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The Flood Pulse Concept in River–Floodplain Systems

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Abstract

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The principal driving force responsible for the existence, productivity, and interactions of the major biota in river–floodplain systems is the flood pulse. A spectrum of geomorphological and hydrological conditions produces flood pulses, which range from unpredictable to predictable and from short to long duration. Short and generally unpredictable pulses occur in low-order streams or heavily modified systems with floodplains that have been leveed and drained by man. Because low-order stream pulses are brief and unpredictable, organisms have limited adaptations for directly utilizing the aquatic/terrestrial transition zone (ATTZ), although aquatic organisms benefit indirectly from transport of resources into the lotic environment. Conversely, a predictable pulse of long duration engenders organismic adaptations and strategies that efficiently utilize attributes of the ATTZ. This pulse is coupled with a dynamic edge effect, which extends a "moving littoral" throughout the ATTZ. The moving littoral prevents prolonged stagnation and allows rapid recycling of organic matter and nutrients, thereby resulting in high productivity. Primary production associated with the ATTZ is much higher than that of permanent water bodies in unmodified systems. Fish yields and production are strongly related to the extent of accessible floodplain, whereas the main river is used as a migration route by most of the fishes.

In temperate regions, light and/or temperature variations may modify the effects of the pulse, and anthropogenic influences on the flood pulse or floodplain frequently limit production. A local floodplain, however, can develop by sedimentation in a river stretch modified by a low head dam. Borders of slowly flowing rivers turn into floodplain habitats, becoming separated from the main channel by levées.

The flood pulse is a "batch" process and is distinct from concepts that emphasize the continuous processes in flowing water environments, such as the river continuum concept. Floodplains are distinct because they do not depend on upstream processing inefficiencies of organic matter, although their nutrient pool is influenced by periodic lateral exchange of water and sediments with the main channel. The pulse concept is distinct because the position of a floodplain within the river network is not a primary determinant of the processes that occur. The pulse concept requires an approach other than the traditional limnological paradigms used in lotic or lentic systems.

river/floodplain/ecosystem theory

Résumé

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Les inondations occasionnées par la crue des eaux dans les systèmes cours d'eau-plaines inondables constituent le principal facteur qui détermine la nature et la productivité du biote dominant de même que les interactions existant entre les organismes biotiques et entre ceux-ci et leur environnement. Ces crues passagères, dont la durée et la prévisibilité sont variables, sont produites par un ensemble de facteurs géomorphologiques et hydrologiques. Les crues de courte durée, généralement imprévisibles, surviennent dans les réseaux hydrographiques peu ramifiées ou dans les réseaux qui ont connu des transformations importantes suite à l'endiguement et au drainage des plaines inondables par l'homme. Comme les crues survenant dans les réseaux hydrographiques d'ordre inférieur sont brèves et imprévisibles, les adaptations des organismes vivants sont limitées en ce qui a trait à l'exploitation des ressources de la zone de transition existant entre le milieu aquatique et le milieu terrestre (ATTZ), bien que les organismes aquatiques profitent indirectement des éléments transportés dans le milieu lotique. Inversement, une crue prévisible de longue durée favorise le développement d'adaptations et de stratégies qui permettent aux organismes d'exploiter efficacement l'ATTZ. Une telle crue s'accompagne d'un effet de bordure dynamique qui fait en sorte que l'ATTZ devient un « littoral mobile ». Dans ces circonstances, il n'y a pas de stagnation prolongée et le recyclage de la matière organique et des substances nutritives se fait rapidement, ce qui donne lieu à une productivité élevée. La production primaire dans l'ATTZ est beaucoup plus élevée que celle des masses d'eau permanentes dans les réseaux hydrographiques non modifiés. Le rendement et la production de poissons sont étroitement reliés à l'étendue de la plaine inondable, tandis que le cours normal de la rivière est utilisé comme voie de migration par la plupart des poissons.

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Dans les régions tempérées, les variations de l'ensoleillement et/ou de la température peuvent modifier les effets de la crue, et l'action de l'homme sur la crue des eaux et sur les plaines inondables limite souvent la production. Une plaine inondable peut cependant se former localement par sédimentation dans un tronçon de cours d'eau modifié par un barrage de basse chute. Aussi, les rives des cours d'eau à faible débit se transforment en plaines inondables suite à la formation de levées alluviales qui les séparent du canal principal.

Les crues sont des phénomènes qui se manifestent par à-coups. Cette situation est différente de celles prises en compte par les concepts qui mettent l'accent sur les processus continus intervenant dans les eaux courantes, tel que le concept du continuum appliqué aux cours d'eau. Les plaines inondables constituent un cas particulier car elles ne sont pas tributaires de la transformation inefficace de la matière organique en amont, même si leur réserve d'éléments nutritifs dépend en partie des échanges latéraux périodiques d'eau et de sédiments avec le canal principal. La crue est un phénomène particulier par rapport aux conditions normales parce que la position d'une plaine inondable dans le réseau fluvial n'est pas un facteur qui détermine de façon fondamentale les processus observés dans ce type de milieu. Les questions soulevées par le phénomène des crues ne peuvent pas être résolues à l'aide des concepts traditionnels de la limnologie utilisés pour étudier les systèmes lotiques et lénitiques.

Hydrologists think of rivers as links in the hydrological cycle, which transport runoff water from the continents to the sea or to the center of endorheic basins (Curry 1972). Since water is a good solvent and flowing water provides kinetic energy, water transport by rivers is linked with the transport of dissolved and solid substances. However, precipitation and river discharge typically vary significantly during the annual cycle. At low discharge rates, rivers flow in well-defined channels, but at high water in natural systems wide floodplains are recurrently inundated.

River-floodplain systems provide important habitats for biota, and ecologists have tried to link the biota of river systems with local environmental conditions and to adopt existing paradigms from other aquatic systems. These attempts have met with two problems: (1) the division of ecology into terrestrial ecology and limnology; and (2) the classification of water bodies into more or less closed, lentic systems with accumulating characteristics (lakes, ponds) as outlined in traditional limnology texts (Ruttner 1952) and open, lotic systems with discharging characteristics (streams, rivers) (Hynes 1970). The transient nature of aquatic habitats in floodplains resulted in biased treatment or in their omission. When studying rivers, most limnologists restricted themselves to river channels; when studying floodplains, they concentrated on floodplain lakes, often treating them as classical lakes.

One recent theoretical construct in river ecology, the river continuum concept (RCC) (Vannote et al. 1980), is based on the hypothesis that a continuous gradient of physical conditions exists from headwater to mouth. Analogous to the energy equilibrium theory of fluvial geomorphologists, the RCC states that structural and functional characteristics of stream communities are adapted to conform to the most probable position or mean state of the physical system. Producer and consumer communities establish themselves in harmony with the dynamic physical conditions of a given river reach, and downstream communities are fashioned to capitalize on the inefficiencies of upstream processing. Both upstream inefficiency (leakage) and downstream adjustment seem predictable. Therefore the RCC purports to provide a framework that permits us to integrate predictable and observable biological features of lotic systems (Vannote et al. 1980).

In our view, the RCC suffers from two basic limitations: (1) it was developed on small temperate streams but has been extrapolated to rivers in general; and (2) it was based on a concept that had been elaborated for the river basin in a geomorphological sense but was in fact restricted to habitats that are permanent and lotic.

Most papers that discuss the RCC recognize these limitations (Winterbourn et al. 1981; Barmuta and Lake 1982; Minshall et al. 1983; Minshall et al. 1985; Statzner and Higler 1985; Sedell et al. 1989) but fail to consider the biological significance of processes within the seasonal, aquatic habitats of floodplains. It may prove acceptable to modify the RCC to account for brief and unpredictable floods in low-order streams, even for catastrophic floods which change the physical environment and "reset" systems (Cummins 1977; Fisher 1983). However, as the size of a floodplain increases, usually along with increasing river discharge, the frequency of floods decreases, and their duration and predictability increase. These changes result in a distinct geomorphological and hydrological system with an increasing ratio of periodically lentic to lotic areas. This system results in adaptations of biota that are distinct from those in systems dominated by stable lotic or lentic habitats.

