# Understanding Large River: Floodplain Ecosystems

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# Understanding Large River–Floodplain Ecosystems

## *Significant economic advantages and increased biodiversity and stability would result from restoration of impaired systems*

Peter B. Bayley

Ecologists, like most scientists, view nature with preconceptions based on their experience and culture. Industrial cultures have modified large river–floodplain ecosystems to the extent that it is difficult to recognize major variables that once regulated the systems and to account for the surviving biota. The natural functions of these systems have practically disappeared, principally because modifications have tended to prevent regular flooding. Studying these and other ecosystems that now have well-defined land/water boundaries has not only produced two classes of ecologists, terrestrial and aquatic, but in aquatic ecology has also given rise to limnologists and stream ecologists whose theories usually presume relatively static water levels (Junk et al. 1989).

Forbes (1895) in the United States and Antipa (1911, 1928) in Europe recognized some of the ecological attributes and value of river-floodplain ecosystems just before industry and modern farming changed overriding physical and hydrological features of the landscape, as well as water and sediment quality. Since then, the use of temperate rivers for bulk transportation, waste disposal, and hydroelectricity; the separation of floodplains from the river for intensive agriculture; and the accelerated drainage of basins due to wetland removal and poor land-use have combined to inhibit productivity of natural resources. Often maintained by governments, these activities produce other problems, for example the constriction of the floodway through artificial levees resulted in the increased flood stages on the Mississippi River in 1973 (Belt 1977) and 1993 (Myers and White 1993).

**Funding for experimental restoration and evaluation should take priority over ecological research on severely impaired ecosystems**

Therefore, ecologists in temperate countries have not benefited from studying relatively unperturbed systems in order to understand how their systems functioned naturally. Also, prevailing economic perspectives of rivers are grossly distorted by government subsidies and the inability of most economists to value natural resources unless they are currently being exploited and thus are in the market economy.

Ecological and economical knowledge has benefited from an appreciation of the value of less-impacted tropical river-floodplains (Bayley 1988, Welcomme 1975, 1979), whose ecological attributes seem to be shared among all such systems (Junk et al. 1989). However, there is a limited window of opportunity, because many tropical developing countries are following the practices of so-called advanced countries in their pursuit of rapid development.

In this article I summarize the ecological knowledge available on naturally functioning river-floodplains and the human benefits derived from those ecosystems. I focus on processes leading to biological productivity in the floodplain in large systems, in which the surface area of rivers is typically small compared with that of the adjoining floodplain. Finally, I discuss the principal gaps in our knowledge that are likely to influence attempts at restoration and evaluation.

## Ecological basis of river-floodplain ecosystems

The dynamic interaction between water and land is the principal process that produced river-floodplains, maintains them, and has affected the adaptations of biota that have evolved therein. The flood-pulse concept was developed to summarize these effects on the biota using available information from tropical and temperate systems (Junk et al. 1989). Earlier ecological concepts did not adequately explain the observations or provide a basis for appropriate hypothesis develop-

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ment. However, despite human modifications, information from processes in temperate wetlands (e.g., Brinson et al. 1980, Gosselink and Turner 1978, Odum 1984, Ward 1989, Wood 1951) contributed to the development of the flood-pulse concept.

The flood-pulse concept, from the aquatic viewpoint, identifies the predictable advance and retraction of water on the floodplain of a pristine system as the principal agent controlling the adaptations of most of the biota. Therefore, the flood pulse is not a disturbance; instead, significant departures from the average hydrological regimen, such as the prevention of floods, should be regarded as a disturbance.

The flood pulse is postulated to enhance biological productivity and maintain diversity in the system. The principal agents associated with this typically annual process are plants, nutrients, detritus, and sediments (Figure 1). A gradient of plant species adapted to seasonal degrees of inundation, nutrients, and light exists along the aquatic/terrestrial transition zone (Junk et al. 1989), which is subsequently referred to as the floodplain. The floodplain is therefore that part of the river-floodplain ecosystem that is regularly flooded and dried, and it represents a type of wetland. Although Figure 1 refers to plants as being terrestrial or aquatic, some species are so well-adapted that they are productive during wet and dry phases and are not well-described by the adjectives *terrestrial* or *aquatic* (e.g., Junk 1970).

