HYDROLOGICAL PROCESSES
Hydrol. Process. **14**, 2861–2883 (2000)

An extension of the flood pulse concept

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Abstract:

The flood pulse concept of Junk, Bayley and Sparks is a major contribution to our understanding of river–floodplain interactions and has become an important paradigm in lotic ecology. The concept is based mainly on large tropical lowland rivers. Floodplains may, however, develop in all geographical areas and at different locations along a river corridor. We extend this concept to temperate areas by including information derived from near-natural proglacial, headwater and lowland floodplains. Specific attention is directed to the role of temperature as a major determinant of floodplain ecology. Further attention is directed to the importance of expansion–contraction cycles occurring well below bankfull ('flow pulse' versus 'flood pulse'). Selected examples are presented that highlight the complexity of expansion–contraction events and their consequences on habitat heterogeneity and functional processes. Habitat heterogeneity is mainly a product of shifting water sources, different flow paths and the relative importance of autogenic processes. In different floodplain systems, expansion may enhance habitat heterogeneity (e.g. glacial floodplain) or create homogeneity (e.g. Danubian floodplain). Further, the ecological consequences of episodic flow and flood pulses are discussed. Finally, a landscape approach is suggested in order to document expansion and contraction processes and to elucidate how these processes influence landscape heterogeneity and biodiversity patterns. Such a landscape-based ecosystem model can be applied to rigorously assess the ecological integrity of river–floodplain systems. Copyright © 2000 John Wiley & Sons, Ltd.

KEY WORDS river; floodplain; flow pulse; temperature; ecosystem process; expansion; contraction; biodiversity; conservation; landscape

INTRODUCTION

The fundamental concepts that underpin current scientific knowledge of riverine ecosystems have been formulated over the past two decades. The river continuum concept (Vannote *et al.*, 1980), the nutrient spiralling concept (Newbold *et al.*, 1981), and the serial discontinuity concept (Ward and Stanford, 1983) all ignored floodplain dynamics in their initial formulations, although subsequent modifications rectified this to some extent (e.g. Sedell *et al.*, 1989; Ward and Stanford, 1995a; Townsend, 1996; Fisher *et al.*, 1998).

The most comprehensive approach focusing on river–floodplain dynamics is the flood pulse concept (FPC; Junk *et al.*, 1989), which promulgated the view that rivers and their fringing floodplains are integrated components of a single dynamic system, linked by strong interactions between hydrological and ecological processes. The major driving force is the pulsing of river discharge that determines the degree of connectivity and the exchange processes of matter and organisms across river–floodplain gradients. The FPC has stimulated a series of studies that examined the ecological significance of flooding across a wide range of fluvial ecosystems (Van den Brink *et al.*, 1993; Bayley, 1995; Heiler *et al.*, 1995; Prach *et al.*, 1996; Knowlton

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Received 11 July 1999
Accepted 1 October 1999

and Jones, 1997; Lorenz *et al.*, 1997; Michener and Haeuber, 1998; Spink *et al.*, 1998; Tockner *et al.*, 1999b; Ward *et al.*, 1999b,c).

The FPC is, however, derived mainly from research carried out in large tropical river–floodplain systems with a predictable flood pulse of long duration (Junk, 1997). Because nearly all rivers in Europe and North America have been 'trained' for many decades or even centuries (e.g. Amoros *et al.*, 1987; Dynesius and Nilsson, 1994), we may have a distorted view of fluvial dynamics and functional processes in temperate rivers. Are biota capable of exploiting the less predictable floods of shorter duration that typically occur in headwater floodplains or the marked expansion–contraction events that occur below bankfull ('flow pulse' versus 'flood pulse'; cf. Puckridge *et al.*, 1998)?

The primary goal of this paper is to extend the FPC to temperate running waters, to floodplains situated in upper and middle reaches, and to expansion–contraction cycles below bankfull. We present data from three semi-natural European floodplains that have been investigated extensively in recent years: (i) the Val Roseg, a glacial floodplain in Switzerland (Tockner *et al.*, 1997; Ward *et al.*, 1999b; Malard *et al.*, 1999); (ii) the Tagliamento River in north-east Italy (Figure 1), the last morphologically intact river corridor in central Europe (Ward *et al.*, 1999c; Tockner *et al.*, in press); and (iii) the Danube River in the Alluvial Zone National Park, Austria (Tockner *et al.*, 1998; Schiemer *et al.*, 1999). These three systems represent a range of formerly widespread temperate floodplain types. The importance of thermal heterogeneity is clearly illustrated and interactions between temperature and flow are documented. We concentrate on the ecological ramifications of connectivity, habitat heterogeneity, functional processes and biodiversity.

