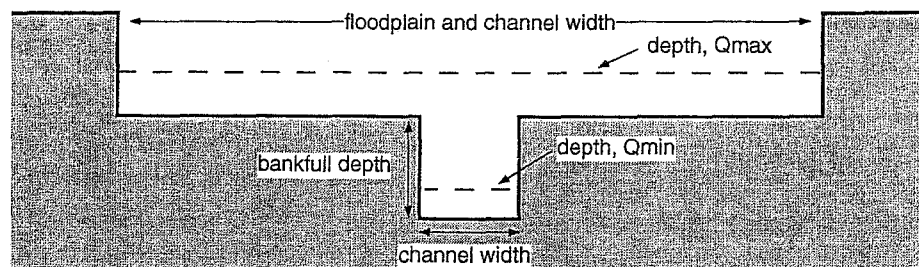


Fig. 2. Food web diagram indicating trophic relationships among groups (solid lines; arrows point from resources to consumers), and conversions (dotted lines) of algae to detritus via mortality, of small fish to big fish via growth, and of big fish to small fish via reproduction.

the model to small changes in key parameter values. Finally, we review other important factors omitted from

a. Floodplain River



b. Hydrograph

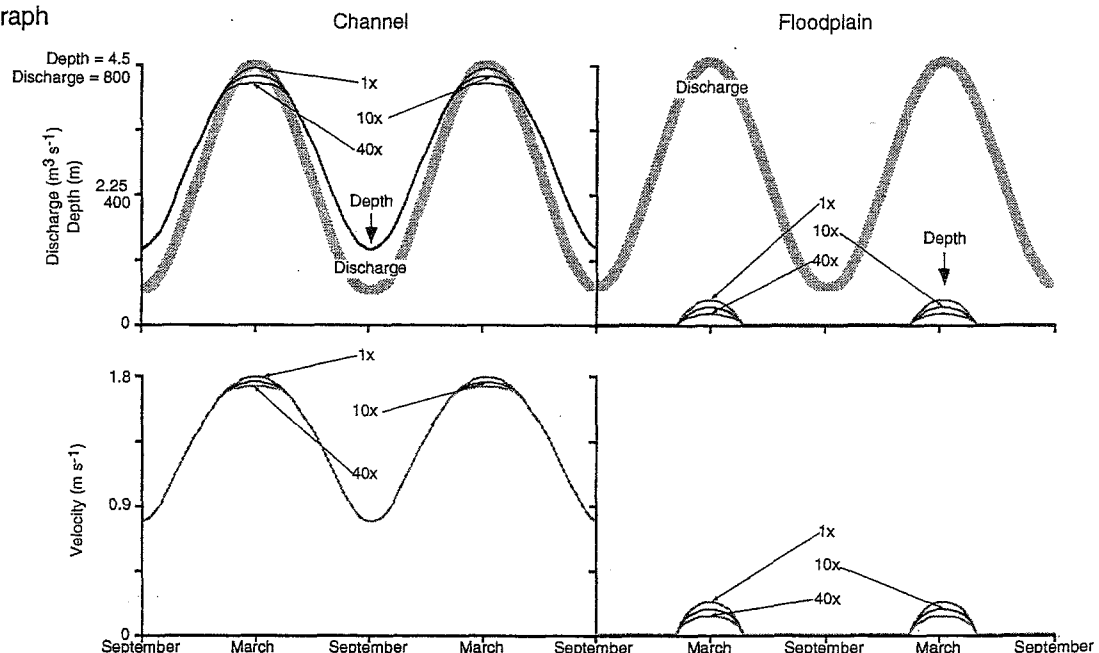


Fig. 1. (a) Diagram showing idealized cross-sectional geometry of modeled rivers, with dashed lines indicating maximum and minimum seasonal depths in the channel and the floodplain. (b) Seasonal hydrographs, showing discharge, flow depth, and flow velocity in three rivers over two years with one high flow and one low flow period per year. The three rivers experience the same discharge, but have floodplain to channel width ratios of one, ten and forty.

Table 1  
Physical parameter values

Channel width	100 m
Floodplain widths	100, 1000, or 4000 m
Bankfull depth	4.0 m
Water surface slope, $S$	0.0004
Manning's coefficients:	
channel, $n_c$	0.03
floodplain $n_f$	0.05
Discharge:	
maximum	800 m <sup>3</sup> s <sup>-1</sup>
minimum	100 m <sup>3</sup> s <sup>-1</sup>
Time step	weekly intervals

the present model, and suggest future directions for both modeling and field research.

#### 4. Modeled hydrology

Ignoring here the complex morphologies of real floodplain rivers, we begin by assuming that the single main channel and its floodplain are simple rectangles in cross-section (Fig. 1a). We will consider three cases: a river with a very narrow floodplain equal to its channel width, like the Colorado River; a river with a floodplain ten times its channel width, like reaches of the upper Mississippi; and a river with a floodplain forty times the width of its channel, like the lower Fly River in Papua New Guinea. Dry season flow is entirely contained within the main channel. When the depth of rising water in the channel ( $d_c$ ) exceeds bankfull depth ( $d_b$ ), 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 determines how the total discharge is apportioned between these two habitats (Henderson, 1966, Parker, 1993).

Channel or floodplain flow velocity,  $u_c$  or  $u_f$ , can be estimated by a relationship between velocity and downstream surface slope of the water ( $S$ ), depth of flow ( $d_c$  or  $d_f$ ), and an empirical Manning's coefficient ( $n$ ) that increases with bed roughness. Manning's  $n$  for the channel ( $n_c$ ) is here taken to be less than Manning's  $n$  for the floodplain ( $n_f$ ) (Table 1) because the scoured

channel bed and walls are smoother than the vegetated floodplain.

Using Manning's relation, channel velocity:

$$u_c = \frac{1}{n_c} d_c^{2/3} S^{1/2}$$

and floodplain velocity:

$$u_f = \frac{1}{n_f} d_f^{2/3} S^{1/2}$$

can then be used to compute discharge,  $Q = wud$ , where  $w$  denotes width,  $d$  denotes depth, and  $u$  denotes velocity. Here the subscript "c" denotes channel properties, and "f" denotes floodplain properties. Floodplain discharge,  $Q_f$ , is zero if  $d_c < d_b$ , where  $d_b$  denotes the bankfull depth of the channel, so  $d_f = 0$ , and is given by:

$$Q_f = w_f d_f u_f = w_f \frac{1}{n_f} (d_c - d_b)^{5/3} S^{1/2}$$

when  $d_c > d_b$ . Total discharge:

$$Q = Q_f + Q_c$$

is then:

$$\frac{1}{n_c} d_c^{5/3} S^{1/2} w_c$$

when  $d_c < d_b$ , and:

$$\frac{1}{n_c} d_c^{5/3} S^{1/2} w_c + \frac{1}{n_f} (d_c - d_b)^{5/3} S^{1/2} w_f$$

when  $d_c > d_b$ .