A major zone of activity is the moving littoral (Junk et al. 1989), which is an inshore zone from the water's edge to a few meters depth. This zone traverses the floodplain as flooding and drawdown take place. High turnover rates of organic matter and nutrients are predicted to occur largely as a result of this movement. The moving littoral traverses a floodplain that is typically many times larger than the area of permanent lotic and lentic bodies. In large pristine systems, such as parts of the Amazon, conditions are more lentic than lotic because water movements occur gradually during approximately six to nine months each year.

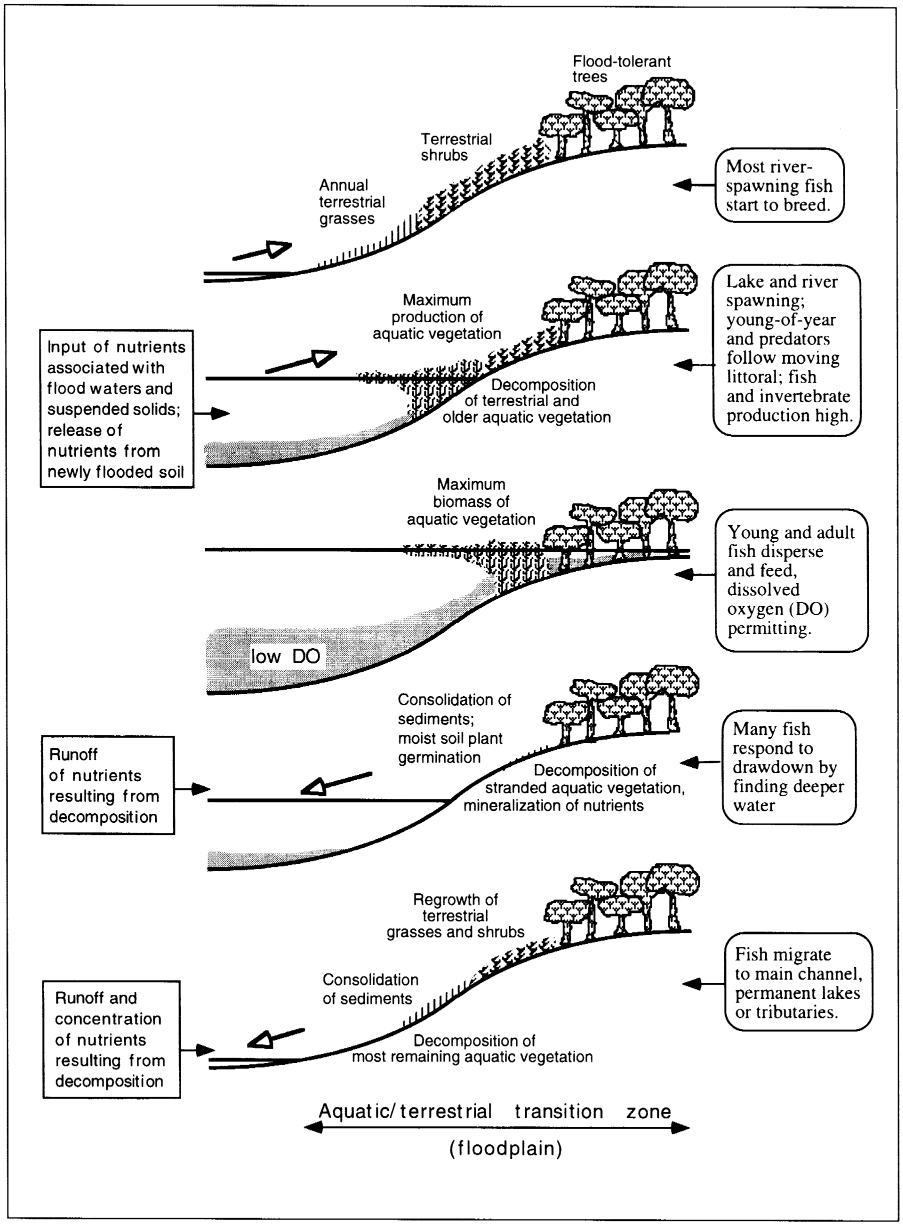

**Figure 1.** Schematic of the flood-pulse concept (derived from Junk et al. 1989) showing a vertically exaggerated section of a floodplain in five snapshots of an annual hydrological cycle. Right-hand column indicates typical life-history traits of fish. DO = dissolved oxygen.