COUPLING FLOW VARIABILITY AND THERMAL HETEROGENEITY

The major physical drivers in river–floodplain systems appear to be fluvial dynamics and temperature (Ward, 1985; Poff and Ward, 1989; Petts and Amoros, 1996; Richter *et al.*, 1997; Poff *et al.*, 1997). These two parameters provide the ecological conditions necessary to assure rich biodiversity and bioproduction through processes that shape habitats and create complexity. Flow regimes show regional patterns that are determined by river size and by geographical variation in climate, geology, topography and vegetation cover. Poff and Ward (1989) and Puckridge *et al.* (1998) analysed hydrographs of a variety of different river systems, identifying distinct groups of rivers that differ in respect to the magnitude, frequency, timing and predictability of their hydrological regime. Therefore, Puckridge *et al.* (1998) suggested that the FPC could be expanded to encompass hydrological variability of large rivers from different climatic regions. The magnitude of the flow and flow (flood) variability are the most significant factors related to biological variables (cf. Clausen and Biggs, 1997); however, there is a considerable unexplained variance in the biological measurements not accounted for by the flow regime. Nutrients and, in particular, temperature resources are additional important variables explaining biological diversity.

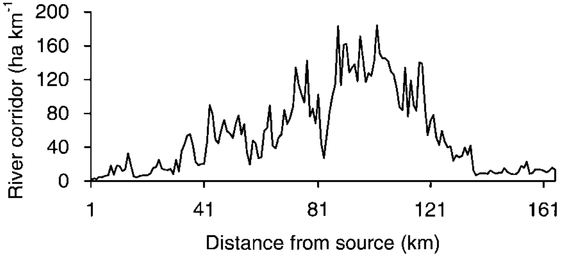

Figure 1. Dimension of the riparian corridor (active floodplain and riparian forest; ha km^{-1}) along the entire course of the Fiume Tagliamento, Italy. Note the alternation of floodplain reaches and constrained reaches along the river corridor (adapted from Ward *et al.*, 1999c)

Relatively little is known about thermal heterogeneity in alluvial floodplains (Neiff, 1996; Petts, 1996). In tropical rivers, temperature is high but remains relatively constant (Figure 2a). Therefore, the regular pulsing of the flow has been considered as the dominant factor for the development of biorhythms, as was the seasonal light–temperature regime in temperate regions. Junk *et al.* (1989) and Bayley (1991) indicated that the timing of a flood might be crucial for the recruitment of fish and for overall productivity. In temperate systems, decomposition rates of organic matter could be faster or slower depending on the timing of inundation. Cold winter floods may decrease decomposition rates, whereas summer floods may accelerate rates. Nutrient uptake also declines or even stops during winter flooding.

Seasonal patterns of flow and temperature in three selected temperate floodplains and a tropical river are compared in order to emphasize the complex interaction between these two principle driving variables (Figure 2). The River Jong is a tropical African river of medium size from which both flow and temperature data are available (Wright, 1982). There, a predictable flood pulse of long duration is associated with relatively stable temperatures (Figure 2a). The Val Roseg floodplain, a glacial system, is characterized by a predictable flow with peaks during the major period of icemelt in mid-summer (Figure 2b). Temperature, however, already levels off in spring when the thermal capacity of the river is still low and solar radiation already high. Temperature remains relatively constant throughout the whole summer till early autumn (cf. Figure 3). The River Danube and the lowland River Morava form an intersection about 50 km downstream of Vienna, Austria (Figure 2c and d). Altitudinal range of the River Morava catchment is between 130 and 1500 m compared with 130 to 4000 m for the Alpine River Danube. Therefore, snowmelt water in the Morava produces a flood during early spring with relatively cold temperatures. However, the Danube carries meltwaters from high elevation areas that generate warmer floods in early summer (Figure 3). In addition, the Danube exhibits a less predictable and a ‘flashier’ flow regime compared with the Morava. The lower section of River Morava is subjected to two floods, one by active river flooding in early spring (low temperatures) and a second one in early summer caused by ponding back (*c.* 30 km) of Danube flood waters (high temperatures). This occurrence of floods of different thermal characteristics has major ecological effects. For example, the floodplain of the lower section of the River Morava is a unique habitat colonized by both warm- and cold-water adapted species (e.g. Löffler, 1993).