Empirical experience (e.g. Parker, 1993) suggests that Manning's coefficients of 0.03 for the channel ( $n_c$ ) and 0.05 for the floodplain ( $n_f$ ) are within the range commonly observed for large lowland rivers. Alternatively, these coefficients could be estimated at the study reach from measured relationships between discharge, channel depth, and water surface slope. The downstream surface slope can be measured in the field, or computed from topographic maps. Channel and floodplain width ( $w_c$ ,  $w_f$ ), and the depth at bankfull,  $d_b$ , are based on field measurements. Discharge as a function of time,  $Q(t)$  is obtained from hydrographs of the study reach. These substitutions give us all that is required to solve the equations for the channel and floodplain discharge, except for depth of flow in the channel,  $d_c$ . A program SPLITQ solves for  $d_c$  iteratively by a Newton–

Raphson method of approximation (Parker, 1993). After  $d_c$  is known, we can solve these equations for the other variables of interest,  $Q_c$ ,  $Q_f$ ,  $d_f$ ,  $u_c$ , and  $u_f$ .

Total discharge varies seasonally. Here, we represent a 12-month cycle with one dry season and one rainy season with a simple oscillating sine wave. Generalization to more realistic hydrographs, however, is not difficult. We do not consider the effect of rain on the floodplain, which in swampy lowland rivers may contribute as much or more than the channel to flooding of the river plain. In rivers with wide floodplains, more of the increase in discharge after spillover is absorbed by expansion of the river's width. In constrained rivers for which floodplain widths are about equal to channel widths, total width cannot change much, so increased discharge is largely apportioned between river depth and flow velocity.

## 5. Web members

We begin our exploration of the ecological effects of hydrologic changes, as constrained by floodplain width, by postulating a seven element, five level food web (Fig. 2). Issue can be taken with our assumptions about web structure and choices of aggregated biotic "players". We view these as place markers to be altered or expanded when the model is tailored to fit a specific river ecosystem. Trophic groups with basic features portrayed here occur in all floodplain river ecosystems, but we may not have captured some groups which dominate in some systems. Much more field research is needed to identify potential "strong interactors" in floodplain river food webs around the world.

Energy enters our model web from two sources, detritus (dead terrestrial and aquatic vegetation and associated microbes), and aquatic vegetation, envisioned here as attached or free-floating macrophytes and algae. Detritus and vegetation are consumed by small invertebrates (e.g. aquatic insect larvae, amphipods, zooplankton). Small invertebrates are eaten by small fish, which we assume to correspond to young life history stages of large fish. Big fish prey on the small fish and the invertebrates. Small fish and big fish are linked trophically, and also by growth and recruitment dynamics. The modeled web would have to be reconfigured to portray river ecosystems in which important herbivore–detritivores include fish (e.g.

Table 2

Biomass balance equations; biomass units: ( $\text{g m}^{-2}$ ), rate of change: ( $\text{g m}^{-2} \text{ week}^{-1}$ )

Detritus, $D$	$\frac{dD}{dt} = L + m_v V - c_{DI}ID - m_D D$
Vegetation, $V$	$\frac{dV}{dt} = b_v V \left(1 - \frac{V}{K}\right) - c_{VI}IV - m_v V$
Invertebrates, $I$	$\frac{dI}{dt} = b_{ID}c_{DI}ID + b_{IV}c_{VI}IV - c_{IJ}JI - c_{IF}FI - m_I I$
Juvenile fish, $J$	$\frac{dJ}{dt} = b_{IJ}J - g_{FJ}J - c_{JF}FJ - m_J J$
Large fish, $F$	$\frac{dF}{dt} = g_{FJ}J - c_{FB}BF - m_F F$
Fishing birds, $B$	$\frac{dB}{dt} = b_{BF}c_{FB}BF - m_B B$

those studied by Power, 1983 and Bowen, 1979) or large crustacea (prawns, crayfish), which would escape in size from small but not large predators.

Big fish in our model are preyed upon by water birds that wade (herons, cranes, egrets, storks) or dive (kingfishers, osprey, fishing eagles, pelicans). We have not included birds that swim underwater, like cormorants, mergansers, or auklets. We are interested in exploring here the impact of various hydrologic regimes in floodplains of different widths on the wader-diver guild, whose fishing is constrained by water depth (Power, 1984, 1987).

Table 2 gives the biomass balance dynamics for the five entities modeled here, with biotic parameters listed in Table 3. Performance variables (rates of birth, death, feeding, growth, or movement between habitats) that govern the nature and strength of interactions among web members will typically respond to physical factors that change as discharge fluctuates (Table 4). We have assumed two hydraulic dependencies: vegetation carrying capacity increases, then declines with velocity (Fig. 3a), and bird fishing success declines with depth (Fig. 3b). These are discussed in more detail below, where we review our present treatment for each food web entity, and discuss potentially important hydraulic dependencies that remain to be explored.

Detritus in our model has two sources: dead aquatic vegetation and litter and fruit from terrestrial vegetation. Floodplains but not large channels support large standing biomasses of terrestrial vegetation that accrue during low water periods (e.g. Junk and Howard-Williams, 1984). A pulse [ $1000 \text{ g (dry wt) m}^{-2}$ ] of this

Table 3  
Biological parameter values

Conversion efficiencies	
$b_{XY}$ is the biomass (g) of X produced from an ingested mass of Y (units: $\text{g g}^{-1}$ )	
$b_{ID}$	0.025
$b_{IV}$	0.050
$b_{JI}$	0.200
$b_{FI}$	0.100
$b_{FJ}$	0.200
$b_{BF}$	0.050
$b_V$ , intrinsic rate of natural increase for vegetation	0.500
$b_J$ , reproductive rate of large fish	see Table 5
$g_{FJ}$ , growth rates of juvenile fish into large fish (units: $\text{week}^{-1}$ )	see Table 5
Ingestion rates, $c_{XY}$ : per predator (Y) ingestion rate of a unit biomass of prey (X) per time [units: $\text{m}^2 \text{g (predator)}^{-1} \text{week}^{-1}$ ]	
$c_{DI}$	0.025
$c_{VI}$	0.025
$c_{IJ}$	0.025
$c_{IF}$	$0.025 [1 - (\text{Veg}/\text{Veg}_{\text{max}})]$
$c_{JF}$	$0.050 [1 - (\text{Veg}/\text{Veg}_{\text{max}})]$
$c_{FB}$	see Table 3
Mortality rates (units: $\text{week}^{-1}$ )	
$m_D$	0.002
$m_V$	0.001
$m_I$	0.001
$m_J$	0.005
$m_B$	0.001
$m_F$	see Table 5
$K$ , vegetation carrying capacity	see Table 4
$L$ , litter infall [ $\text{g (dry wt) m}^{-2} \text{week}^{-1}$ ]	3.0

dead plant material is made available to the food web each year when the floodplain is first inundated. This pulse approximates estimates of Junk and Howard-Williams (1984) of an annual production (during the dry period) of 8 t (dry weight)  $\text{ha}^{-1}$  of dead plant material on Amazonian varzea. Except for this pulse, we assume the rate at which terrestrial litter is made available to aquatic consumers is constant during periods of inundation.

We have modeled aquatic vegetation as a single entity that grows logistically until it reaches an asymptote at the carrying capacity ( $K$ ) of the environment. The vegetation is grazed by invertebrates, and dies from other causes at a density-independent rate  $m_V$ , augmenting detritus.

We envision floodplains as supporting large standing crops of grasses (e.g. *Echinocloa* or *Paspalum* in Amazonia, or *Saccharum* sp., dominant along the Fly

River). After spillover, inundated grasses quickly develop a coating of periphytic algae available to grazers. We model this as a pulse [ $100 \text{ g (dry wt) m}^{-2}$ ] of vegetation entering the food web upon spillover, as we did for floodplain detritus.