During flooding, nutrients previously mineralized during the preceding dry phase are dissolved. Additional nutrients dissolved in the flood waters or associated with suspended sediment are brought in from the main river. High primary production and decomposition rates also occur during flooding, with production outstripping decomposition. For example, annual net production of a floodplain grass species in the Amazon was estimated at 99 tons of dry matter per hectare (Piedade et al. 1991), which far exceeds total primary production measured in other productive natural environments (e.g., Lieth and Whittaker 1975). Herbaceous macrophyte and tree litter production have been estimated to make up 69% and 24%, respectively, of total annual net production (the remaining 7% was phytoplankton and periphyton) in a partially deforested area of the Amazon floodplain (Bayley 1989). Despite this high production from vascular plants, the alternating terrestrial and aquatic phases decompose plant matter at a rate similar to that at which it is produced, and accumulation of detritus has not been observed in regularly flooded areas (Junk and Furch 1991).

When the water level stops rising, decomposition processes increase relative to production, resulting in generally increased dissolved oxygen deficiency (Figure 1), which is sometimes associated with production of hydrogen sulfide from sulfate reduction. When the moving littoral reverses during drawdown, nutrient runoff and concentration occur, which can result in increased phytoplankton production. At the same time, exposed mud banks are stabilized by drying and the germination of terrestrial plants.

The responses of much of the higher biota, including fish, mammals, and invertebrates, to the flood cycle are expressed in characteristic adaptations across all river-floodplain ecosystems (Figure 1; Junk et al. 1989). The moving littoral during flooding provides excellent nursery grounds for fish and near optimal environments for many invertebrates, especially those associated with macrophytes (Junk 1973), and adult fish. Therefore most fish species anticipate these conditions by spawning before or during the water rise. During drawdown, production is also expected to be high due to effects of nutrient accumulation. Fish need to grow quickly through the flood period to reach sufficient size to reduce predation losses when the water volume subsequently reduces to its minimum and to reduce overwinter mortality in temperate systems.

River-floodplain biota in general have high annual growth and mortality rates (r-selected traits; Pianka 1970). They have evolved life-history strategies that enable them to quickly colonize large areas. This ability helps species to persist, because variability in the flood regime from year to year results in different areas of the floodplain being accessible and optimal for growth and survival.

Figure 1 approximates the average conditions for a well-vegetated (nondesert) floodplain with low wind velocities. There are a number of deviations expected from these average conditions. Variability in dissolved oxygen among localities and systems is high, being influenced by wind velocity and fetch, water currents, thermocline effects, and decomposition effects that occur to some extent throughout the hydrological cycle.

The effect of seasonal temperature changes in the temperate zone is likely to depend on timing with respect to the flood pulse. In many temperate basins a spring flood results from seasonal rains, snow melt, and/or changes in evapotranspiration rates. While many fish species spawn during the rise of the flood when conditions are best for dispersal of eggs or young, water temperatures may be optimal for high somatic production during the period of drawdown, when invertebrate prey would be expected to benefit from nutrient runoff. Also, decomposition rates of flooded herbaceous vegetation are slower at the lower temperatures, resulting in more vegetative cover and substrate for fish and invertebrates during drawdown. Therefore, aquatic production may be enhanced by a slow rate of drawdown under these conditions. In the upper Mississippi, the flood pulse now tends to occur earlier and more briefly than it did last century (Grubaugh and Anderson 1988). Therefore, it would be expected that more flooded area would have received the benefit of higher temperatures during the original hydrological regimen.

In the temperate winter, a low decomposition rate is expected to result in greater carry-over of detritus from previous years than for a tropical system. Also, in temperate basins, ice-cover can exacerbate the winter's low, dissolved oxygen conditions (Bodensteiner et al. 1990), whereas in the tropics, high decomposition rates and thermocline effects can locally limit dissolved oxygen at higher water levels. I would expect the latter condition to also be common during the summer in hydrologically restored temperate systems.

None of these deviations from average conditions suggest that annual productivity would be reduced due to the presence of the flood pulse. An important question is how much productivity is enhanced by the flooding process.

## Benefits of river-floodplain ecosystems

The benefits of maintaining genetic and species diversity and preserving unique natural phenomena should be self-evident. Less obvious is the benefit of enhanced production.