Recently, the importance of river-floodplains to fish populations in temperate, subtropical, and tropical regions has been shown by Lambou (1959), Holčík and Bastl (1976, 1977), Bryan and Sabins (1979), Welcomme (1979, 1985, 1989), Bayley (1980, 1981a, 1983), Junk (1980, 1984), and Littlejohn et al. (1985). These studies have signaled a renewed appreciation of pioneer work by Antipa (1911, 1928) and Richardson (1921). The status of the forest in subtropical river-floodplain systems has been summarized by Gosselink et al. (1981) and Wharton et al. (1981). The biases and inadequacies of limnological paradigms when applied to floodplain systems were recently discussed by Bayley (1980, 1983), Junk (1980, 1984), and Junk and Welcomme (1989) based on their experience in tropical systems. Amoros et al. (1986) and Bravard et al. (1986), who analysed the impact of flood regulation on plant and animal communities of the Rhône R. floodplain, stressed the importance of lateral and vertical dimensions of the river–floodplain system. Davies and Walker (1985) emphasized that considerable modification of the RCC was required before it could be applied to large river systems.

In this paper we synthesize evidence that suggests a complementary concept, the "flood pulse", that attempts to explain the relationship between the biota and the environment of an unmodified, large river–floodplain system. This concept is based on our experiences in relatively pristine systems in the neotropics and Southeast Asia and in the Upper Mississippi R. We derive this concept from the known ecology of typical biota that have adapted to the geomorphology and hydrology of large river–floodplain systems.

The Flood Pulse Concept

We propose that the pulsing of the river discharge, the flood pulse, is the major force controlling biota in river–floodplains. Lateral exchange between floodplain and river channel, and nutrient recycling within the floodplain have more direct impact on biota than the nutrient spiralling discussed in the RCC (Vannote et al. 1980). We postulate that in unaltered large river systems with floodplains in the temperate, subtropical, or tropical belt, the overwhelming bulk of the riverine animal biomass derives directly or indirectly from production within the floodplains and not from downstream transport of organic matter produced elsewhere in the basin.

The effect of the flood pulse on biota is principally hydrological. We postulate that if no organic material except living animals were exchanged between floodplain and channel, no qualitative and, at most, limited quantitative changes would occur in the floodplain (Bayley 1989). The relative importance of imported versus recycled inorganic nutrients in floodplains is not clear and probably varies between systems. Given similar hydrological conditions, the longitudinal position of a floodplain in the drainage network is of little importance with respect to the biota.

The Highway Analogy

Faunal life histories in unaltered large river–floodplains can be viewed as analogous to vehicles on a highway network. Were non-terrestrials to investigate this network, they would observe numerous bodies traveling in opposite directions and might well surmise that resources for those bodies were derived from the highways. If funds permitted a detailed study, it would reveal that four-wheeled creatures need to leave highways periodically for sustenance, along with their apparently symbiotic occupants. Eventually, major sources of production would be identified in farms, oil fields, and mines, vehicles consuming and distributing resources via the highway network as a response to production cycles and long-term economic changes.

The life histories of major plant and animal groups, in particular fish, in large river–floodplains are beginning to be understood sufficiently to contribute to the theory that the river network in a river–floodplain system is in many ways analogous to a highway network with the vehicles corresponding to the fish. Detritivores, herbivores, and/or omnivores support large fisheries in the main channel (Petrere 1978, 1982; Welcomme 1979; Quirós and Baigún 1985), but the highest yields are associated with adjoining floodplains (Richardson 1921; Lowe-McConnell 1964; Petrere 1983) and most of their production is derived from floodplain habitats (Welcomme 1979; Bayley 1983). The main channel is used principally as a route for gaining access to adult feeding areas, nurseries, spawning grounds, or as a refuge at low water or during winter in temperate zones. An analogous situation is found in large north-temperate and arctic rivers where most of the ichthyomass is anadromous; here the main feeding grounds are found in the delta area or in the sea (Grainger 1953; Andrews and Lear 1956; Foerster 1968; Roy 1989).

We will describe the functions of the floodplain and main channel in large river–floodplain systems with respect to the biota and evaluate the links between them and the nonfloodable watershed in the light of recent data.

Definition of a Floodplain

Terms applied to classical limnological and terrestrial systems can be inappropriate for explaining concepts in river–floodplains. This is not merely a semantic discussion because the classical terms are understood to define features and functions in their respective systems.

The “active floodplain” of a river is defined by North American hydrologists as the area flooded by a 100-year flood (Bhowmik and Stall 1979). This period is arbitrary, longer than most existing records, and has little ecological meaning. Bayley (1981b) noted that huge areas of shallow, very acidic, largely deoxygenated swamp occur in the Peruvian Amazon. These areas are distant from the main channels and inhospitable to the bulk of aquatic animals. He proposed an active floodplain that excluded these peripheral swamps in order to compare fish production and fishery yields among systems.

We define floodplains as “areas that are periodically inundated by the lateral overflow of rivers or lakes, and/or by direct precipitation or groundwater; the resulting physicochemical environment causes the biota to respond by morphological, anatomical, physiological, phenological, and/or ethological adaptations, and produce characteristic community structures”. This ecological definition recognizes that flooding causes a perceptible impact on biota and that biota display a defined reaction to flooding. Furthermore, it implies that the impact of water level pulsing on biota is independent of the nature of its source and that there are many ecological similarities between floodplains adjacent to, for example, pulsing lakes or reservoirs and pulsing rivers. The definition encompasses a wide hydrological spectrum from short- to long-duration floods and from unpredictable to predictable timing. Our examples from large river systems exhibit predictable flood pulses of long duration.

We have termed the floodplain area the “aquatic/terrestrial transition zone” (ATTZ) because it alternates between aquatic and terrestrial environments. We use this term to stress our more specific definition of floodplain, because ‘floodplain’ has often been defined to include permanent lentic and lotic habitats. The inshore edge of the aquatic environment that traverses the floodplain (ATTZ) we have termed the “moving littoral”. The floodplain or ATTZ has unique properties that have been considered to comprise a specific ecosystem (Junk 1980; Odum 1981).

Hydrologists consider the river and its floodplain as one unit since they are inseparable with respect to the water, sediment, and organic budgets. We term this unit the “river–floodplain system”. Therefore, this system comprises permanent lotic habitats (main channels), permanent lentic habitats, and the floodplain (ATTZ). Many limnologists have difficulty defining floodplains viz a viz other aquatic systems, and they have defined artificial, stable borders between land and water. Conversely, floodplains are ecosystems with water boundaries that recurrently traverse large areas. The environmental change from the aquatic to the terrestrial phase at a specific point in a floodplain (ATTZ) may be as severe as the change from a lake to a desert. Classical limnological terms describing morphological features of lakes or rivers (e.g., shoreline, littoral, profundal, size, depth) are unsuitable and must be redefined or qualified, because they have become time-dependent in the floodplain. This time dependency is important because it affects the productive processes and the life cycles of plants and animals. Pieczyńska's (1972) definition of eulittoral appears to have functional parallels with our definition of a floodplain; however, the eulittoral occupied a very small part (±5 %) of the nonfloodplain lakes in her study and responded to a pulse amplitude of only about 40 cm. Also, we are cautious about drawing close parallels with the intertidal zone because the time scale of the tidal pulse is so much shorter, and is brief compared with the generation times of the higher biota.

Distinctions between aquatic and terrestrial organisms and processes have proved useful in studies of rivers and lakes with well-defined borders. The ecologist's view of floodplains, however, may vary according to the group of organisms being studied. Many of the organisms colonizing floodplains have developed adaptations that enable them to survive during an adverse period of drought or flood and even to benefit from it; thus neither a purely aquatic nor a wholly terrestrial view is appropriate.

Fisheries biologists tend to consider main channels and their floodplains as a single unit, because both are essential for the survival of fish stocks (Holčík and Bastl 1976; Welcomme 1979; Bayley 1980, 1981a, 1983). Conversely, studies of floodplains linked to African rivers or reservoirs show that they are also important for terrestrial game animals in adjacent nonflooded savannas, because the floodplains determine survival rates during the dry period (Sheppe and Osborne 1971; Davies 1985).

Were we to follow the arguments of hydrologists, all plant and animal material produced in a river–floodplain system would be autochthonous because it derives from riverine sediments and dissolved nutrients. Allochthonous would refer to the material introduced from outside the river–floodplain system. In limnological literature, however, the term autochthonous is applied to biota produced in the aquatic environment, and all terrestrial material is thereby classified as allochthonous. Oscillation between aquatic and terrestrial phases in floodplains makes the limnological differentiation of organic material according to its origin misleading. Similarly, the riparian zone, as understood in temperate areas, is difficult to define in a river–floodplain system. Consequently, we avoid unqualified references to these terms.

We have defined floodplain (ATTZ), river–floodplain system, and moving littoral, and explained why traditional limnological and hydrological paradigms are not appropriate from an ecologist's view. We now use examples to describe the effects of the flood pulse on biotic and abiotic components of the river–floodplain system.