Channel flows in large rivers are too deep and swift for rooted macrophytes (Junk and Howard-Williams, 1984, pers. observ.), but channels can support floating macrophytes with attached algae until flow velocities exceed washout thresholds ( $u_{\text{scour}} = 1 \text{ m s}^{-1}$ ; Table 4). A fraction (0.2) of floating macrophytes and algae is washed between the channel and the floodplain with currents that accompany spillover and reconfinement.

We have modeled vegetation carrying capacity as a hump-shaped function of flow velocity (Fig. 3a), curve-fitting with a parabolic equation that specifies a maximum carrying capacity ( $K_{\text{max}}$ ) at an optimal flow velocity of  $0.1 \text{ m s}^{-1}$ , and small residual standing crops

Table 4

Specification of discharge-dependent variables in biomass balance equations

Vegetation carrying capacity ( $K$ ), a function of flow velocity,  $u$

$$K = \begin{cases} K_{\min} & \text{if } u > u_{\text{scour}} \\ au^2 + bu + c + K_{\min} & \text{if } u < u_{\text{scour}} \end{cases}$$

$$a = \frac{-K_{\max}}{u_{\text{scour}}^2 - 2u_{\text{opt}}u_{\text{scour}} + u_{\text{opt}}^2}$$

$$b = -2au_{\text{opt}}$$

$$c = K_{\max} + au_{\text{opt}}^2$$

$$K_{\max} = 1000 \text{ (g m}^{-2}\text{)}$$

$$K_{\min} = 100 \text{ (g m}^{-2}\text{)}$$

$$u_{\text{opt}} = 0.1 \text{ m s}^{-1}$$

$$u_{\text{scour}} = 1.0 \text{ m s}^{-1}$$

Birds capture rates of large fish ( $c_{\text{FB}}$ ), a function of depth,  $d$

$$c_{\text{FB}} = \begin{cases} 0 & \text{if } d > d_{\text{escape}} \\ \frac{-C_{\text{FB,max}}}{d_{\text{escape}}^X} d^X + C_{\text{FB,max}} & \text{if } d < d_{\text{escape}} \end{cases}$$

$$d_{\text{escape}} = 0.3 \text{ m}$$

$$C_{\text{FB}} = 0.5 \text{ m}^2 \text{ g}^{-1} \text{ week}^{-1}$$

$$X = 0.5$$

( $K_{\min}$ ) persisting (in implicitly assumed slack water refuges) at flows greater than  $u_{\text{scour}} = 1.0 \text{ m s}^{-1}$ . Our reasoning is as follows: Carrying capacity initially increases from zero flow to low flow, because of improved nutrient exchange (Whitford and Schumacher, 1964) and wafting which could periodically expose lower layers of vegetation to the light (Koehl and Alberte, 1988). If flow velocities were to increase past an optimum, however, carrying capacity would diminish because increasing turbidity would limit light for rooted vegetation, and increasing turbulence could damage or overturn floating vegetation or even entrain it below the water surface.

Invertebrates in our model increase by converting the vegetation and detritus that they eat to offspring. We assume that detritus (with microbes of high food quality infesting low quality dead organic matter) and vegetation (with high quality algae coating low quality macrophytes) are equal in food quality, as reflected by invertebrates' conversion ( $b_{\text{ID}} = b_{\text{IV}}$ ) and ingestion rates ( $c_{\text{DI}} = c_{\text{VI}}$ ). These quality-related parameters, however, would depend on dynamics of microbial conditioning or algal colonization and growth, which are not incorporated in the present model. We also assume that attack rates are constant in accordance with Holling's "Type 1" functional responses: consumers do

not satiate or change efficiencies over the range of prey densities they experience Holling (1959). This assumption may not be realistic if food organisms proliferate much faster than their consumers.

Invertebrates are lost by predation to small fish and to big fish, and via density independent mortality. Because size affects maneuverability, we assume that invertebrates have no effective structural refuges from small fish. Vegetation does provide refuges for small fish and invertebrates from large fish, as has been demonstrated in a number of studies (Crowder and Cooper, 1982, Werner et al., 1983, Werner and Gilliam, 1984, Mittelbach, 1988, Power, 1990). We incorporate refuge effects by allowing attack coefficients of large fish on invertebrates and small fish to decline linearly with vegetation density (Table 3)

We portray size structured processes that characterize fish populations, allowing juveniles to grow into big fish at a rate proportional to their collective food intake (Table 5). For juvenile fish, the conversion rate  $b_{\text{II}}$  is the rate at which somatic tissue, rather than offspring, is elaborated from invertebrates, allowing individual growth to the large size class. Juveniles are

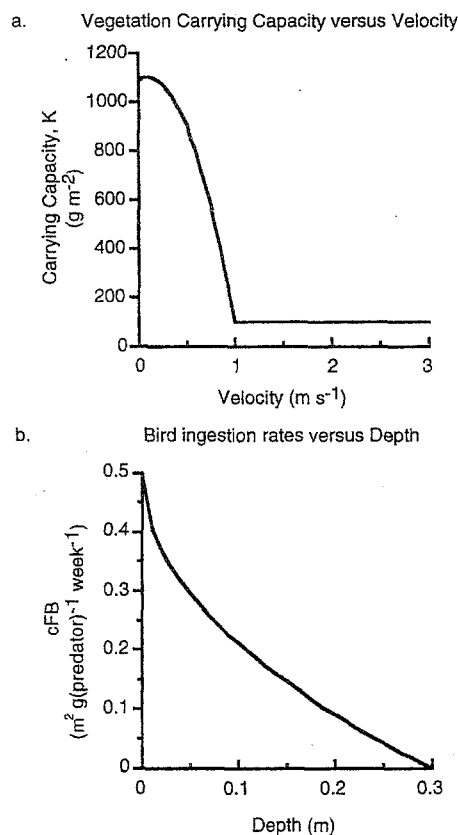


Fig. 3. Relationship of plant carrying capacity to flow velocity (a) and bird fishing rate to depth (b).

Table 5

Life history and trophic coupling of large (F) and small (J) fish

Allocation by large fish (F) to reproduction of small fish (J);  $b_J$  [units: g (small fish)  $g^{-1}$  (large fish)  $week^{-1}$ ]

$$b_J = \begin{cases} reprod_{min} & \text{if } \frac{stores}{F} < ration_{min} \\ reprod_{min} + reprod_{scope} & \text{if } \frac{stores}{F} > ration_{max} \\ reprod_{min} + reprod_{scope} \left( 1 - \frac{(ration_{max})F - (stores)F}{ration_{max} - ration_{min}} \right) & \text{if } ration_{min} > \frac{stores}{F} > ration_{max} \end{cases}$$

$$Stores = b_{JF} c_{JF} JF + b_{IF} c_{IF} IF$$

$$ration_{max} = 0.5 \text{ [g (prey) } g^{-1} \text{ (predator) } week^{-1}]$$

$$ration_{min} = 0.1 \text{ [g (prey) } g^{-1} \text{ (predator) } week^{-1}]$$

Mortality rate of large fish,  $m_F$ :

$$m_F = \begin{cases} mort_{min} & \text{if } \frac{stores}{F} > ration_{min} \\ \left( 1 - \frac{stores}{ration_{min}F} \right) scope_{mort} + mort_{min} & \text{if } \frac{stores}{F} < ration_{min} \end{cases}$$

$$scope_{mort} = 0.005 \text{ (week}^{-1}\text{)}$$

$$mort_{min} = 0.0005 \text{ (week}^{-1}\text{)}$$

Growth rate of juvenile fish into large fish,  $g_{FJ}$ 

$$g_{FJ} = b_{JI} c_{IJ} JI$$

consumed by large fish, which also give birth to them at a rate proportional to their collective intake and conversion efficiencies of both invertebrates and juvenile fish. If food intake by large fish is below some minimum per capita ration, reproductive rates drop and mortality rates increase (Table 5).