The flood-pulse concept implies that biological production is enhanced through a variety of processes during the flooding cycle. I previously hypothesized that an optimal rate of increase in water level exists that would maximize production (Bayley 1991). If the rate were too fast, biological processes in the moving littoral would not be able to keep up with the advance of water level. Conversely, if the rate were too slow, oxygen deficiency might inhibit fauna and decomposition rates.

Also, on an annual cycle fast rates of rise and fall would limit the time that aquatic biota could spend on the floodplain, whereas low rates would limit how much floodplain would be inundated. Therefore, rates of rise and fall would be expected to influence the annual production of aquatic biota, as well as the timing of temperature regimens.

Although special studies are needed to examine specific hypotheses that consider elements of the hydrological cycle, the available data allow testing of the more general hypothesis that a flood-pulse advantage would increase biological productivity per unit water area above the level expected from equivalent stable water bodies. Fish yield from all multispecies fisheries can be regarded as integrating a variety of aquatic and terrestrial production processes in the river-floodplain. Data collected worldwide (Bayley 1988, 1991), in which comparisons between yield or biomass could be made in ecologically comparable, but hydrologically distinct, systems are summarized in Figure 2.

If the fishery yields per mean unit area were no different from equivalent lentic yields, implying that flooding increased production merely because it increased surface area, values would be expected to