Hydrology

The hydrological regime of rivers reflects the climate of its upstream catchment area. Low order streams have an irregular flood pattern with numerous peaks because they are strongly influenced by local precipitation. This influence generally diminishes with increasing size of the watershed and is almost imperceptible in the hydrograph of very large rivers.

The hydrological buffering capacity of a large catchment area results in a rather smooth and predictable flood curve. In mainly tropical or subtropical systems with large watersheds, the hydrograph reflects seasonality in precipitation, and typically shows only one pronounced flood peak per year. A few tropical rivers, e.g., the Zaire R., show two flood peaks due to two rainy seasons in their catchment areas. In temperate and cold climates, the impact of precipitation on the hydrograph is modified by the temperature regime. For example, minor flooding occurred in autumn in the Upper Mississippi R. prior to dam construction (Grubaugh and Anderson 1989a) because evapotranspiration rates decrease as temperature drops. Also, water accumulates as snow and ice in winter, which then contribute to the spring flood by melting.

Due to the size of large river basins, the effects of seasonal climatic changes may be felt downstream only after several weeks or even months. This time lag can be of ecological importance in downstream parts of large river systems. In the central Amazon the river is still rising at Manaus after the termination of the major rains; the flood peak follows the rainy season by 4–6 weeks. On the lower Mississippi R., cold water from melting snow in the head waters passes when the temperature in the backwaters of the floodplain is already much higher (Bryan et al. 1976; Holland et al. 1983).

The shape of the hydrograph depends not only on the discharge characteristics of the river, but also on valley slope, floodplain size, and vegetation. Although the Illinois R. has a mean discharge of only 627 $m^3 \cdot s^{-1}$ (Fitzgerald et al. 1986), it has protacted floods characteristics of a much larger river because it occupies a wide river valley carved by the ancestral Mississippi and Teays rivers. Because the valley has filled with alluvium, its gradient is very flat and the river drops only 1.6 $cm \cdot km^{-1}$.

At a given rate of discharge increase, the water level rises more slowly as the floodplain begins to fill. In larger floodplains the rate of rise is slower, the period of inundation increases, and more lentic habitats develop. As the water recedes, processes in the floodplain become less dependent on the river channel and more subject to local climatic events. During the terrestrial phase, the amount and distribution of local rains greatly affects the composition and productivity of plant communities as well as the life cycles of many animals. When local precipitation at low water is high, floodplains are forested, e.g., in the middle and upper Amazon, Zaire, and Mississippi rivers. Conversely, when local precipitation is low, savannas with gallery forest develop, e.g., in the floodplains of the lower Nile, Zambezi, and Volta rivers. Some lakes and swamps are isolated from the main channel for many months or even years. Their hydrological regimes are therefore independent of the main channel except during periods of high water.

Nutrients

According to hydrologists, a river's chemistry reflects its catchment area. This holistic view has been applied successfully to streams with respect to their nutrient budgets (Hynes 1975; Vannote et al. 1980). Nutrients can roughly be divided into inorganic and organic fractions; these in turn can be subdivided into gaseous compounds, dissolved solids, and particulate matter. The floodplain receives all classes of nutrients directly from the main channel, and its basic nutrient status would be expected to correspond to that of the river. Floodplains, however, tend to establish their own cycles since organisms and environmental conditions that influence the biogeochemical cycles differ considerably from those in the main channel. The effects of rain, runoff, groundwater, and input from floodplain tributaries may also be important.

The Inorganic Fraction

Gaseous Compounds

Gases such as CO_2, O_2, H_2S, CH_4, and N_2 are produced and/or consumed in the floodplain independently of processes in the main channel in systems with slow, regular flood pulses. Residence time of floodplain water and temperature modify concentrations. The lack of persistent thermal and chemical stratification in most Atchafalaya floodplain lakes is due to the short period of lentic conditions during warm weather (Bryan et al. 1974). In contrast, the water column becomes chemically stratified over large areas soon after entering the Amazon floodplain; the daily thermocline with a temperature difference of 1–3 °C is sufficient to inhibit circulation deeper than 2–6 m during periods of several weeks or even months. Large amounts of organic material under decomposition at high temperatures result in high rates of oxygen consumption and CO_2 release near the bottom. Hypoxic, or even anoxic conditions accompanied by H_2S and CH_4 production, are often found at a few metres depth (Schmidt 1973a; Melack and Fisher 1983; Junk et al. 1983).

In addition to nitrogen input from the river, high nitrogen fluxes to and from the atmosphere occur. These fluxes are related to oxygen levels and to organisms in water and soils, both of which change drastically between flood and dry periods. Denitrification in wetlands is well documented (Kemp and Day 1984) and has even been used in the treatment of wastewater (Dierberg and Breszonic 1984). Various nitrogen-fixing organisms, e.g., cyanophytes and bacteria, that are often associated with higher plants such as Leguminosae counteract denitrification by fixing atmospheric nitrogen (Heller 1969; Richey et al. 1985). Despite the high potential for denitrification, Brinson et al. (1980) consider tupelo-cypress swamps to be nitrogen sinks due to high nitrogen levels in the litter.

Dissolved Solids

River water is the major source for dissolved inorganic compounds, including plant nutrients. Abiotic and biotic processes in the floodplain, however, may considerably alter the total amount and ionic composition of dissolved materials. Increased evaporation may raise salinity in backwaters above the levels found in the river, in particular in arid climatic zones. Biogenic modifications are reported from Amazonian floodplain lakes where ten to twentyfold increases in total salinity have been measured in small pools at low water (Furch et al. 1983). A major change in ionic composition, such as an increase in potassium, has been principally associated with leaching of decomposing aquatic and terrestrial macrophytes (Furch 1984a, 1984b; Furch et al. 1983).

Further changes in ionic composition result from dilution by local rains or by mixing with lateral inflows of surface and ground water from nonflooded areas. During low river stages in the Amazon, water seeping through floodplain sediments has an electric conductance up to 200 times that of the Amazon R. water, with high levels of iron and manganese (Irion and Junk, unpublished data).

Levels of dissolved nutrients are seldom limiting factors for primary production in the main channels of large rivers. In the floodplain, however, phosphorous and/or nitrogen often limit productivity, and inflowing river water replenishes the nutrient levels, as shown for phytoplankton production in Amazonian floodplain lakes (Fisher 1979). In lake and swamp habitats receiving minimal influence from the Atchafalaya R., heterotrophic phytoplankters (flagellated euglenophytes and pyrrophytes) predominated during low water levels in association with minimal inorganic nutrients (Bryan et al. 1976; Seger and Bryan 1981).

Little is known concerning the amount of dissolved inorganic compounds released from the floodplain into the main channel, and findings are contradictory for phosphorous (Yarbro 1983) and nitrogen (Brinson et al. 1983). Release and storage may be related to the flood cycle and to vegetation cover, and in temperate regions, to the growth cycle of the vegetation (Klopatek 1978; Brinson et al. 1980). Because large floodplains represent a mosaic of habitats with different physical and chemical conditions supporting diverse biotic communities, they may act either as a sink, or as a source with respect to each nutrient, depending on the circumstances.

Particulate Matter

Particulate inorganic matter in suspension is normally considered an unimportant source of plant nutrients in the river channel. Conversely, such particles hinder growth of phytoplankton and submersed aquatic macrophytes due to shading. In floodplains, however, they become a basic part of the nutrient pool available to primary producers in the dry phase and during part of the wet phase. Fertility of floodplains depends largely upon the quality of deposited sediments. Irion (1983) states that transport and deposition of sandy and kaolinitic material produce an infertile floodplain (e.g., Rio Negro in Brazil), whereas the montmorillonite and illite of the Amazon and Mississippi rivers result in high floodplain fertility. However, an impoverishment of some mobile elements (Fe, Mn, Zn) was detected in the upper 10 m-layer of Amazon sediments, which are only a few hundred years old (Irion et al., unpublished data). Conversely, weathering of the sediments, which is accelerated in tropical climates, adds dissolved inorganic materials.

The Organic Fraction

According to the RCC, aquatic animal communities of low-order streams depend mainly upon material from the nonflooded watershed. Medium-order streams have an increased instream production. Fauna of high-order rivers lacking floodplains depend mainly on organic material from upstream areas because primary production in the main channel is very low (Vannote et al. 1980).

Practically all litter must be processed by microorganisms if it is to become attractive to higher consumers. A considerable portion continues to be practically indigestible, such as fine particulate organic material in the Amazon main channel (Hedges et al. 1986). Ertel et al. (1986) reported that humic materials comprised 60 % of the dissolved organic carbon of the Amazon main channel; this carbon in turn made up about 50 % of the total organic carbon. The comparatively low BOD of the water from the main channel of the Amazon itself contrasts sharply with values in its floodplain (Junk, unpublished data).