Big fish in our model are preyed upon by water birds that wade (herons, cranes, egrets, storks) or dive (kingfishers, osprey, fishing eagles, pelicans). These birds, like piscivorous fish, can track their prey to much greater depths, but like fish they are gape limited, and must swallow their prey whole. We are interested in exploring here the impact of various hydrologic regimes in floodplains of different widths on the depth-constrained wader-diver guild (Power, 1984, 1987). Predators in the wader-diver guild do not require whole-body streamlining, and therefore can tear prey apart before swallowing them with appendages that would compromise their hydrodynamics. Because their prey is warned of attack at the instant of predator “splashdown”, however, these birds fish effectively only in shallow water (Kramer, 1983; Power, 1984), typically less than 20–30 cm. We have modeled large fish capture rates by birds as very high when water is so shallow (a few cm) that fish are stranded helplessly.

In deeper water, bird attack rates decrease abruptly to zero at and beyond 30 cm (Fig. 3b).

Bird impacts on fish may be minor if they feed primarily on stranded individuals in shrinking floodplain pools that would die anyway before the next inundation. Bonetto et al. (1969) estimated that a large fraction of the Parana river fishes died from seasonal stranding. Kushlan (1976) has even documented counter-intuitive beneficial effects of bird predation. In shrinking water bodies, more fish survived when their numbers were thinned by birds, preventing the remaining fish from depleting oxygen to lethal levels. While we have not explicitly modeled birds as “donor controlled” (depending on fish for food, but having only weak impacts on fish densities), our simulation results suggest this relationship (see below).

The birds we model suffer no predation. Birds may be more free of predation than other taxa, because adults can fly to escape, and vulnerable young life stages are protected by their parents. Birds do suffer density independent mortality, which sets the rate at which they starve when fish are unavailable. As active homeotherms, birds would starve in the absence of food more quickly than other predators. In our model, food would be unavailable for birds during low water when



fish leave the floodplain. When floodplains are dry or too deep to fish, bird mortality rates would be higher than those we have assumed ( $m_B = 0.001 \text{ week}^{-1}$ ), unless some alternative energy sources for maintenance were available. These alternative food resources (e.g. terrestrial insects, fish stranded in shrinking floodplain pools, amphibious or terrestrial vertebrates) for birds are assumed, but not explicitly modeled here. High metabolic costs for birds are also reflected in the relatively low conversion rates of fish to bird biomass ( $b_{BF} = 0.05$ , so that much is allocated to maintenance rather than production of offspring). Real birds would migrate to track fluctuating resources along and between river drainages. Our model cannot portray this strategy, as longitudinal dynamics to portray migrations have not been included. This model is therefore only a very preliminary exploration of the question of how wide floodplains need to be in order to support populations of wading or diving birds.

## 6. Simulation results and discussion

As expected, rivers with wider floodplains sustained a larger total biomass of all trophic groups (Fig. 4–6). Trophic biomass was distributed as a pyramid in all channels, with vegetation and detritus making up most of the organic matter in the food web, and invertebrates, then big fish constituting most of the consumer biomass (Fig. 4).

All trophic groups except birds were at, or close to, equilibrium after about twenty simulated years (Fig. 5). Birds equilibrated by this time only in the  $10\times$  channel. Birds fed on fish when these entered the shallow floodplain during spillover. Fish colonizing floodplains from the channel were most dilute on the  $40\times$  floodplain, and most concentrated on the  $1\times$  floodplain. At initial densities of ( $0.1 \text{ g m}^{-2}$ ), birds equilibrated on the  $10\times$  floodplain, but steadily decreased on the  $40\times$  floodplain, and slowly increased on the  $1\times$  floodplain, over the 100 year simulation (Fig. 5d). Because bird population dynamics are portrayed with the simplest possible Lotka–Volterra equation (Table 2), it is possible to compute the density of big fish required to support an equilibrium bird population as  $F^* = m_b / (b_{BF} \times c_{FB})$ . Given parameter values we used (Table 3), this value would be  $0.04 \text{ g fish m}^{-2}$  if water were always sufficiently shallow to permit

birds their maximum fishing efficiency,  $c_{FB} = 0.5 \text{ m}^2 \text{ g}^{-1} \text{ week}^{-1}$ . In our model, however, fishing efficiency decreased with depth of water on the floodplain, so this fish density greatly underestimates that actually required to sustain birds. On the  $1\times$  floodplain, bird biomass finally stabilized (after 667 simulated years) when maximum spillover fish density was about  $1.8 \text{ g m}^{-2}$ . On the  $10\times$  floodplain, bird biomass stabilized at a lower fish density, ca.  $0.8 \text{ g m}^{-2}$ , presumably because birds had longer periods of efficient fishing due to longer episodes of shallow inundation than occurred with the narrower floodplain. On the  $40\times$  floodplain, however, densities of fish at spillover were never high enough to support birds, which approached extinction after 667 simulated years, despite more prolonged favorable fishing conditions.

Fish biomass did not respond to these long-term trends in bird biomass, suggesting weak or absent “top down control” (regulation of lower trophic levels by predators). In fact, despite small increases in birds on the  $1\times$  floodplain, a slight step increase in the biomass of big fish occurred after 50 years, which coincided with small increases in lower trophic levels and juvenile fish, suggesting that ‘bottom-up’ trophic effects and recruitment trends dominated. This inference was confirmed by running the model without birds (Table 7). Responses by big and small fish to the absence of birds were 6% or less, and, interestingly, in some cases, fish biomass was slightly higher with birds present (e.g. big fish on the  $1\times$  floodplains). Invertebrates responded more to the presence or absence of birds, usually showing increases (of 9–17%) with birds present. Birds had stronger indirect than direct effects on lower trophic levels because of some of the assumptions about refuges, feeding efficiencies of large versus small size classes, and size structure built into our model. Bird predation actually increased big fish biomass on the  $1\times$  floodplain, apparently by relieving juvenile fishes of predation and competition with adults enough so that their recruitment to adult size classes was enhanced. On the  $1\times$  floodplain, where birds had the briefest foraging time, their beneficial modification of fish size structure apparently outweighed their direct predatory impact.