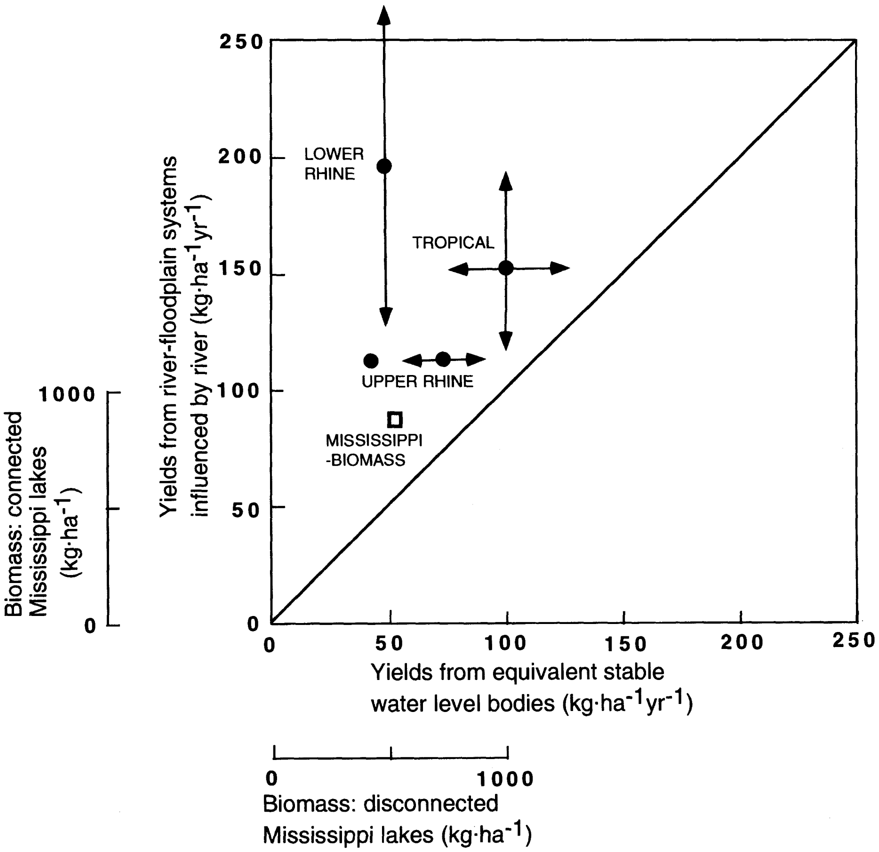

**Figure 2.** Multispecies fish yield (solid circles) or biomass (open square) from floodplains (ordinate) versus multispecies fish yield or biomass from equivalent bodies with stable water levels (abscissa). Maximal yields of tropical river-floodplains (based on 15 annual yield estimates from 12 systems) and tropical lakes (based on 31 lakes and reservoirs) were derived from models of river-floodplains and lakes, respectively, that related yield to fishing effort (Bayley 1988). The floodplain data were based on maximal area flooded. Mean depth had a relatively low effect on yield, and there was considerable overlap in mean depths between the lakes and river-floodplains used (Bayley 1991). Temperate river data obtained for regularly inundated backwaters on the upper Rhine River averaged 115 kg·ha$^{-1}$yr$^{-1}$ (ordinate), whereas backwaters separated from the river and an impounded reach yielded 63–84 kg and 42 kg·ha$^{-1}$yr$^{-1}$, respectively (two values on abscissa; Kriegsmann 1970 in Lelek 1989). On the lower Rhine River, regularly inundated backwater lakes yielded 125–270 kg·ha$^{-1}$yr$^{-1}$ (ordinate; Lelek 1989) compared with 45 kg·ha$^{-1}$yr$^{-1}$ (abscissa) from the main river (Kriegsmann 1970 in Lelek 1989). Biomass estimates in floodplain lakes connected to the Atchafalaya River (lower Mississippi) averaged 860 kg·ha$^{-1}$ compared with 550 kg·ha$^{-1}$ for lakes separated from the river by high levees (Bryan and Sabins 1978). Those authors observed that the former value from connected lakes was higher than biomass densities in virtually all southeastern reservoirs.

cluster around the 45° line in Figure 2. All available data indicated that yields were higher in river-floodplains, including individual, temperate floodplain lakes that were connected to the river. In the case of the tropical data, yields were only available for maximal river-floodplain area and therefore underestimate the predicted optimal yields compared with those of lakes. The combined surface area of rivers and permanent lentic bodies is small compared with the average inundated area of the associated floodplains, and many riverine species depend on resources from the floodplain (Junk et al. 1989, Welcomme 1985). Therefore, the minority of fish species that do not depend directly or indirectly on floodplain production cannot contribute significantly to the yield. Moreover, yields in river-floodplains tend to be underestimated compared with lakes, because of the inadequacy of most estimation methods in accounting for the highly dispersed fishing activities in river systems (Bayley and Petrere 1989).

A restoration process should require a return of natural flooding conditions (or some simulated equivalent on a smaller scale if technologically feasible) and regular access of water and biota to previously isolated floodplains, in addition to water or sediment quality improvements. Restoration of water quality in systems naturally poor in nutrients might result in lower productivity when the principal disturbance is excessive nutrient input. Although many river-floodplains receive additional nutrients from farming practices and municipal waste, their potential productivity is almost certainly depressed by physical alterations to the landscape and hydrology, which result in a highly unpredictable flood pulse and denial of access of water to much of the floodplain. The evidence synthesized here from multispecies fisheries indicates that flood pulses in large floodplains provide a bonus in production above that which would be expected merely from the increase in water area. This indication, plus evidence of high primary productivity in natural floodplain systems, suggests that tangible economic and recreational benefits should be expected from restoration attempts, in addition to increased biodiversity and decreased probability of catastrophic flooding.

## Research strategies

Research approaches to understanding and predicting ecological structure and function in river-floodplain ecosystems must explicitly account for effects of scale. At small spatial (e.g., meters or tens of meters) and temporal (e.g., hours or days) scales in the floodplain, a large variety of mechanisms affecting individuals or populations (e.g., Welcomme 1985) is conceivable, which is probably a major cause of the observed high variances in the quantities and compositions of flora and fauna. It is difficult and costly to attempt microcosm approaches to determine what mechanisms are most likely to regulate biotic processes on the much larger scales (e.g., kilometers and hydrological seasons) necessary for understanding principal system functions, estimating limits of resource exploitation, and planning conservation and restoration strategies.

Therefore, we need to initially design studies that can be more readily interpreted at these large spatial and temporal scales. The choice of variables is critical. Practical, statistical units for sampling in hypothesized ecological patches (Picket and White 1985) should be defined by hydrology and geomorphology, not geographic position. These units are like mobile quadrats and are referred to as templets. In a given floodplain, such templets would be largely determined by depth, flow, and plant association. The scale of templets is likely to be heavily dependent on the available sampling technology, whose accuracy and cost are likely to determine the power to distinguish effects. Research is required on different scales before relationships between templets and ecologically based patches can be developed. These relationships are important for the development of more generally applicable models and for providing a sound theoretical basis for the comparative analysis of independent systems.

Given the foregoing operational guidelines, there are several specific questions that need to be answered in order to predict effects of prevalent anthropogenic disturbances, refine concepts of sustainable exploitation, and plan restoration strategies. Information is accumulating on relatively pristine tropical systems in some areas of South America and Africa, but it is sparse in the few temperate systems (e.g., in Asia) that have not been heavily impacted. Therefore, what we know from the tropical systems can only be applied to temperate systems by understanding how processes may deviate from a general, conceptual model such as the flood-pulse concept. In this regard, the effects of temperature interactions with hydrological regimes on biota are critical. Annual primary and secondary production in many temperate systems may depend more on mechanisms occurring during drawdown than those occurring when the water is rising.