In the glacial floodplain of Val Roseg, peak flow in summer is associated with low temperatures and high sediment loads that may reduce the beneficial effect of such ‘flow pulses’ (Ward, 1994; Tockner *et al.*, 1997). Uehlinger *et al.* (1998) identified two potential windows of time, one in late spring (4–6 weeks) and a second in early autumn (6–10 weeks), during which conditions (elevated water temperature but low turbidity) may favour the accrual of benthic algae and the occurrence of benthic invertebrates. Concomitantly, low water periods in spring and autumn are likely to be very sensitive to human impact (e.g. climate change). For example, in the Danube River at Linz (catchment area: 79 490 km^2), an average increase in water temperature of *c.* 0·8°C has occurred since 1901 (Webb and Nobilis, 1994). During low water periods in autumn and early winter, however, water temperature increased more than 2°C.

Traditionally, river temperature has been recorded only in the main channel (Figure 2). Including records from different floodplain water bodies demonstrates that thermal heterogeneity across a river–floodplain transect can be as high or even higher than along the entire main river course. Based on preliminary data from the Tagliamento River, dramatic increases in thermal complexity occur when moving from single-thread headwaters downstream to island braided floodplains (Figure 4). The low-order streams with single channels showed very similar seasonal and diel temperature patterns despite their location in different subcatchments and different stream orders (Figure 4a). In headwater floodplains, although groundwater–surface-water interactions create relatively low diel and seasonal variations in temperature, individual floodplain water bodies exhibit markedly different temperature regimes (Figure 4b). In lowland floodplains, differences in surface water temperature of 15°C have been measured at a given time across a river–floodplain transect (Figure 4c). In braided New Zealand rivers, Mosley (1983) observed a similar maximum temperature range between 17·2 and 35°C. In the Tagliamento River, the high thermal heterogeneity reflects the presence of a variety of floodplain water bodies and the complexity of surface and subsurface