Changes in abundance of vegetation and detritus available to consumers were simple linear functions of floodplain width (Fig. 6A), because their seasonal and longer term dynamics were dominated by the (per

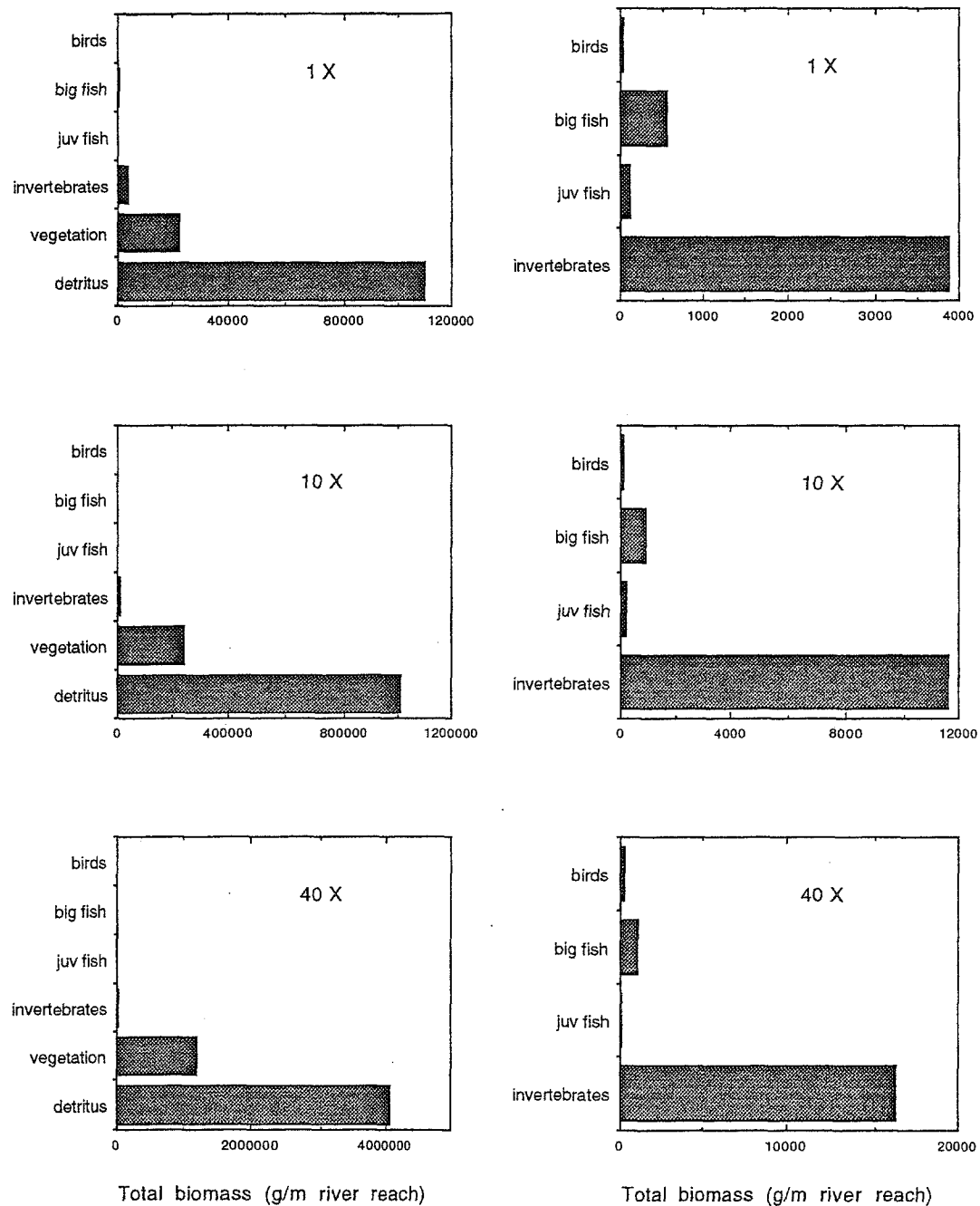


Fig. 4. Left-hand column: equilibrium standing stocks [seasonal maxima total biomass, where total biomass ( $\text{g m}^{-1}$  river reach) = density ( $\text{g m}^{-2}$ )  $\times$  channel width (m) during low flow; = density  $\times$  (channel + floodplain width) during high flow] of detritus and vegetation available to river consumers, and of invertebrates, juvenile fish, big fish, and birds in rivers with floodplains one, ten, and forty times the width of their channels. Right-hand column shows same values for consumers only. Note changes of scale on the x-axes.

area) pulse that accompanied spillover. The detritus pulse was intended to mimic that contributed by the production and death of terrestrial vegetation during the dry period on the floodplain (following Junk and Howard-Williams, 1984). Vegetation did not accrue in the channel, due in our model (as in real floodplain river channels) to the high channel flow velocities that limited carrying capacities via scour and turbidity. Veg-

etation appeared as a pulse of growth with continued production when the floodplain was inundated with slacker water.

For invertebrates and both size classes of fish, increases in total equilibrium biomass between floodplains that were one times ( $1\times$ ) and ten times ( $10\times$ ) the widths of the river channel were larger than increases in floodplain widths from ten times to forty