Part of the organic carbon transported in the main channel passes on to the floodplain. This amount, however, is negligible in comparison with in situ production of organic material in the floodplains of rivers (Bayley 1989). Estimates of the productivity of the Amazon floodplain show that annual primary production is of the same order of magnitude as the total amount of carbon transported by the river to the Atlantic Ocean (Richey et al. 1980; Junk 1985a).

The direct impact of floodplains on the carbon budget of main channels is not well known. Some evidence suggests that floodplains can be a source for particulate and dissolved carbon (Chowdhury et al. 1982; Martins 1982; Junk 1985a; Furch and Junk 1985; Grubaugh and Anderson 1989b). Conversely, retention mechanisms, such as settling of particulates, uptake by organisms, and retention of most macrophytes by stranding or trapping during falling water (Junk 1980) contribute to the recycling of most carbon in the floodplain and strongly reduce leakage to the river channel. Carbon export from floodplains also depends on hydroperiod, flushing rate, and in temperate regions, on the growth cycle of floodplain vegetation. Data from floodplains are limited, but Odum and de la Cruz (1967) estimated that the rate of export of organic material from a Georgia tidal marsh was directly proportional to volumetric flow rates.

Gosslink et al. (1981) assumed that flooding during winter and spring provides more detritus to main channels than during summer in temperate regions. In the tropics, consistently high temperatures favor high production and rapid processing of organic material throughout the year.

Biota in the River Channel

The channel is well defined in large, pristine rivers, and is delineated from the floodplains by natural levées and/or a marked increase in water velocity. In rivers modified by navigation dams, such as the Mississippi, broad, slow-flowing main channel borders are found on either side of the narrow main channel, which is defined by the thalweg (Fremling et al. 1989). These borders, which constitute a developing floodplain, are discussed separately below; however, the main channels of modified rivers have much in common with those in more pristine systems.

Plants

Great water depth, high suspensoid load, considerable turbulence, and strong current make the main channel unfavorable for primary production. Aquatic macrophytes and periphyton normally colonize shores and, in some transparent tropical rivers, rocky substrates (Podostemaceae). In slow-flowing tropical and subtropical rivers floating macrophytes may become important. Phytopotamoplankton density increases with stream order, transparency, and decreasing current velocity, but absolute values are low (e.g., Berner 1951). In most large rivers, physical factors, in particular light, rather than mineral nutrients limit primary production (Fisher 1979). Average primary production per unit area in the main stems of large turbid river systems such as the Amazon, Mekong, Ganges, and Mississippi can be only a small fraction of that in their floodplains.

The extent to which floodplain water bodies contribute to populations of potamoplankton and floating macrophytes in large rivers is unknown. The considerable increase of potamoplankton downstream of reservoirs, e.g., in the Nile (Brook and Rzóska 1954; Talling and Rzóska 1967; Hammerton 1976) and the increase of floating macrophytes in the Amazon main channel at rising and high water (Junk 1970) are due to high production of these plants in associated lentic habitats.

Invertebrates

Little information is available about colonization by animals of the bottoms of large rivers. The bed loads of large rivers in alluvial plains, e.g., the Mississippi, are sandy (Schumm 1977). Large river channels mostly consist of a monotonous sequence of slowly moving sand dunes unsuitable for benthic organisms. The Amazon R., for example, transports its bed load of coarse sand as dunes 6–8 m high (Sioli 1984).

High suspensoid loads hinder benthic and epizoic animals (Hynes 1970). Junk (1973) found a decrease in number and biomass of principally filter-feeding perizoon in floating macrophyte vegetation as amounts of inorganic suspensoids increased.

Although some invertebrates can live in the dominant sandy substrates of main channels (e.g., the chironomids *Gillotia*, *Cyphonella*, *Robackia*, and *Saetheria* [Coffman and Ferrington 1984]), densities are low. Berner (1951) and Morris et al. (1968) indicated average fresh invertebrate biomasses in the main channel of only 0.001 $g \cdot m^{-2}$ and 0.007–0.048 $g \cdot m^{-2}$, respectively, for the Missouri R., and attributed these low values to shifting substrates, siltation, fluctuating water levels, swift current, and absence of aquatic vegetation. In the Atchafalaya distributary, which receives 80 % of the Mississippi R. discharge, Bryan et al. (1976) reported a mean quantity of 327 benthic individuals per m^2 in riverine habitats compared with densities up to ten times greater in floodplain habitats.

Logs and rocks provide stable substrates for organisms in a channel environment that is otherwise dominated by shifting alluvium. Over 10^6 logs were pulled from channels in the lower 1600 km of the Mississippi during a 5-year period (Harmon et al. 1986). The average fresh animal biomass colonizing logs in the Kaskaskia R., Illinois, varied between 0.57 and 1.65 $g \cdot m^{-2}$ (Nilsen and Larimore 1973). Nord and Schmulbach (1973) reported a range of 0.2–3.2 $g{\cdot}m^{-2}$ dry weight in the Missouri R. Assuming an average surface area per log of 5 m^2, a dry biomass density of 2 $g{\cdot}m^{-2}$ of log, and an average width of the lower Mississippi channel of 900 m, the overall biomass density of this fauna would be only 0.007 $g{\cdot}m^{-2}$.

Vertebrates

Vertebrates, particularly fish, are important consumers in the main channel. In subtropical and tropical rivers, freshwater dolphins, capybaras, manatee, hippos, turtles, and crocodiles may contribute considerably to the main channel biomass. White whales and seals occur in arctic rivers; beavers, muskrats, and otters in temperate rivers; and waterfowl and shorebirds in both. However, few higher animals have adapted to utilize main channel habitats exclusively. Those that do tend to be predators whose prey depends largely on production in floodplain habitats, such as large, piscivorous catfishes (Goulding 1981), to some extent river dolphins (Ferreira da Silva 1983), and fish that consume aquatic invertebrates (Lundberg et al. 1987). In the main channels of the Mississippi and Missouri rivers, pallid sturgeon (*Scaphirynchus albus*), blue sucker (*Cycleptus elongatus*), blue catfish (*Ictalurus furcatus*), and several chubs (*Hybopsis* spp.) feed largely on invertebrates, and, with respect to large pallid sturgeons and blue catfish, on fish (Pflieger and Grace 1987).

Most vertebrates use the main channel temporarily as migration routes, for spawning, as refuge during droughts or freeze-up, or for hibernation. Tropical rivers are famous for large-scale migrations of fish for dispersal and/or spawning in the main channel or floodplain, that result in large biomass densities in the main channel during falling or low-water periods (Godoy 1967; Bonetto et al. 1969a; Bayley 1973; Ribeiro 1983). Large channel catfish (*Ictalurus punctatus*), flathead catfish (*Pylodictis olivaris*), and freshwater drum (*Aplodinotus grunniens*) use drop-offs, scour holes or obstructions in or along the main channel of the Upper Mississippi R. for a winter refuge (Hawkinson and Grunwald 1979).

Except for limited amounts of potamoplankton, benthos, and predators, the biota of the main channel concentrate close to the river shoreline, to islands, or in the main channel border areas described below, areas where habitat diversity increases and food supply improves (edge effect). Therefore the "bank coefficient" (Sedell et al. 1989) is an index of the productivity potential of a river channel in the absence of a floodplain. Conversely, when a regularly inundated floodplain is present, most of the vertebrates found in the main channel depend to a great extent directly or indirectly on primary production in the laterally linked floodplain habitats.

Biota in the Floodplains

Flood Pulsing and Life Cycles

Life cycles of biota utilizing floodplain habitats are related to the flood pulse in terms of its annual timing, duration, and the rate of rise and fall. Timing is important in temperate rivers where seasonal temperature and light cycles also regulate productivity.

Because the ATTZ has pronounced aquatic and terrestrial phases, there are strong selective pressures on aquatic organisms to colonize it at rising or high water because of the feeding opportunities (Bonetto et al. 1969b; Welcomme 1979; Bayley 1983, 1988). Conversely, terrestrial organisms that occupy nonflooded habitats along the floodplain borders are adapted to exploit the ATTZ at low water levels (Sheppe and Osborne 1971; Fredrickson 1979; Davies 1985).

In low-order streams, the level of adaptation to flooding is rather low. For many organisms, unpredictable floods correspond to catastrophic events that periodically "reset" the physical and biotic environment (Cummins 1977; Fisher 1983). Obligate aquatic organisms concentrate mostly in the main channel because flood periods are too short and irregular to develop profitable strategies for occupying the ATTZ.