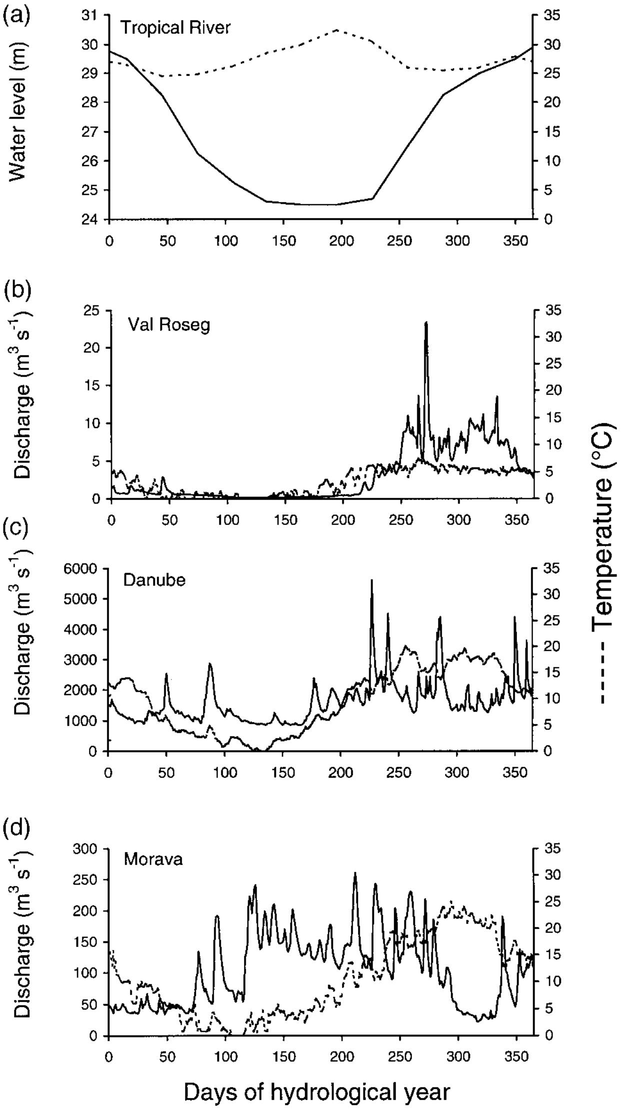

Figure 2. Temporal relationship between flow and temperature regimes in four river systems (hydrological year, 1 October to 30 September). (a) Tropical River Jong in Sierra Leone (catchment: 7500 km^2, Wright, 1982; average monthly values). (b) Glacial river Val Roseg in Switzerland (catchment: 66·5 km^2, Tockner *et al.*, 1997; U. Uehlinger, personal communication). (c) Danube River in Austria (catchment: 104 000 km^2, WSD, Vienna). River Morava in Lower Austria (catchment: 26 600 km^2, WSD, Vienna)

hydrological connectivity. In pools far from the low flow channel ('pool far', located at the outer side of the active floodplain), frequent surface connections ('flow pulses', indicated by arrows, Figure 4c) lead to sharp decreases in temperature (up to 10°C within a day). Backwaters, fed by upwelling alluvial groundwater, in contrast, exhibit low and relatively constant temperatures. In summer, these backwaters may serve as important 'cold-water refugia' for fish and aquatic insects. In these locations, water temperature may be as much as 7°C lower than in the adjacent main channel. In winter, however, the groundwater-fed channels exhibit higher temperatures than any other channel type (D. Arscott, personal communication). In this lowland river section of the Taliamento (20 m a.s.l.) cold-adapted and warm-adapted species co-occur, albeit

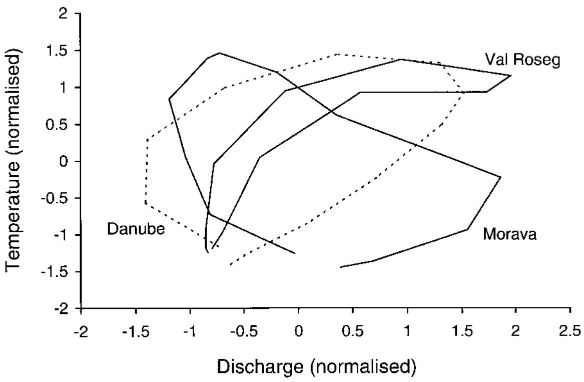

Figure 3. Temporal variations in discharge and temperature (normalized deviations from mean values based on monthly averages) in three central European floodplains (Val Roseg, Danube, Morava). Discharge data for Danube and Morava from WSD Vienna (1969–1995) and for Val Roseg from Swiss Hydrological and Geological Survey (1955–1994); temperature data from U. Uehlinger, personal communication (1997–1998)

in different floodplain water bodies. For example, cold alluvial groundwater habitats are occupied by high densities of salmonids (mainly the grayling, *Thymallus thymallus*); whereas isolated floodplain lakes provide habitats for characteristic lowland species such as *Tinca tinca* and *Esox lucius* (Tockner *et al.*, in press). The high within-reach thermal heterogeneity characterizing intact river–floodplain systems (Ward, 1985; Stanford *et al.*, 1996) was ignored in the development of classic fish zonation concepts.

In summary, temperature is a fundamental property contributing to high habitat heterogeneity. Effects of temperature and hydrological regimes on biota are likely to be critical; therefore, both temperature and flow patterns need to be considered in order to understand floodplain functioning.

FLOODPLAINS AS EXPANDING AND CONTRACTING SYSTEMS

Rapid changes in ecosystem size, although generally neglected by stream ecologists, is a fundamental property of lotic systems (de Vries, 1995; Stanley *et al.*, 1997). This is especially true for riverine floodplains that are by their nature expanding and contracting (and often fragmented) ecosystems (Ward *et al.*, 1999b; Malard *et al.*, 1999). The flood pulse concept is based upon overbank inundation as the key ecological determinant of river–floodplain system function. However, distinct expansions and contractions of river floodplains occur well below 'bankfull'. The bottom photograph in Figure 5 shows a 'flood pulse', but the upper two photographs clearly illustrate marked changes in surface waters below bankfull ('flow pulse'). Moreover, overflow of river water is not the only cause of inundation in river–floodplain systems.