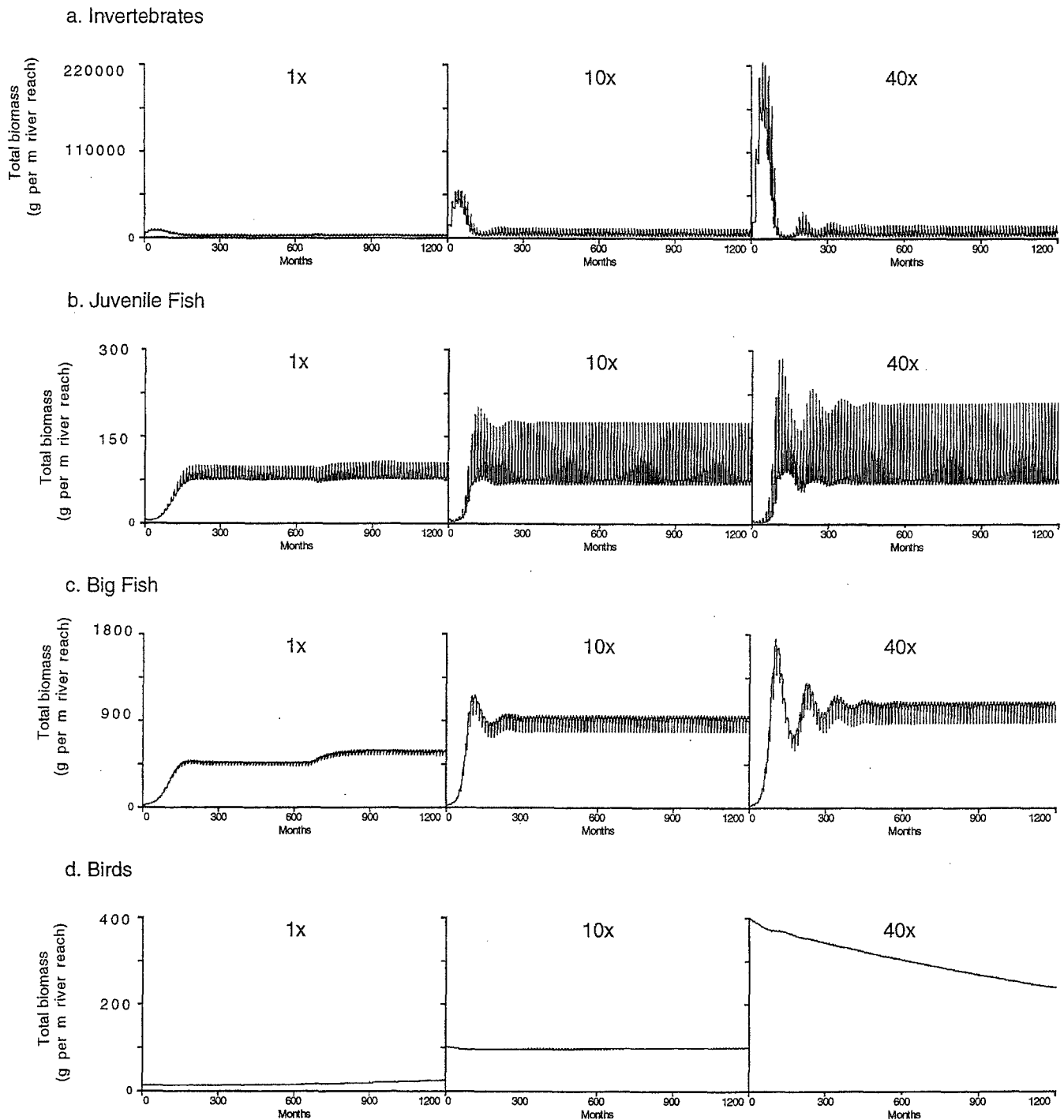


Fig. 5. Total biomass of (a) aquatic invertebrates, (b) juvenile fish, (c) large fish, and (d) birds in rivers with floodplains one ( $1\times$ ), ten ( $10\times$ ), and forty ( $40\times$ ) times the width of their channels. Time period shown is 1200 months, or 100 years.

times the channel width (Fig. 6B, C) Birds, in contrast to other consumers, increased nearly linearly with floodplain width from the 1000 to the 4000 m wide floodplain simulation (Fig. 6D).

Our interpretations of these different trends in total consumer biomass with floodplain width are as follows: Invertebrates, and hence the fish that fed on them, did

not respond proportionately to floodplain habitat expansion because they could not completely track the seasonal pulses in their detrital and vegetation foods on wider floodplains, as their feeding time on floodplains was cut short by reconfinement. Invertebrates also suffer higher rates of predation when concentrated in refuge-free channels with fish during low flow. In addition

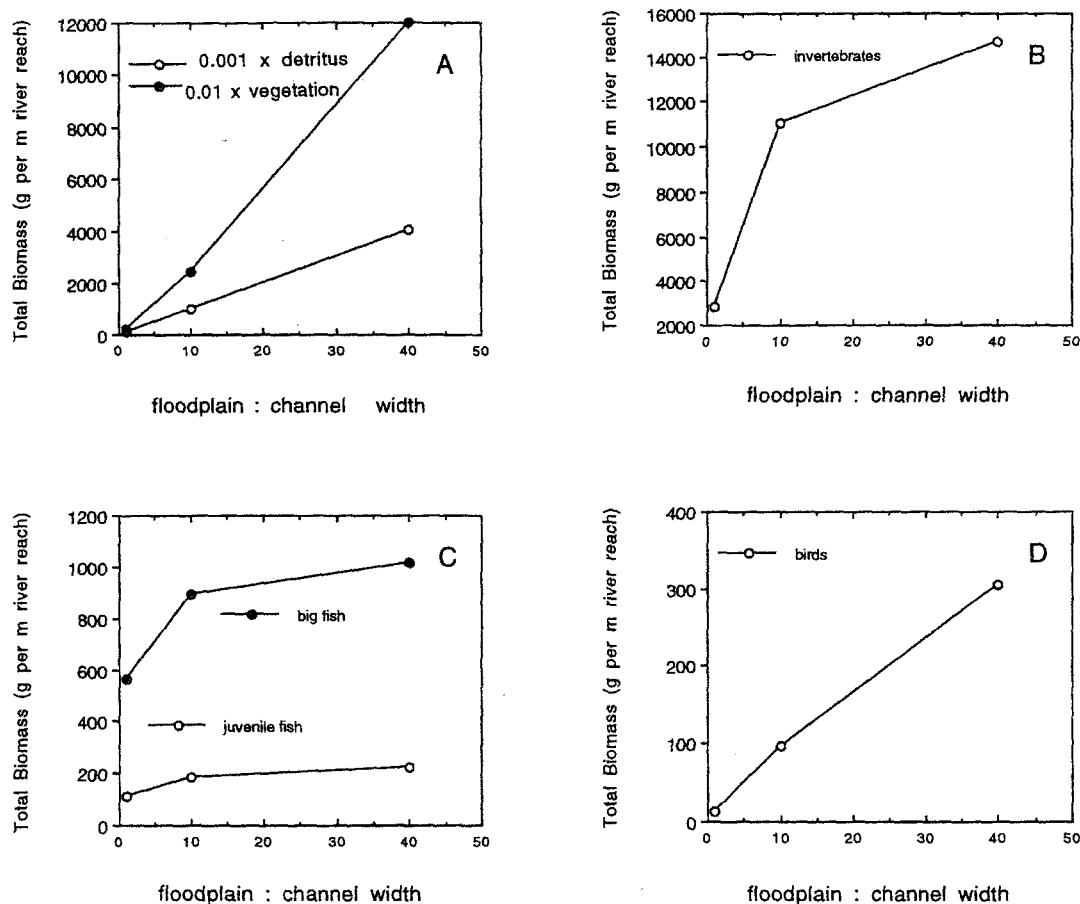


Fig. 6. Changes with floodplain width in total biomass for (A) detritus and vegetation (available to aquatic consumers), (B) invertebrates, (C) juvenile and big fish, and (D) birds. Values are seasonal maxima at year 100. At this time, seasonal biomasses had attained equilibria for all trophic groups except birds in  $1\times$  and  $40\times$  floodplains (see text).

to food limitation, juvenile fish suffered a similar loss to predatory big fish, which prevented increases in their low flow season (minimal) biomass with floodplain width expansion (Fig. 5b). Limitation of juveniles of course would lower their recruitment to large size classes, which damped increases of big fish from the  $10\times$  to the  $40\times$  floodplain simulation (Fig. 6C).

Sensitivity analyses, in addition to checking the robustness of the model, give insights into the importance of particular "species traits" for components of the modeled floodplain river food web. Sensitivity analyses were performed by running the model with eight key parameters changed, one at a time, to values 0.8 and 1.2 times those used in the basic simulations. For these analyses, the floodplain width was 1000 m ( $10\times$  the channel width), and simulations continued for 50 years. As before, all trophic groups equilibrated. Table 6 gives the responses in seasonal maximum and minimum total biomasses by all six trophic groups.

The model was reasonably robust; a 33% change in parameter values typically produced responses of less than 33% in seasonal maxima and minima of total biomass for the various trophic groups. One of the stronger responses was by invertebrates to a parameter,  $X$ , which affected the relationship between water depth and fishing effectiveness by birds (Table 4b). As  $X$  increased, bird fishing effectiveness at given depths less than the escape depth of 30 cm also increased. Interestingly, invertebrates showed a proportionately large decreases with increasing  $X$ , apparently mediated through small increases in the biomass of big fish, which, although they preyed on invertebrates, also reduced the densities of small fish by predation. Small fish were modeled as twice as efficient at converting invertebrates to growth as big fish were at converting invertebrates to offspring (Table 3,  $b_{FI} = 2b_{FI}$ ), and through this indirect life history mechanism, had stronger effects than big fish on invertebrate abundance.