In temperate and tropical systems, the effects of variance in the hydrological regime, especially seasonal contingency (Colwell 1974), are expected to be critical, which is not meant to imply that a regular annual flood pulse of consistent amplitude is desirable. Biota have evolved under considerable hydrological variation among years that, for example, reset parts of the floodplain by periodically flushing out peripheral swamps and recycling accumulated organic matter and nutrients.

A considerable proportion of organic matter exists in the form of detritus in floodplains. Therefore, any study of energy transfer among trophic levels should explicitly account for seasonal accumulation and breakdown rates of the various forms of particulate and dissolved organic matter. These processes are likely to be slowed in temperate winters. Consequently, differences in the state of the hydrological cycle when low temperatures occur are likely to produce differences among temperate systems, as well as between tropical and temperate ones.

Lag effects of recycling of organic matter or nutrients at cooler temperatures may result in qualitatively different production processes or different emphases on processes. For example, secondary processes that depend on released nutrients and plant growth may be fast enough to accompany the moving littoral in tropical systems, whereas at cooler temperatures other processes may use the nutrient regeneration later on in permanent lentic or lotic zones after the flood has subsided.

Finally, systems under restoration require special consideration. Landscaping of the floodplain is problematic, because it requires accurate prediction of the dynamics of water and sediment transport, of the effects of those dynamics on vascular plant colonization and maintenance, and vice versa. Attempts to landscape could prove to be counterproductive until these processes are understood.

To avoid expensive mistakes and to gain the maximal amount of information, restoration of river-floodplains needs to begin with an experimental approach in which different hydrological alternatives are evaluated with respect to natural responses of the landscape and flora. Detailed, expensive studies of higher fauna of human interest, such as fish and waterfowl, should be postponed until the physical nature and woody vegetation of the restored floodplain have become relatively stabilized. Such an experimental approach is essential in order to demonstrate what can be expected and what can be gained from a genuine, basin-wide restoration, which requires a sustained improvement of land- and water-use practices on a large scale.

## Conclusions

Our understanding of naturally functioning river-floodplain ecosystems leaves much to be desired. However, large-scale processes and benefits common to relatively pristine systems in some tropical areas are sufficiently known to indicate that significant economic advantages, in addition to benefits associated with increased biodiversity and stability, would result from restoration of impaired systems.

However, our cultural development has caused river-floodplain ecosystems in most temperate and some tropical areas to be more adversely affected than most other natural systems. It has also almost destroyed our ability to study their ecology.

We cannot gain more useful information in most temperate systems without first attempting to restore, or at least emulate, the natural hydrological regimes. Therefore, I believe that funding for experimental restoration and evaluation should take priority over ecological research on severely impaired river-floodplain systems.

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## References cited

Antipa, G. P. 1911. Fischerei und Flussregulierung. Allgem. *Fischerei-Zeitung, München* 16/17: 1–5.

______. 1928. Die biologischen Grundlagen und der Mechanismus der Fischproduktion in den Gewässern der unteren Donau. *Academie Roumaine, Bulletin de la Section Scientifique* 11: 1–20.

Bayley, P. B. 1988. Accounting for effort when comparing tropical fisheries in lakes, river-floodplains, and lagoons. *Limnol. Oceanogr.* 33: 963–972.

______. 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.

______. 1991. The flood pulse advantage and the restoration of river-floodplain systems. *Regul. Rivers Res. & Manage.* 6: 75–86.

Bayley, P. B., and M. Petrere Jr. 1989. Amazon fisheries: assessment methods, current status, and management options. *Can. Spec. Publ. Fish. Aquat. Sci.* 106: 385–398.

Belt, C. B. Jr. 1977. The 1973 flood and man's constriction of the Mississippi River. *Science* 189: 681–684.

Bodensteiner, L. R., R. J. Sheehan, and W. M. Lewis. 1990. Differences in the physical environment of the upper Mississippi River as factors in the overwinter survival of fish. Pages 109–117 in *The Restoration of Stream Fish Habitat.* Rivers & Streams Technical Committee, North-Central Division of the American Fisheries Society.