Several water sources, referred to as 'local water', may contribute to the expansion of flooded surfaces: direct rainfall, tributary water, overland runoff, soil water and rising groundwater. Hughes (1980) and Lewin and Hughes (1980) summarized the hydrological processes involved in the movement of water between a river and its floodplain and also showed that these processes operated in a specific order as a flood rose (inundation sequence) and receded (recession sequence). Each flooding process is likely to have a specific effect on various ecosystem attributes. For example, flooding with hyporheic water may result in a pulse of nutrients that stimulates primary production but does not allow fish migration. Active overflow may simultaneously produce a pulse of nutrients and favour fish migration but a strong current generally depresses primary production. Finally, backwater flooding may have a positive effect on both primary production and fish migration. Thus, the flood pulse is likely to have little beneficial effect on production if active flow predominates over seepage and backwater flow. Increase in the extent of lentic waters during flooding occurs when a floodplain is traversed by a slowly moving littoral (e.g. 'creeping flow'). Although this

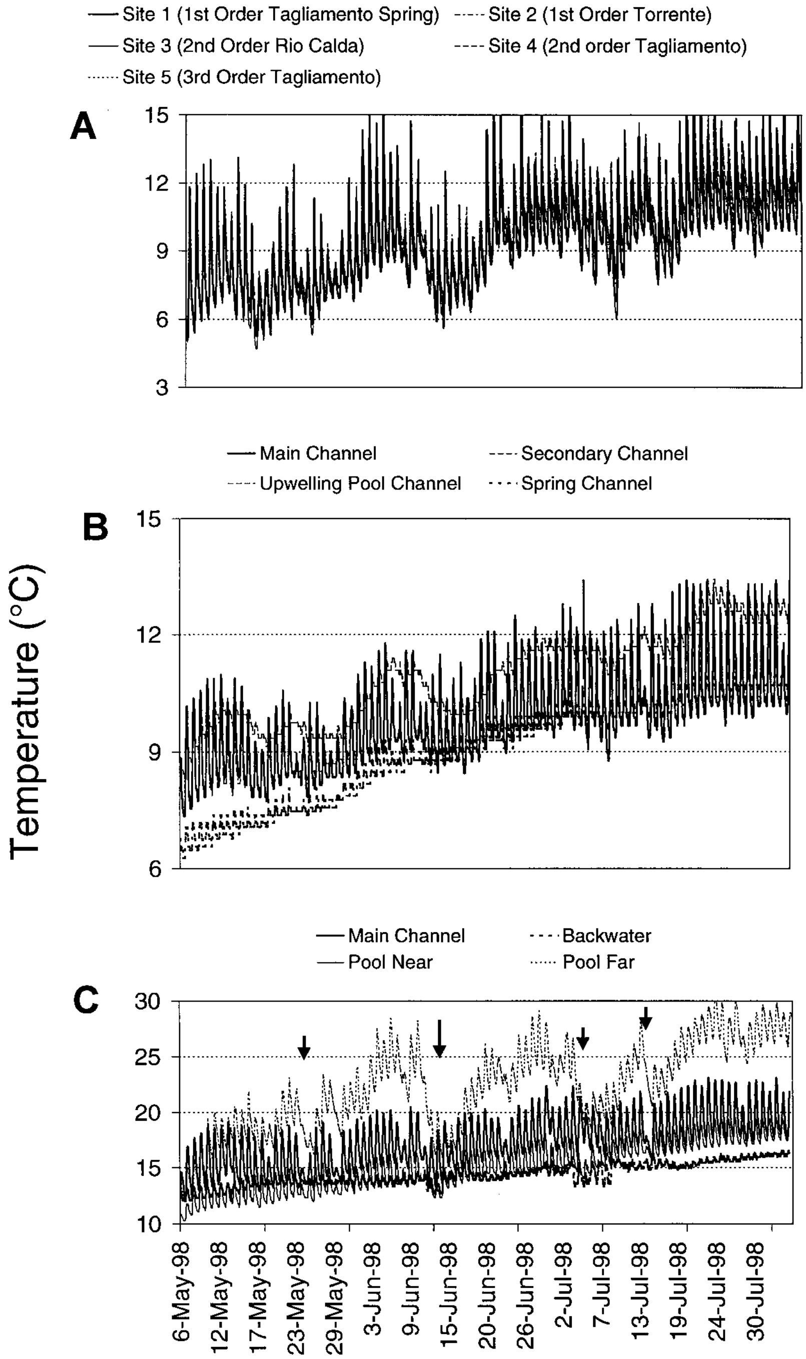

Figure 4. Temperature patterns (May to August 1998) in different aquatic habitats of three river reaches of the Tagliamento River. (a) Headwater constrained reach including three tributaries (river-km 1–5); (b) Headwater floodplain (river-km 13); (c) Island-braided lowland reach (river-km 120). (D. Arscott and K. Tockner, unpublished data). Arrows mark 'flow pulses'. Please note different scales

Figure 5. Tagliamento River downstream of Pinzano (river-km 83) at low, mean and flood water levels (Photographs: K. Tockner). At this location, active corridor width is *c.* 1·0 km

typically happens in many large lowland river systems such as parts of the Amazon (Bayley, 1995), this is far from being the case in all natural river–floodplain systems (e.g. Figure 6). Mertes (1997) examined the inundation patterns along several reaches of large rivers using remote sensing and showed that a variety of water sources led to flooded conditions prior to inundation from overflow of river water. In many cases, this early filling with relatively clear water impeded the intrusion of silty water arising from the overbank flow of the river. With analogy to the hyporheic zone, Mertes (1997) introduced the term 'perirheic zone' to denote the transition zone where river water mixes with local water.

Although changes in size are thought to exert major control on environmental conditions, as well as biodiversity patterns and ecological processes, very few studies have examined patterns and processes associated with below bankfull flooding in river–floodplain systems (Lewin and Hughes, 1980; Mertes *et al.*,