Table 6

Sensitivity analyses of key parameters, showing response of total biomass to values 0.8 and 1.2 times those used in the model. Floodplain width = 1000 m ( $10 \times$  channel width); results show seasonal minima and maxima during year 49–50. Parameters:  $c_{FB}$  (attack rate by birds on fish);  $X$  (exponent relating bird fishing rates to water depth);  $b_{FI}$  (conversion efficiency of invertebrates to big fish);  $b_{ID}$  (conversion efficiency of detritus to invertebrates);  $c_{DI}$  (ingestion rates of detritus by invertebrates);  $m_j$  (mortality rates of juvenile fish);  $scope_{mort}$  (scope of mortality for big fish);  $vel_{opt}$  (optimum velocity for vegetation). See Table 3 and text for more complete definitions

Parameter, Values		Detritus	Vegetation	Invertebrates	Small fish	Large fish	Birds
$c_{FB \max}$	$\times 0.8 = 0.4$	241–1006845	0–247923	1272–10725	71–186	756–911	87–87
	$\times 1.2 = 0.6$	226–1006594	0–242630	1386–11482	70–183	742–905	105–106
Percent differences		(6) (0.02)	(0) (2)	(8) (7)	(1) (2)	(1) (0.6)	(18) (18)
$X$	$\times 0.8 = 0.4$	202–1006088	0–231838	1622–12975	75–184	740–897	95–96
	$\times 1.2 = 0.6$	263–1007191	0–255759	1116–7889	67–185	754–913	96–97
(Percent differences)		(23) (0.1)	(0) (9)	(31) (39)	(11) (0.5)	(2) (2)	(1) (1)
$b_{FI}$	$\times 0.8 = 0.4$	227–1006601	0–242624	1384–11467	67–184	748–906	95–96
	$\times 1.2 = 0.6$	361–1008164	0–278317	702–6519	144–240	745–898	97–98
(Percent differences)		(37) (0.2)	(0) (13)	(49) (43)	(53) (23)	(0.4) (0.9)	(2) (2)
$b_{ID}$	$\times 0.8 = 0.02$	159–1006578	0–255642	1406–8709	69–167	632–766	88–89
	$\times 1.2 = 0.03$	0–1006530	0–235920	1203–13631	73–201	860–1043	104–105
(Percent differences)		(100) (0)	(0) (8)	(14) (36)	(5) (17)	(27) (27)	(1) (1)
$c_{DI}$	$\times 0.8 = 0.02$	298–1007215	0–255494	1401–8871	69–169	643–779	89–90
	$\times 1.2 = 0.03$	0–1006008	0–236171	1221–13303	73–198	844–1022	102–103
(Percent differences)		(100) (0.1)	(0) (8)	(13) (33)	(5) (15)	(24) (24)	(13) (13)
$m_j$	$\times 0.8 = 0.16$	234–1006741	0–245663	1319–11044	71–185	750–908	96–96
	$\times 1.2 = 0.24$	233–1006718	0–245175	1330–11112	71–184	750–908	96–96
(Percent differences)		(0.4) (0)	(0) (0.2)	(0.8) (0.6)	(0) (0.5)	(0) (0)	(0) (0)
$scope_{mort}$	$\times 0.8 = 0.004$	135–1006799	0–246945	1293–10869	71–186	754–911	96–97
	$\times 1.2 = 0.006$	130–1006662	0–243944	1356–11286	70–184	746–906	95–96
(Percent differences)		(0.4) (0)	(0) (0.1)	(0.5) (0.4)	(1) (1)	(0.1) (0.5)	(1) (1)
$vel_{opt}$	$\times 0.8 = 0.08$	133–1006732	0–245358	1323–11070	71–185	750–908	96–97
	$\times 1.2 = 0.12$	133–1006732	0–245531	1323–11073	71–185	750–908	96–97
Percent differences		(0) (0)	(0) (0)	(0) (0)	(0) (0)	(0) (0)	(0) (0)

Invertebrate biomass responses were nearly proportional to two other parameter value changes: decreased efficiency of conversion of invertebrate biomass to juvenile fish with drops in adult birth rates ( $b_{FI}$ ), and increases with invertebrate ingestion rates of detritus ( $c_{DI}$ ). Increases in birth rates ( $b_{FI}$ ) also increased the seasonal minima of juvenile fish, but did not lead to notable increases in densities of big fish, probably due to food limitation of growth for the small fish size classes. The only other large changes noted from varying these parameters were in the seasonal minima of detritus that accrued during low water in the channel. Increases of 33% in conversion efficiencies and feeding rates of invertebrates ( $b_{ID}$  and  $c_{DI}$  respectively) were sufficient to allow them to deplete detritus completely

from channels during the low flow period. The significance for overall food web dynamics of this depletion was not great, however, because of the seasonal renewal of detritus upon spillover. This annual pulse was critical in maintaining river consumers, but was not depleted by them, as in real floodplain rivers.

In summary, consumers with biologically reasonable parameters had no “top down” influence on seasonally pulsed floodplain vegetation or detritus over a simulated 100 year period. Invertebrates were limited by feeding time: the period of their exposure to abundant floodplain detritus and vegetation during high flow. Invertebrates also appeared predator limited, and the two predators on invertebrates, juvenile and big fish, appeared largely food limited. Juvenile fish were also

Table 7

Effect of birds on equilibrium total biomass (seasonal minima and maxima) of other consumers

	Floodplain: Channel widths					
	1		10		40	
	min	max	min	max	min	max
<i>Invertebrates</i>						
Birds –	550	587	1145	9854	1122	12756
Birds +	503	550	1323	11073	1357	15188
Percent difference	9	6	13	11	17	16
<i>Small fish</i>						
Birds –	81	114	73	189	74	225
Birds +	79	109	71	184	73	222
Percent difference	2	4	2	3	1	1
<i>Big fish</i>						
Birds –	902	2804	774	917	862	1043
Birds +	964	2922	750	908	841	1057
Percent difference	6	4	3	1	2	1

limited by adult cannibalism. Food limitation, not predation, accounted for the declining rate of increase in fish biomass with floodplain width (Fig. 6C).

The steeper rise in modeled bird biomass with floodplain width (Fig. 6D) did not reflect differential responses by birds to wider or shallower floodplains, but were simply due to the slow decay from initial conditions, as discussed above. Birds, although exerting only weak direct effects as predators on large fish (Table 7), had interesting indirect effects, as in the 10 × floodplain, via their influence on fish size structure and the impact of this on invertebrate abundance.

## 7. Future directions

We have explored the influence of floodplain width for a simple food web with four trophic levels, two energy sources, and coupled life-history and trophic linkages between size structured fishes. Most models assume that the context for the modeled system is constant (Walters, 1986), which is probably never true for ecosystems. We have relaxed this assumption by making some parameters in our food web model explicit functions of physical conditions that change with seasonal river discharge. The price of this realism is added complexity. Although our model is a vast over-simpli-

fication of nature, it is nevertheless too parameter rich to calibrate in the field. Field studies of specific systems or subsystems are needed in order to identify components of food webs that are crucial to either species of interest, or to overall dynamics. These must be studied in greater detail, so that less critical or less dynamic components can be dropped or represented by more aggregated parameters (Tilman, 1990, Schaeffer, 1981).