Brinson, M. M., H. D. Bradshaw, and J. B. Elkins Jr. 1980. Litterfall, stemflow, and throughfall nutrient fluxes in an alluvial swamp forest. *Ecology* 61: 827–835.

Bryan, C. F., and D. S. Sabins. 1978. Management implications in water quality and fish standing stock information in the Atchafalaya Basin, Louisiana. In *Proceedings of the Third Coastal Marsh and Estuary Management Symposium.* Louisiana State University, Baton Rouge, LA.

Colwell, R. K. 1974. Predictability, constancy, and contingency of periodic phenomena. *Ecology* 55: 1148–1153.

Forbes, S. A. 1895. Illinois State Laboratory of Natural History, Champaign, Illinois. Biennial Report of the Director. 1893–1894. Pages 39–52 in *Illinois Fish Commissioner's Report for 1892–1894.* Illinois State Laboratory of Natural History, Champaign, IL.

Gosselink, J. G., and R. E. Turner. 1978. *The Role of Hydrology in Freshwater Wetland Ecosystems.* Academic Press, New York.

Grubaugh, J. W., and R. V. Anderson. 1988. Spatial and temporal availability of floodplain habitat: long-term changes at pool 19, Mississippi River. *Am. Midl. Nat.* 119: 402–411.

Junk, W. J. 1970. Investigations on the ecology and production biology of the floating meadows (Paspalo-Echinochloetum) on the Middle Amazon, Part 1: the floating vegetation and its ecology. *Amazoniana* 2: 449–495.

______. 1973. Investigations on the ecology and production biology of the floating meadows (Paspalo-Echinochloetum) on the Middle Amazon, Part 2: the aquatic fauna in the root zone of floating vegetation. *Amazoniana* 4: 9–102.

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.

Junk, W. J., and K. Furch. 1991. Nutrient dynamics in Amazonian floodplains: Decomposition of herbaceous plants in aquatic and terrestrial environments. *Verh. Internat. Verein. Limnol.* 24: 2080–2084.

Kriegsmann, F. 1970. Gutachten über die Rhienfischeri und die Wirkung der Teilkanalisierug zwischen Breisach und Kehl. In Anon. 1976. *Umweltprobleme des Rheins.* Kohlham, Stuttgart, und Mainz, Germany.

Lelek, A. 1989. The Rhine River and some of its tributaries under human impact in the last two centuries. *Can. Spec. Publ. Fish. Aquat. Sci.* 106: 469–487.

Lieth, H., and O. H. Whittaker. 1975. The primary production of the biosphere. Springer-Verlag, Berlin, Germany.

Myers, M. A., and G. E. White. 1993. The challenge of the Mississippi flood. *Environment* 10 (12): 6–35.

Odum, E. P. 1984. Wetlands as vital components of the nation's water resources. In R. Arora and L. Gordray, eds. *The Water Resources of Georgia and Adjacent Areas.* Georgia Department of Natural Resources, Atlanta, GA.

Pianka, E. R. 1970. On r- and K-selection. *Am. Nat.* 104: 592–597.

Picket, S. T. A., and P. S. White, eds. 1985. *The Ecology of Natural Disturbance and Patch Dynamics.* Academic Press, Orlando, FL.

Piedade, M. T. F., W. J. Junk, and S. P. Long. 1991. The productivity of the $C_4$ grass *Echinochloa polystachya* on the Amazon floodplain. *Ecology* 72: 1456–1463.

Ward, J. V. 1989. Riverine-wetland interactions. Pages 385–400 in R. Sharitz and J. Gibbons, eds. *Freshwater Wetlands and Wildlife.* CONF-8603101. US Department of Energy, USDOE Office of Scientific and Technical Information, Oak Ridge, TN.

Welcomme, R. L. 1975. The fisheries ecology of African floodplains. Technical Paper 3. CIFA/T3. FAO Committee for Inland Fisheries of Africa, UN Food and Agriculture Organization, Rome, Italy.

______. 1979. *The Fisheries Ecology of Floodplain Rivers.* Longman, London, UK.

______. 1985. River fisheries. FAO Fisheries Technical Paper No. 262. UN Food and Agriculture Organization, Rome, Italy.

Wood, R. 1951. The significance of managed water levels in developing the fisheries of large impoundments. *J. Tenn. Acad. Sci.* 26: 214–235.