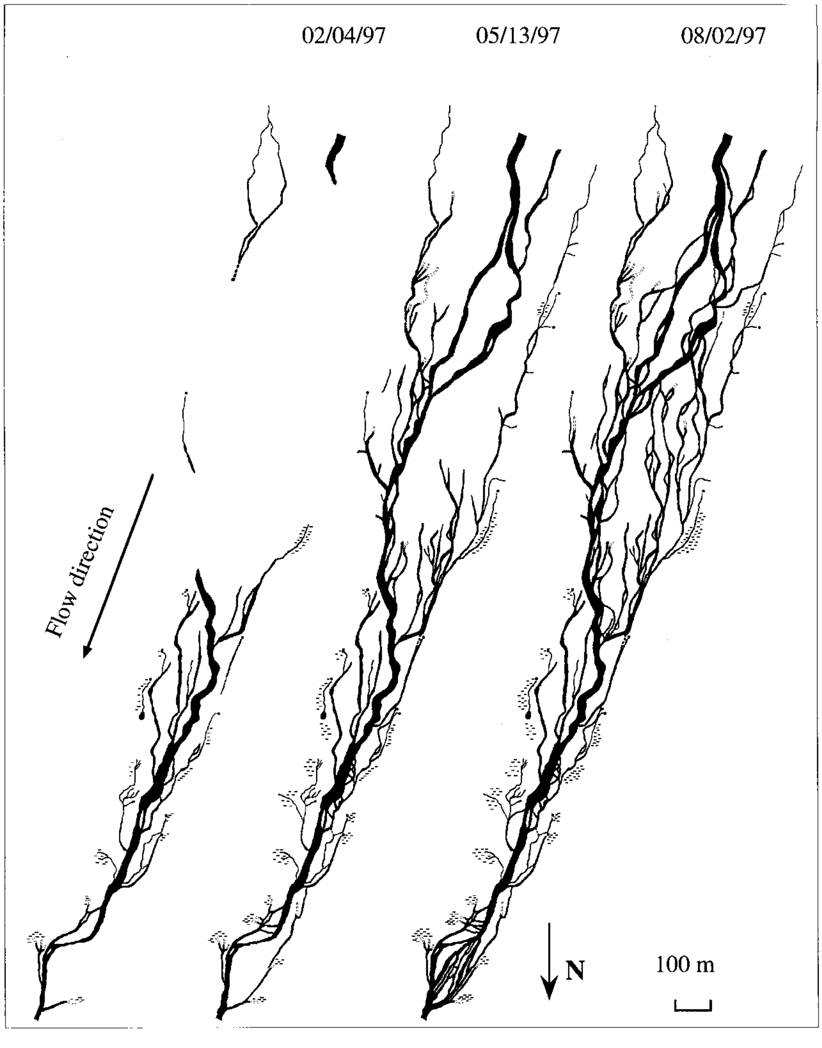

Figure 6. Expansion and contraction cycle in a glacial floodplain (Val Roseg, Switzerland; modified from Malard *et al.*, 1999)

1995; Mertes, 1997; Galat *et al.*, 1998). The following section documents patterns of expansion and contraction events in three European rivers, the Roseg River (Switzerland), the Rhône River (France) and the Danube River (Austria).

The annual cycle of expansion and contraction of the glacial floodplain of the Roseg River (Switzerland) was analysed in detail by Malard *et al.* (1999). The authors demonstrated that the seasonal changes in the extent and spatial pattern of the channel network were linked to the shifting dominance of different hydrological reservoirs and flow paths within the catchment. The expansion of the channel network comprises two distinct phases (Figure 6). During the first phase of expansion, recharge of hillslope and floodplain aquifers by snowmelt water resulted in a progressive rise of the groundwater table. As river discharge (Q) increased from 0·3 to 1·5 $m^3 s^{-1}$, total channel length increased from 6 to 15 km. However, increased surface flow was largely restricted to groundwater-fed tributaries and alluvial channels and occurred without substantial changes in upstream surface connectivity between the river and floodplain water bodies. Expansion of the channel network reflected the linkage between the floodplain and groundwater reservoirs of the catchment (Figure 7). During the second phase, increase in discharge (from 1·5 to 6 $m^3 s^{-1}$) was caused successively by the melting of the snow pack on the glacier surface and the ablation of ice. This resulted in a further expansion of the channel network from 15 to 21·4 km and a marked increase in upstream surface connectivity (Figure 7). In this glacial floodplain, water was confined to stream channels during the seasonal flow pulse. Even larger unpredictable flood events ($Q > 20\ m^3 s^{-1}$) caused by extreme rainfall did not increase the proportion of lentic habitats. With the exception of marshes on the floodplain terraces, the aquatic habitats consist only of lotic waters.