The predictable and prolonged flood pulse typical of large rivers favors the development of anatomical, morphological, physiological, and/or ethological adaptations of terrestrial and aquatic organisms in order to colonize the ATTZ as shown by Adis (1979) and Irmler (1981) for Amazonian terrestrial invertebrates and by Uetz et al. (1979) and Wharton et al. (1981) for N. American floodplains.

In the humid tropics, regular flooding and drying of floodplains provoke a pronounced seasonality in an otherwise unseasonal environment. Many Amazonian floodplain trees show distinct annual growth rings, because inundation causes a "physiological winter" through oxygen stress (Worbes 1985, 1986). Seed production is timed with the flood for dispersal by water or by fish (Gottsberger 1978; Goulding 1980). Terrestrial arthropods from central Amazonian floodplain forests show a defined reproduction period (Adis and Mahnert 1986; Irmler 1986) but are polyvoltine in neighboring dryland forests (Adis and Sturm 1989). The flood cycle has been hypothesized as the driving force behind species selection ("taxon pulse", Erwin and Adis 1982) and the acquisition of an annual seasonality that enabled tropical insects to colonize temperate zones (Paarmann et al. 1982; Adis et al. 1986). The regular pulsing of large rivers may have been as important for the development of biorhythms in the tropics as was the pulsing of the light/temperature regime in temperate regions or the change between dry and wet periods in the arid and semiarid tropics.

Because many vertebrates living in the main channel depend on the floodplain for food supply, spawning, and shelter, they have developed strategies to utilize periodically available habitats. High mobility is required, as witnessed by the extensive migrations referred to earlier. Such strictly aquatic animals as fish and manatees depend on the flood cycle of the river, which controls access to the floodplain. Others less strictly aquatic, such as hippos, beavers, or capybaras, make feeding trips out of the water.

The importance of lateral migration of animals between the floodplain and main channel of large river systems has been underestimated because modern civilization has substantially modified the hydrograph and separated floodplains from main channels. These modifications dominate large temperate river systems. The biologist's typical view of fish in temperate rivers has been that they complete their life cycles within the river channel. Indeed, fish have no alternative in sections of some highly altered systems such as major stretches of the Mississippi R. Their persistence in these areas attests to their great plasticity in coping with habitat change.

Fishes that depend on seasonal colonization of floodplain habitats dominate the fisheries, the biomass, and the production in river–floodplain systems (Bonetto et al. 1969a; Welcomme 1979; Bayley 1981a; Goulding 1981; Bayley 1983; Littlejohn et al. 1985). Spawning of many species occurs at the beginning or during some period of the rising flood, resulting in timely colonization of the floodplains for feeding and shelter (Bayley 1983, 1988; Holland et al. 1983; Welcomme 1985). Conversely, when the water recedes, fish find refuge in main channels, in residual floodplain water bodies, or in permanent tributaries (Welcomme 1979).

Adults of many species show seasonality in food uptake related to flood cycles, as shown for the Rupununi R. by Lowe-McConnell (1964) and for the large rivers of the Amazon basin by Goulding (1980, 1981) and Ribeiro (1983). Periods of fasting coincide with low or falling water levels and are associated with decreases in seasonal fat content in many adult fish (Junk 1985b). Studies of diets at rising and high water show that many species directly use pollen, fruits, seeds, and the small portion of terrestrial insects that drop into the water from the canopy of the forest (Goulding 1980).

Detritus plays a major part in the food webs in floodplains (Welcomme 1985). Fish are major detritivores in the tropics. For example, fine particulate organic matter (FPOM) is consumed directly by the highly specialized Prochilodontidae and Curimatidae in South America, and by Citharinidae and *Labeo* species in Africa (Bowen 1984; PBB, pers. obs.). Coarse particulate organic matter (CPOM) features in the diet of many omnivores in the Amazon (Almeida 1980; Santos 1981).

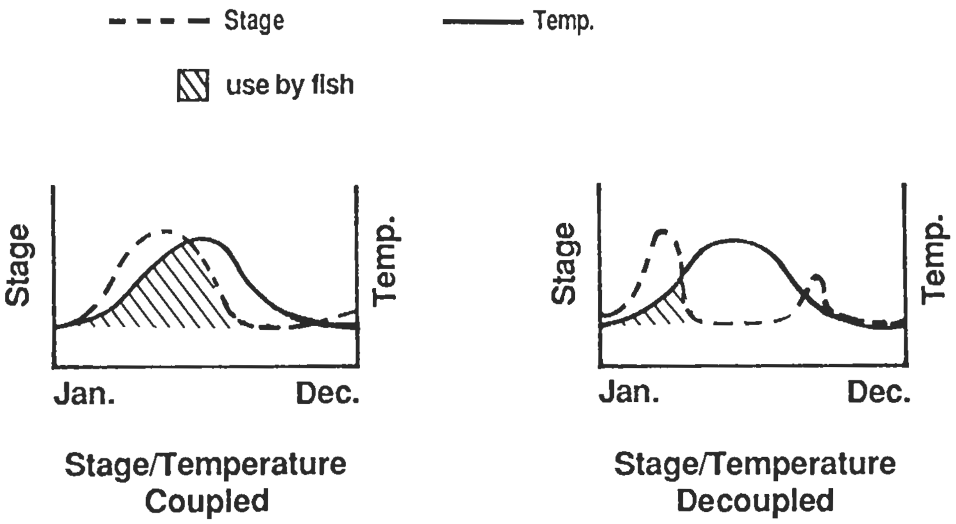
FPOM is also an important feature of the gut contents of large catostomids and *Dorosoma* in large N. American rivers, but its nutritional importance has only recently been indicated (Ahlgren 1988). Most of the commercially important fishes are bottom feeders utilizing macroinvertebrates, which in turn ingest detritus (Fremling et al. 1989).

The importance of remnant floodplain areas in the Mississippi and its tributaries was indicated by Risotto and Turner (1985), who found that 55 % of the variation in average fish catch was explained by bottomland hardwood area (as a proxy to floodplain area), fishing effort, and latitude. Because some bottomland forest is now cut off by manmade levees and not all floodplains are forested, the relationship might be improved with direct measurements of the active floodplain areas.

Adaptations to survive hypoxic conditions favor the colonization of periodically stagnant waters typical of many floodplains. Air breathing and other adaptations to low oxygen concentrations are frequently found in neotropical fishes (Carter and Beadle 1931; Kramer et al. 1978; Junk et al. 1983), other tropical floodplain rivers (Welcomme 1979), and in fish of the Mississippi drainage (e.g., gars, *Lepisosteus* spp. and bowfin, *Amia calva*; see also Marvin and Heath 1968).

In the temperate Upper Mississippi R. floods can reduce the overwinter survival of young-of-the-year freshwater drum (*Aplodinotus grunniens*) by the influx of channel water at 0°C into backwater thermal refuges where the temperature is 4°C (Bodensteiner and Sheehan, in press). The winter biology of fishes in large North American rivers has been little studied, and the recruitment of other species may be strongly affected by winter temperatures and flood patterns. From spring through summer, the timing and duration of the flood is critical to species which gain access to the ATTZ and permanent backwaters for feeding and spawning. Ideal conditions for spring spawners occur during years in which the flood and temperature rise are coupled; conversely, recruitment is poor if the flood retreats too soon during the warm growing season (Fig. 1). Finger and Stewart (1987) found that the timing and duration of flooding controlled the year-class dominance of spring- versus summer-spawners in Missouri floodplain forests.

In polar, sub-arctic, and taiga rivers the timing of the flood is predictable because of massive snow melt in the spring. However, the flood is accompanied by ice that scours the floodplains and subsequently recedes rapidly,



Stage/Temperature Coupled

Stage/Temperature Decoupled

FIG. 1. Schematic of combinations of river stage and water temperature in temperate river–floodplain systems (see text).

creating an inhospitable environment for fishes (Roy 1989). The severe springtime conditions may explain why fish in high latitudes avoid the flood by spawning in the fall (R.A. Ryder, personal communication).

Tree growth is mainly retarded by floods because the rhizosphere becomes deoxygenated (Huffman 1980; Huffman et al. 1981). Gosselink et al. (1981) postulated that floods during winter or spring have a positive effect on the floodplain forest because they distribute nutrients and water to the soil before plant growth commences. Data on flood tolerance of tree species often appear to be contradictory because the timing of floods relative to growth and resting periods is not stated (Dister 1980).