Detrital fluxes and processing rates are crucial in floodplain rivers, where the huge expansion and contraction of habitat prevent aquatic consumers from ingesting more than a small proportion of the primary production. This limitation may be intensified by anthropogenic impacts. Junk (1975) points out that humans have intensively hunted herbivorous vertebrates, including turtles, manatees, and capybaras, that once may have had strong grazing impacts on the floodplains of Amazonia. An interesting counter-example is occurring in the grassy floodplain of the lower Fly River, which is now subjected to grazing from huge expanding herds of alien deer (*Cervus timorensis*) introduced to New Guinea around 1900 (Nowak, 1991). These deer exert a novel type of herbivory on a largely native flora, and the consequences for that floodplain-river ecosystem would be of great interest. While it seems unlikely that even vertebrate herbivores could regulate vegetation biomass in seasonal river floodplains, they might affect its quality through selective grazing. For example, magpie geese (*Anseranas semipalmata*) recruitment appears to track year to year variation in standing crops of wild rice (*Orzias*) (P.S. Lake, Monash University, Australia, pers. commun.), one of the most nutritious plants in the Fly River floodplain. During good years, enormous flocks of these geese settle on the grassed floodplain, converting vegetation to nutrients. If introduced deer suppressed wild rice, they could exert indirect ecosystem level effects on nutrient cycling (via food competition with geese) which could alter microbial and algal growth, hence the quality and quantity of foods available for invertebrates and other lower trophic level consumers in the system. In most floodplain rivers, however, as in our model, floodplain vegetation probably plays a primarily structural role during periods of inundation, providing substrates for algal growth and refuges for prey from predators (Junk, 1975).

Several hydrologically driven processes could influence detrital fluxes and processing, and should be incorporated into more realistic models of floodplain rivers. The magnitude, rate of change, and duration of flood-imposed stress (water, deposited sediments) on terrestrial plants will affect the rates at which they die or shed parts as litter (Rau, 1994). Seasonally deciduous trees will also provide discrete litter inputs whose correspondence with the flood pulse will vary among tropical and temperate rivers, and between northern and southern hemispheres (Cummins, 1973, Bunn, 1986). Microbial conditioning of litter will enhance its food quality over time (Anderson and Cummins, 1979, Petersen et al., 1989), affecting the efficiency with which this food is converted into invertebrate tissue or offspring ( $b_{ID}$ ) and/or the rate at which they will ingest it upon encounter ( $c_{DI}$ ). Microbial conditioning rates are affected by oxygen availability (Godshalk and Wetzel, 1978), and slow when water depths on floodplains exceed depths of oxygen diffusion or wind stirring (Bayley, 1995). If inundated floodplains are deep enough to stratify, depth-related temperature regimes could also affect microbial processing rates (Bayley, 1995). Loss rates of detrital carbon from the food web ( $m_d$ ) to the atmosphere as  $CO_2$  or  $CH_4$ , and losses by burial below areas accessible to aerobic consumers, are also influenced by depth-mediated temperature and oxygen levels.

Vegetation in our model is clearly overly aggregated. Ecologically important traits of aquatic plants vary with size (microphytes or algae vs macrophytes), growth habit (attached or free floating), and metabolic pathways (C3 plants are more edible than C4 plants). In the Amazon, C4 grasses like *Paspalum* and *Echinochloa* account for over half the annual primary production (Junk, 1985), but stable isotope studies (Forsberg et al., 1993) indicate that these macrophytes provide only 2–18% of the carbon assimilated by fish, while algae and C3 macrophytes account for 82–98% of fish carbon. Other studies (e.g. Mayer and Likens, 1987) also suggest that algae are the most important aquatic plants directly fueling river food webs. For simplicity, however, we have initially modeled algae and macrophytes as one entity, reasoning that attached algae are often limited by substrate, which macrophytes provide. As macrophyte biomass increases, therefore, so should the biomass of attached algae which is more directly available to higher trophic levels. Interactions of

attached algae, phytoplankton, and macrophytes are complex (Engle and Melack, 1989, Moss, 1990), however, and outcomes can vary with factors such as nutrient availability, flow velocity, and their interactions (Stevenson and Stoermer, 1982). In more realistic treatments, therefore, algae and macrophytes should be modeled as separate, interacting entities.

Other hydrologic processes influence the impact of vegetation and detritus on food webs. Periodically, the accrual and decay of large amounts of vegetation can produce catastrophic de-oxygenation and fish kills, particularly if sudden temperature changes (e.g. “friadas” in the Amazon (Welcomme, 1985)), wind stirring or abrupt stage changes in channels relative to floodplains bring deeper hypoxic water up into zones inhabited by fish. In addition, vegetation can affect hydrology. Rooted vegetation is a major source of bed roughness which slows flow over shallow areas. Macrophytes, at low flow velocities, reduce bank erosion and the suspension of sediment. This impact is important in that it maintains clear water (Sparks, 1995), enhancing below-surface photosynthesis, and also affects visual encounters between predators and their prey. These are among the interactions that should be explored in more realistic detailed models focused on the lower trophic levels of floodplain river food webs.

The hydraulic food chain modeling approach could be used to explore consequences of other physical or biotic factors of potential importance. Biotic factors include food web configuration, and attributes posited for web members, for example, their size, feeding efficiency, birth, growth, and mortality rates, and the sensitivities of these to dynamic physical factors. Physical factors include longer term hydrologic variation, for example, the influence of runs of dry or wet years, during which periods of floodplain inundation could vary. The results of our present simulation suggest that variation in the time during which invertebrates could build up their populations by harvesting floodplain vegetation and detritus would have a profound effect on food web structure and dynamics. These exposure times, and other important biotic processes would also be influenced by permanent off channel water bodies, which are features of real floodplains not yet incorporated in our model. The numbers, dimensions, and elevation (inundation frequencies) of these water bodies, whether or not rivers have access to floodplains or are cut off by levees (Power et al., 1995), and the amount

of refuge for organisms from high flows or from predators are other aspects of the physical habitat that should be investigated in future models and field work.

The present version of the model is one dimensional in the sense that all dynamics move only laterally, back and forth between the floodplain and the channel. While much could be explored with this one-dimensional version, two and three-dimensional models would be needed to incorporate vertical and longitudinal dynamics. Vertical dynamics important in lakes would also affect slack-water areas of inundated floodplains and off river water bodies. Influential vertical processes include changes in oxygen stratification, overturn, mixing as a function of depth, and the vertical diel migration of some algae, many invertebrates, and some fish. Longitudinal dynamics would represent the upstream and downstream migrations of large fish schools, translocations of nutrients or colonists, and downstream passage of flood pulses. Longitudinal dynamics would be needed both to understand impacts of migratory species on local reaches, and the fate of these species under longitudinally as well as temporally varying river conditions.

The hydraulic food chain approach, like any dynamic model, is limited in the real complexity it can represent, and as stressed above, should be primarily a tool for guiding field studies. For example, the long term trends or cycles that arise from simulated population interactions could suggest how long monitoring programs should continue to detect cycles that are driven by factors with longer than annual variability. Models might also give us clues about the nature of variation that we must maintain in regulated rivers to save or salvage floodplain ecosystems. In real floodplain rivers, annual variation in precipitation and discharge can perturb and reset populations, for example by creating years that are good for fish and bad for birds, or vice versa (Sparks et al., 1990). These fluctuations mitigate against long-term, biotically driven extinctions, for example of prey by predators. Organisms in real rivers have adapted to track and quickly exploit favorable conditions, and to avoid or endure adverse conditions long enough to survive. It is when we engineer away this environmental variability that we threaten the long term persistence of riverine species.

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