Flooding of the French Rhône exhibited a quite different pattern. The spatial pattern of inundation during a 50-year flood of the Rhône River was mapped using aerial photographs and field measurements (Figure 8; Roux, 1982). Active overflow from upstream to downstream was restricted to a relatively narrow band of circa 2 km width that comprised permanent anastomosed channels and the low elevation islands separating them. On all other surfaces, flooding was caused by a 'backwater effect'. The main-channel water back up through low elevation areas, including old meander bends, tributaries and drainage channels. This double flooding process has a differential effect on several physical and biological processes, including erosion and sediment deposition, organic matter transport and processing, and primary production (Galat *et al.*, 1998; Sparks *et al.*, 1998). For example, Irion *et al.* (1997) have shown that initial backwater flooding into a floodplain lake of the Amazon River resulted in the deposition of fine silts and clays, whereas coarse silts and fine sands were deposited during periods of upstream connection (high-water periods).

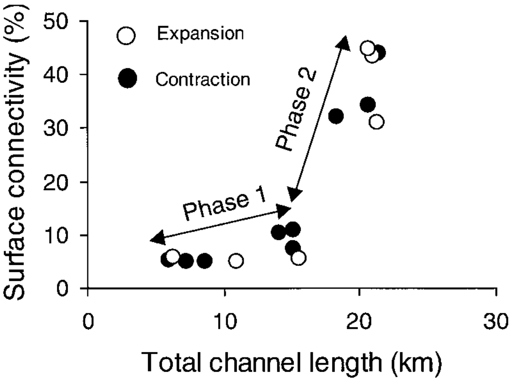

Figure 7. Relationship between surface hydrological connectivity and channel expansion over an annual cycle in the Val Roseg floodplain. Surface connectivity: relative proportion (%) of total channel length having an upstream connection with the main channel/total channel length (modified from Ward *et al.*, submitted)

Figure 8. Inundation patterns of the Rhône river–floodplain system during a 50-year flood event (8 February 1980; discharge = 1800 $m^3 s^{-1}$; IR images, 2300 m above ground level; after Roux, 1982. Reproduced by permission of CNRS Editions.)