The Mississippi R. is a major migratory flyway for waterfowl, shorebirds, gulls, and eagles. The dabbling ducks (mallard, pintails, greenwing and bluewing teal, black duck) utilize mast in floodplain forests, waste grain in adjacent harvested fields, and invertebrates associated with macrophytes in shallow water bodies, as well as the seeds, tubers, and plant leaves in the floodplain (Bellrose 1941). The diving ducks (canvasback, lesser scaup) utilize submerged macrophytes and macroinvertebrates that grow in deeper water (Thompson 1973). Aquatic and moist-soil vegetation in the Illinois and Upper Mississippi floodplains requires a period of shallow, stable water levels during the summer growing season (Bellrose et al. 1979). The summer's primary production is made more accessible to migratory waterfowl by the autumn rise in water levels. If an autumn flood does not occur, managers of refuges and duck clubs create one by pumping water from the river into the floodplain. They also pump water out of the same impoundments if the flood is too slow to retreat in the summer, so they can sow millet or allow native plants to grow (Bellrose et al. 1979).

Flood Pulsing and Plant Community Structure

Under given climatic conditions, plant communities become established in the ATTZ of large rivers according to the flood regime. Every place in this zone can be considered a point on a gradient reflecting the degree of annual flooding. Every plant has its optimum position on this gradient. The optimum, however, can be modified by such factors as stability, structure, and fertility of the substrate, groundwater level, and biogenic processes (e.g., accumulation of organic material, nitrogen fixation, and interspecific competition) (Lindsey et al. 1961; Bedinger 1979; Burgess et al. 1973; Johnson and Bell 1976; Bell 1980; Dister 1980, 1983; Gosselink et al. 1981; McKnight et al. 1981). Distributions of animals are also affected by this gradient in spite of their mobility (Wharton et al. 1981; Larson et al. 1981).

Basic changes in plant community structure occur mainly through a shift of the gradient, such as a rise of the floodplain surface due to additional inorganic or organic sediment deposition (allogenic or autogenic succession), a lowering by erosion, or a change in the hydrograph due to climatic change, tectonic movement, or human influence such as the construction of a dam or lateral dikes.

Plant communities, however, are characterized by smaller changes. There is strong pressure on communities to proceed to a later successional stage when the period of the flood pulse is reduced. The shape of the pulse often varies within large limits, thereby causing communities to respond. Annual plants react to annual differences whereas forest communities are affected by extreme annual floods, droughts, or even periods of successive years of extreme flood events that may occur every 10, 20, or 100 years. Establishment of tree seedlings in low-lying areas requires a period of exceptionally low water for several years, as Demaree (1932) found for *Taxodium distichum*. Aquatic communities tend to fill up periodically isolated water bodies with organic debris, thereby causing autogenic succession to marsh and swamp vegetation when the flood pulse fails. This process has been estimated to require about 200 years in the temperate Rhône R. (Amoros et al. 1986). Extreme floods clean these water bodies and "reset" communities to earlier successional stages. Resets can be especially severe when floods occur during the ice season in temperate rivers because trees and channels can be scoured by wind- or water-driven ice (Sigafoos 1964). Consequently, the observed community structure in floodplains is a result of short-, medium-, and/or long-term effects of the flood pulse. Shelford (1954) estimated that about 600 years were required to develop the late subclimax tulip-deer-oak communities on the lower Mississippi R. Most communities receiving the full amplitude of the flood pulse can be viewed as being in a dynamic equilibrium at an early successional level (pulse-stability, *sensu* Odum 1959; see also Margalef 1968).

Flood Pulsing and Production

Primary and secondary production in the river–floodplain system is the sum of production during terrestrial and aquatic phases. As indicated previously, the basic fertility of the floodplain depends on the nutrient status of the water and on the sediments deriving from the river. This fertility, however, may be modified by tributaries and by runoff from the local catchment area of the floodplain. Length, amplitude, frequency, timing, and predictability of the flood pulse determine occurrences, life cycles, and abundances of primary and secondary producers and decomposers, abundances which affect the level of exploitation and regeneration of the nutrient pool as well as its supply.

Gosselink and Turner (1978) proposed a classification of wetland systems according to a hydrodynamic energy gradient. They suggested that a positive relationship existed between productivity and water flow. Their theory may be valid within limits in a river–floodplain system; however, short-duration pulsing can flush out considerable organic matter and nutrients into the main channel (or into the estuary from a salt marsh as shown by Teal [1962]) and limit in situ productive processes and access by aquatic animals. In such systems, the aquatic biologist studying production is concerned with how the ATTZ benefits the river or the permanent lentic areas in the floodplain. Conversely, slow inundation of the same floodplain allows sufficient time for in situ processes along the moving littoral (Fig. 2), which traverses the ATTZ with each pulse. Aquatic and terrestrial biologists studying production in river–floodplain systems with slow pulsing should be concerned with how the river benefits the floodplain.

The flooding phase of the moving littoral (Fig. 2) finds its closest parallel to a reservoir in the process of being flooded (Wood 1951), with mineralized products from any preceding aquatic cycle and the current terrestrial one being

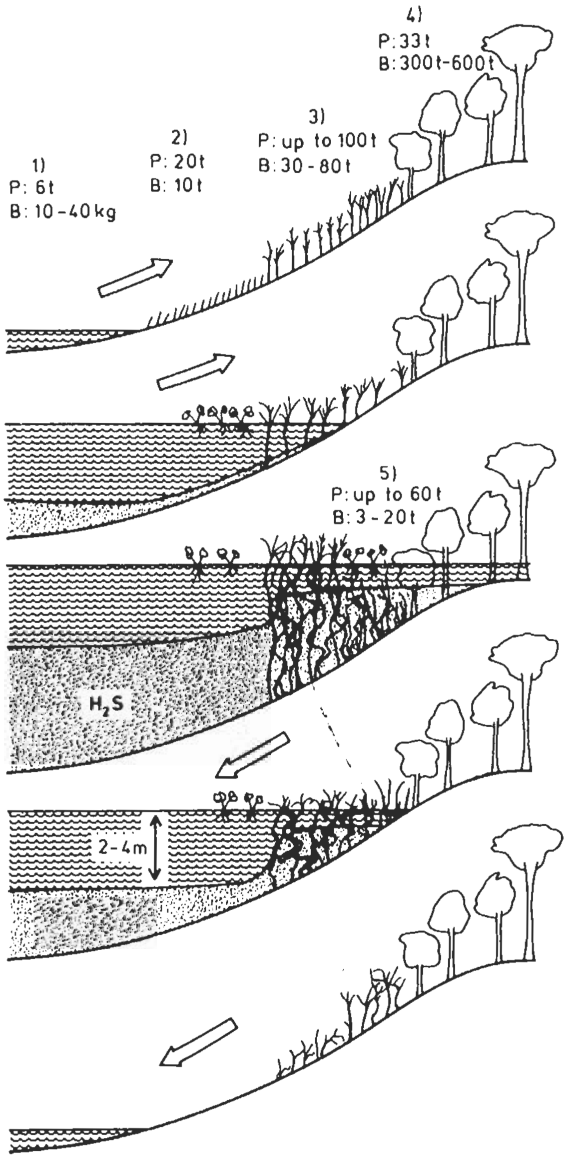


FIG. 2. The moving littoral in the transition zone (ATTZ) of a river-floodplain system in the central Amazon, with estimates of annual production (P) and biomass (B). Estimates are as dry weight per hectare. The H_2S zone has no dissolved O_2. The indicated zones are as follows: (1) Phytoplankton C14 (Schmidt 1973b), (2) annual terrestrial plants, (3) perennial grasses, (4) floodplain (várzea) forest, and (5) emergent macrophytes (from Junk 1985c and unpubl. data). Periphyton are not included, but preliminary data of periphyton on macrophytes from T. R. Fisher (pers. comm.) indicate a total productivity in the floodplain of the same order as phytoplankton (Bayley 1989).

released into the water. The various sources of primary production have high values (Fig. 2) but varying production to biomass ratios. When integrated over areas appropriate for each season in the floodplain, phytoplankton contributed less than 6 % of the total carbon production in the central Amazon várzea floodplain (Junk 1985a; Bayley 1989).

Most carbon sources, including considerable detrital biomass, are important to some animals at some time (Welcomme 1979, 1985; Junk 1984), but their quantitative importance is unknown. Organic material produced in floodplains varies considerably with respect to consistency, protein content, digestibility, and availability, that result in large differences in decomposition time and in the types of organisms involved in decomposition processes. Phytoplankton and periphyton are easily decomposed in only a few hours or days. In the Amazon, aquatic and terrestrial herbaceous plants lose about 50 % of their weight after 2-3 weeks in water (Howard-Williams and Junk 1976). Tree leaves vary widely according to species; some are as quickly decomposed as herbaceous plants whereas others remain little modified throughout months and even years. Softwood plants are destroyed in a few years, whereas hardwood plants may remain little modified for years and even decades (Junk, unpublished data).

Strong evidence suggests that the change between terrestrial and aquatic phases accelerates the decomposition of organic material, as the circumstantial evidence of Wood (1951) indicated. Terrestrial arthropods play an important role in the decomposition of leaf litter and wood as shown for cockroaches by Irmler and Furch (1979) and for termites by C. Martius (pers. comm. to WJJ). Oxygenation of sediments during dry periods promotes processing of organic material; later, when reflooding occurs, plant nutrients are recycled into the water, thereby enhancing productivity. This effect, sometimes in combination with a crop plantation or fallow period for an entire year, has been utilized for many years in European fish culture. Wood (1951) proposed the management of water levels in impoundments by changing them seasonally to increase fish production. Lambou (1959) suggested that the processes described by Wood explain the high productivity of backwater lakes due to natural water fluctuations in the Mississippi floodplain. In the Amazon floodplain during the period of rising water, mean growth increments by weight of 12 common fish species were 60 % higher than during the remainder of the year (Bayley 1988).

Food supply in fertile floodplains during the flood phase can be so abundant that factors other than food may limit individual growth and population density of fish and other aquatic animals. Limitations during the flood phase include spawning success, lack of habitats with sufficient dissolved oxygen (Junk et al. 1983), and predation (Bayley 1983). Limitations at low water include higher levels of predation, a probable reduction in food supply, or even death by drought. Bayley (1988) found that growth of juveniles of 11 abundant fish species tested did not indicate a density-dependent relationship with potentially competing species guilds during the period of rising water. Only two out of eight species indicated density-dependency at $P < .05$ during the shorter falling-water period.

The preceding ideas have very little to do with traditional concepts of productive processes in rivers. The RCC predicts that lower reaches of river systems have low ratios of production to respiration (P/R) due to processing of material from upstream and reduced in situ production. Wissmar et al. (1981) noted that Amazon floodplain lakes have high respiration rates, and Melack and Fisher (1983) noted that carbon loss due to respiration exceeds the carbon contributed by phytoplankton. However, these are limnological perspectives that describe only part of the system. The evidence offered here for the lower reaches of the river–floodplain system indicates high in situ production and low importation of organic matter from upstream. Therefore, we predict high P/R ratios for large river–floodplain systems.

Flood Pulsing and Diversity of Habitats and Species

Sediments, which are deposited in the floodplain in well-defined geomorphological units, form bars, levees, swales, oxbows, backwaters, and side channels. Flowing water grades sediments according to grain size. The floodplain soils are stratified horizontally and vertically in a small scale pattern (Irion et al. 1983; Amoros et al. 1986), but the wind-induced transport of sediment may modify the water-induced sediment pattern.

The main river and its connecting channels represent the lotic part of the river–floodplain system; oxbow lakes, abandoned channels, and backwaters represent the lentic one. Both harbour sets of organisms which colonize the much more extensive, periodically flooded ATTZ and increase species numbers occurring in the floodplain.

Differences in the duration of flooding, in soil structure, and in vegetation result in small-scale habitats in the form of narrow, roughly parallel zones. This arrangement multiplies the edge effect far beyond that represented by the main channel and its islands. In addition to these topological edges, there are many physico-chemical edges in the form of sharp vertical and horizontal boundaries in oxygen, temperature, dissolved or suspended matter; in the main channel these are encountered only at confluences with tributaries or near the substrate. In the Amazon, oxygen levels in surface water may drop from about 5 mg·L^{-1} in the main channel to 0.5 mg·L^{-1} in the floodplain 50 m away (Junk et al. 1983).

Habitats shift horizontally and vertically according to the waterlevel (Fig. 2). In addition to this instability due to the moving littoral is another instability caused by sediment deposition and erosion by the river. Depending on the position of the river channel and its dynamics, habitats may be ephemeral or rather stable over decades or centuries. This affects such stationary organisms as trees.

Nonflooded areas inside and adjacent to the floodplain perimeter, as well as emergent vegetation or the floodplain forest canopy, can be termed terrestrial habitats. All of them harbour an abundance of plants and animals that colonize the ATTZ, increasing considerably the total number of plants and animals occurring in the system.

No attempt to explain the total diversity in all habitats has been made; however, studies on specific plant and animal groups show some tendencies and some apparent inconsistencies. Species diversity would be expected to be limited in aquatic and terrestrial taxa that are sedentary and experience the full impact of the physiological stress resulting from the change between the aquatic and terrestrial phase. Worbes (1983) showed that the central Amazon floodplain forest has a much lower plant species diversity than the nonflooded forest. Salo et al. (1986), however, state that high diversity in tree species characterizing the upper Amazon lowland forests occurs in existing and relict floodplains, but they did not present species numbers or diversity indices. They describe a mosaic of small habitats created by large-scale, continuous disturbance by lateral erosion and sedimentation from the river channel, with high diversity between habitats. They reason that the high diversity in the relatively short-lived habitats of the present floodplains was due to insufficient time to allow competitive exclusion, supporting Connell's (1978) intermediate disturbance hypothesis. In the former floodplain formations that are about 5 000–10 000 years old, habitats are very stable, and the high species diversity between habitats was attributed by them to allopatric speciation.

Diversity would be expected to increase with the ability of organisms to avoid the physiological stress in the ATTZ. High diversity in floodplains occurs in mobile groups, such as fish (Lowe-McConnell 1975; Welcomme 1985) and nonaquatic birds (Remsen and Parker 1983).

The drastic change between terrestrial and aquatic phases results in high seasonal losses for most plant and animal populations, but these losses tend to be recovered by quick growth, early maturity, high reproduction rates for *r*-strategy organisms (Pianka 1970), and fast dispersal. Many of the most persistent and productive tropical aquatic weeds (e.g., *Eichhornia crassipes, Salvinia auriculata, Ceratopteris pteridoides*, and *Alternanthera philoxeroides*) are endemic to neotropical river–floodplains. In floodplains they are periodically decimated during the dry phase, allowing coexistence of many plant species with similar habitat requirements. In hydrologically stable conditions, they become dominant due to their strong competitive ability. Conversely, many persistent weeds in agricultural crops dominate in the early successional stages of floodplain vegetation at low water due to their *r*-strategy traits and recurrent disturbance of the ATTZ by the flood pulse (Seidenschwarz 1986; WJJ, unpublished data).

Many plants and animals show an impressive resilience with respect to short-term catastrophic events; an example is the rapid response of fishes following extreme drought, overfishing, or poisoning. Due to their highly effective reproduction strategies and to their mobility which allows access to dispersed low-water refuges, fish recover quickly when the flood pulse returns (Welcomme 1979). An *r*-strategy is effective only when sufficient nutrient and food resources are available to fully utilize the growth potential. Floodplains of extremely low nutrient status may therefore favor *K*-selection (Pianka 1970), such as Magalhães and Walker (1989) have indicated for Amazonian freshwater shrimps.

If we consider the total number of species in a river–floodplain system, circumstantial evidence suggests that a physical factor, the flood pulse, produces and maintains a highly diverse and dynamic habitat structure, thereby allowing a high species diversity despite stresses in the ATTZ. This is consistent with the intermediate disturbance hypothesis of Connell (1978) and parallels the observations of Statzner and Higler (1986) and Statzner (1987) who noted that physical factors (stream hydraulics) affected zonation patterns of benthic invertebrates, and that longitudinal zones of transition were associated with higher species richness.

Man-Made River-Floodplains

Dams have altered the hydrology and created artificial sedimentation basins covering thousands of square kilometres in rivers worldwide. Dam construction continues. For example, about 100 large reservoirs totalling 100 000 km^2 are projected to utilize the hydroelectric potential of Amazon R. tributaries (Junk and Melo 1987).

The hydrological changes often remove the flood pulse from floodplains downstream and sometimes permanently inundate floodplains upstream.

In the longer term, sedimentation and the modified flood pulse produce man-made river–floodplains. The 26 mainstem navigation dams on the Upper Mississippi R. downstream from Minneapolis, Minnesota, divide the river into reaches where the entire floodplain width immediately upstream of the dam is currently inundated, but where sedimentation is creating shallows that will become levées, side channels, or backwaters, and eventually floodplains (Fig. 3A to H). Of course, former floodplains now behind manmade levées will remain isolated from the river, assuming no long-term changes in flood stages or flood protection policy. The new floodplains upstream from some of these dams will experience the full amplitude of the flood cycle because the dams maintain water depths for navigation only during low flows but have little effect on flood levels. Indeed, the gates are raised completely out of the water and the relatively low earthen weirs that connect the locks and gates to the bluffs are overtopped during floods. The extent to which these developing floodplains contribute to secondary production, fish yield, and waterfowl utilization should be measurable during the next 50 years, assuming that other factors (e.g., pollution) remain constant or are taken into account. Thus the flood pulse concept can be investigated by measuring changes in one system through time since the navigation dam construction.

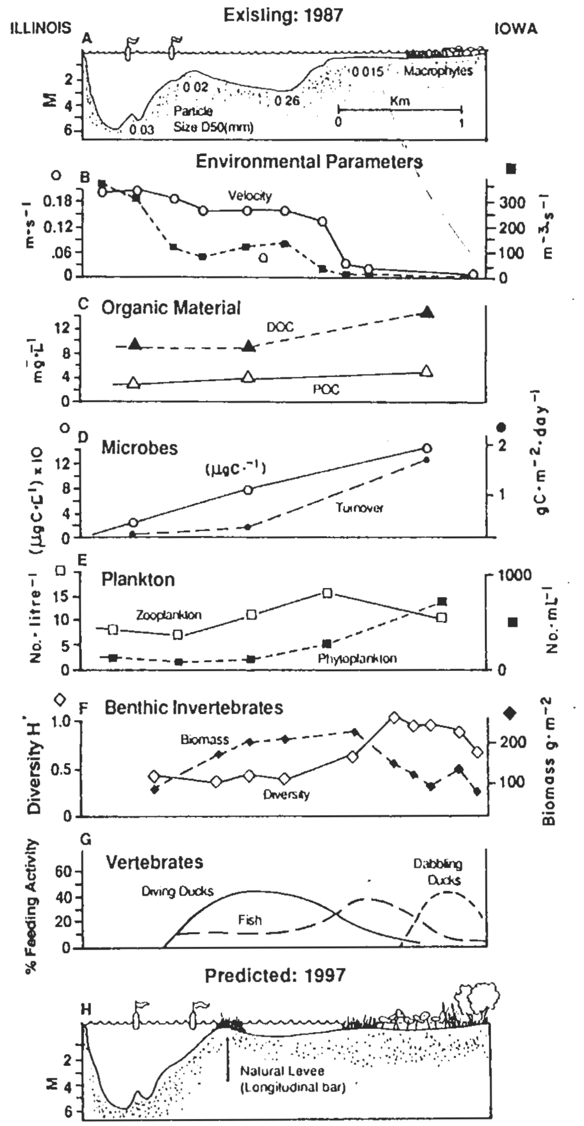


FIG. 3. A section of lower Keokuk Pool on the Upper Mississippi (A-G) with a projection of the stabilized system by the end of the century (H) (unpublished data from R. V. Anderson, R. E. Sparks, J. W. Grubaugh, K. S. Lubinski, and R. W. Gorden).

Even now, in an intermediate stage of succession in the Mississippi pools, the channel borders, not the main channel, are centers of production. Concentrations of particulate and dissolved organic carbon, plankton, and microbes are higher closer to the fringing plant beds and diminish toward the channel (Fig. 3C, E, and D). The greatest biomass of benthic macroinvertebrates are the burrowing filterers and collectors (mayflies of the genus *Hexagenia* and sphaeriid clams, *Musculium* and *Sphaerium*), which occur in beds just offshore of the macrophytes (Fig. 3F). These invertebrates apparently did not appear in high densities (up to 100 000 clams·m^{-2}) in the oldest pooled reach of the Mississippi R., the Keokuk Pool, until the 1960's (Gale 1969; Sandusky et al. 1979), when sedimentation raised the channel border bottom to the 1-m euphotic zone, thereby triggering autochthonous production by macrophytes. Diving ducks, which feed on concentrations of these invertebrates, only began using this pool in substantial numbers in the mid 1960's (Mills et al. 1966; Thompson 1973; F.C. Bellrose, pers. comm.). If phytoplankton or upstream sources had fueled the clams and mayflies, dense populations of these invertebrates should have been present in Keokuk Pool (but evidently were not) when Ellis (1931a, 1931b) made his biological surveys 18 years after the dam was closed, which was sufficient time for the accumulation of substrate suitable for burrowers. Organic matter was not being trapped behind upstream dams before it could enter the pool because these dams were not constructed until the late 1930's and early 1940's. The historical evidence from the Upper Mississippi R. thus supports the idea that a high level of secondary production requires a nearby center of primary production, rather than long-distance transport of organic matter from upstream sources via the main channel.

Conclusions

From a hydrological aspect, floodplains are part of the drainage system of rivers and are periodically affected by transport of water and dissolved and particulate material. From an ecological point of view, they represent transition zones (ATTZ) that alternate between aquatic and terrestrial states and link river channels with permanent lentic bodies and permanently dry land. Most large river systems have geomorphological settings that produce floodplains that are large relative to the lotic surface area (Welcomme 1985), and, in unmodified watersheds, produce a pulse of long duration that results in extensive but temporary lentic areas covering the ATTZ. Conversely, flood pulses of short duration, which are typical of low-order streams or of some modified systems, are associated with ATTZ's that are frequently covered by flowing water for short periods.

The flood pulse is the driving force for river–floodplain systems and maintains them in dynamic equilibrium. The system responds to the rate of rise and fall and to the amplitude, duration, frequency, and regularity of the pulses. Unpredictable pulses generally impede the adaptation of organisms and are counterproductive for many of them. Conversely, a regular pulse allows organisms to develop adaptations and strategies for efficient utilization of habitats and resources within the ATTZ, rather than depend solely on permanent water bodies or permanent terrestrial habitats. In temperate regions, the light and/or temperature regime may modify the biological effects of the pulse; timing of the pulse becomes important. In polar, sub-arctic, and taiga rivers where ice scouring occurs, the contribution to productivity from the ATTZ is not realized. In semiarid regions, local precipitation has a strong influence on the floodplain biota during the dry phase.

A variety of physical structures in combination with the flood pulse results in great habitat diversity. This diversity is coupled with the dynamic effect of the moving littoral, which extends the edge effect of the littoral over the entire ATTZ, thereby rendering channel banks bordering lotic zones insignificant by comparison. Organisms tend to invade the ATTZ from the terrestrial side also. Regular pulsing coupled with habitat diversity favors high diversity of aquatic and terrestrial plants and animals, despite considerable stress that results from the change between terrestrial and aquatic phases.

Aquatic and terrestrial productivity of river–floodplain systems depend mainly on the nutrient status of the water and sediments, on the climate, and on the flood pulse. Cycles specific to the floodplain, however, are decoupled to some extent from the nutrient status of the main channel. The moving littoral prevents permanent stagnation, thereby allowing the rapid recycling of organic matter and nutrients and resulting in a productivity that we predict to be greater than if the ATTZ were either permanently inundated or dry. Primary production associated with the ATTZ is much higher than that of permanent water bodies in unmodified systems and can often exceed that of permanent terrestrial habitats.

Transport of organic carbon from upstream catchment areas into the floodplain (spiralling) is of little importance to the productivity of the system. Conversely, primary and secondary production of the floodplains is essential to fauna in the main channels. A major component of energy transfer between floodplains and main channels is effected by animal migration, in particular of fish that also migrate upstream for considerable distances. Some bird species transfer nutrients from terrestrial areas or flooded mudflats, where they feed, to floodplain lakes, where they rest and defecate; other species do the reverse. The main function of the river channel in relation to plants and animals in the river–floodplain system is that of a migration route and dispersal system to access resources and refuges.

In conclusion, for those interested in the principal driving forces responsible for the structure, function, and evolutionary history of the biota in river–floodplain systems, we believe that the concept offered here will prove of heuristic rather than merely descriptive value. There is a fundamental dichotomy in the river–floodplain system: both continuous (e.g., the RCC) and batch processes occur. The latter, represented by the flood pulse concept, is dominant in systems with floodplains (ATTZs), in particular when the pulse is regular and of long duration. It is distinct because processes in floodplains do not depend on inefficient processing of organic matter upstream, although their inorganic nutrient pool may be replenished with periodic lateral inflows of water and sediments from the main channel. The pulse concept differs in that the position of the floodplain in the system relative to the river network is not a primary determinant of the processes that occur, although hydrological circumstances do not normally favor floodplain development in extreme upper reaches. However, examples do occur in upper reaches, such as the Pantanal of the Paraná system and the extensive Bolivian and Peruvian floodplains in the Amazon.

This concept implies an approach to studying the system different from the traditional limnological paradigms for either lotic or lentic systems. The space and time scales appropriate for understanding the mechanisms differ from those related to longitudinal processes in lotic channels. We hope that the flood pulse concept will help ecologists improve the design of studies and frame hypotheses that will lead more directly to a better understanding of river–floodplain systems. This is an urgent goal considering the modifications that continue to be proposed and that are sometimes put into practice in many tropical and temperate systems.

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