Yet another pattern of flooding occurs in the Alluvial Zone National Park of the Austrian Danube (Figure 9; Tockner *et al.*, 1998, 1999b). Based on the relationship between the water level of the Danube and the surface water dynamics in the floodplain, three major phases of hydrological connectivity were apparent: (1) a disconnection phase, (2) a seepage connection phase and (3) an upstream surface connection phase. During the disconnection phase, floodplain water bodies covered an area of 75 ha and were dissected into different water bodies. Floodplain water level was relatively stable and about 1 m higher than that of the river. During the second phase, upstream surface connection with the river was not established but the extent of floodplain water bodies increased in response to seepage inflow through porous aquifers. Because water was retained in the floodplain channels by check-dams, there was almost no change in floodplain discharge to the main river channel. Upstream surface connection with the river (via inflow channels) resulted in a sharp increase in floodplain discharge and a further expansion of flooded areas (phase 3). As in the Roseg River floodplain, overbank flow of river water corresponded to a critical threshold during which the degree of hydrological connectivity and the relative proportion of lotic habitats suddenly increased. However, at very high water level (*c.* 147 m a.s.l.; Figure 9), the relative extent of lentic water bodies increased again drastically because large areas of the floodplain forest were inundated. Tockner *et al.* (1999b) have demonstrated that each of the three phases of river–floodplain connectivity has an ecological corollary. This is described below.

EXPANSION–CONTRACTION EVENTS AND RIVERINE LANDSCAPE HETEROGENEITY

In the following section, we used the term landscape in its simplest sense, i.e., a spatially heterogeneous area (Turner and Gardner, 1991; Wiens, 1995). The riverine landscape corresponds to the surface area composed of intersecting terrestrial and aquatic units that are directly influenced by the river (i.e., aquatic habitats, floodplain surface, and riparian zone) while the term ‘riverscape’ refers only to the aquatic components of the riverine landscape. The pulsing of the river discharge creates a shifting mosaic of aquatic and terrestrial habitats that is responsible for the high habitat heterogeneity that generally characterises riverine floodplains (Junk *et al.*, 1989; Ward and Stanford, 1995a). The manner in which a flow pulse generates spatial heterogeneity depends upon the connectivity across the riverine landscape, i.e. its capacity to facilitate exchange between resource patches (Taylor *et al.*, 1993).

Two different processes, erosive flooding and flow pulses, acting at different time-scales control connectivity in a riverine landscape. At the annual or supra-annual scale, erosive floods create and maintain habitat patches in a diversity of successional stages that determine the overall permeability and complexity of the landscape matrix (Galat *et al.*, 1997; Metzger and Décamps, 1997). Kollman *et al.* (1999), for example, investigated changes in the landscape pattern of the island-braided floodplain of the Tagliamento River based on aerial photographs taken in 1984, 1986 and 1991. Erosive floods caused dramatic changes in landscape configuration although the composition, i.e. the relative proportion of river channels, gravel bars and vegetated islands, remained very constant. Between 1984 and 1986, the turnover of landscape elements ranged from 15% for established islands to 83% for large woody debris and pioneer islands. In meandering and forested (‘low energy’) floodplains, however, channels can be relatively stable even for decades (Harper *et al.*, 1997). At shorter time-scales (days to months), and for a given riverine landscape matrix, hydrological connectivity between existing landscape elements varies in response to water level fluctuations well below bankfull (‘flow pulses’). Expansion–contraction are thus expected to result in repeated changes in landscape heterogeneity. Few data are, however, available to compare landscape heterogeneity in river–floodplain systems characterized by distinct patterns of expansion or to analyse temporal changes in spatial heterogeneity at the floodplain scale in response to fluctuating discharge. Mertes *et al.* (1995) used percentage cover and semivariance calculated from three Landsat Thematic Mapper images to examine the relationships between spatial heterogeneity of seven wetland classes and the pattern of flooding in three geomorphologically distinct reaches of the Amazon River in Brazil. The highest diversity of wetland classes, as measured

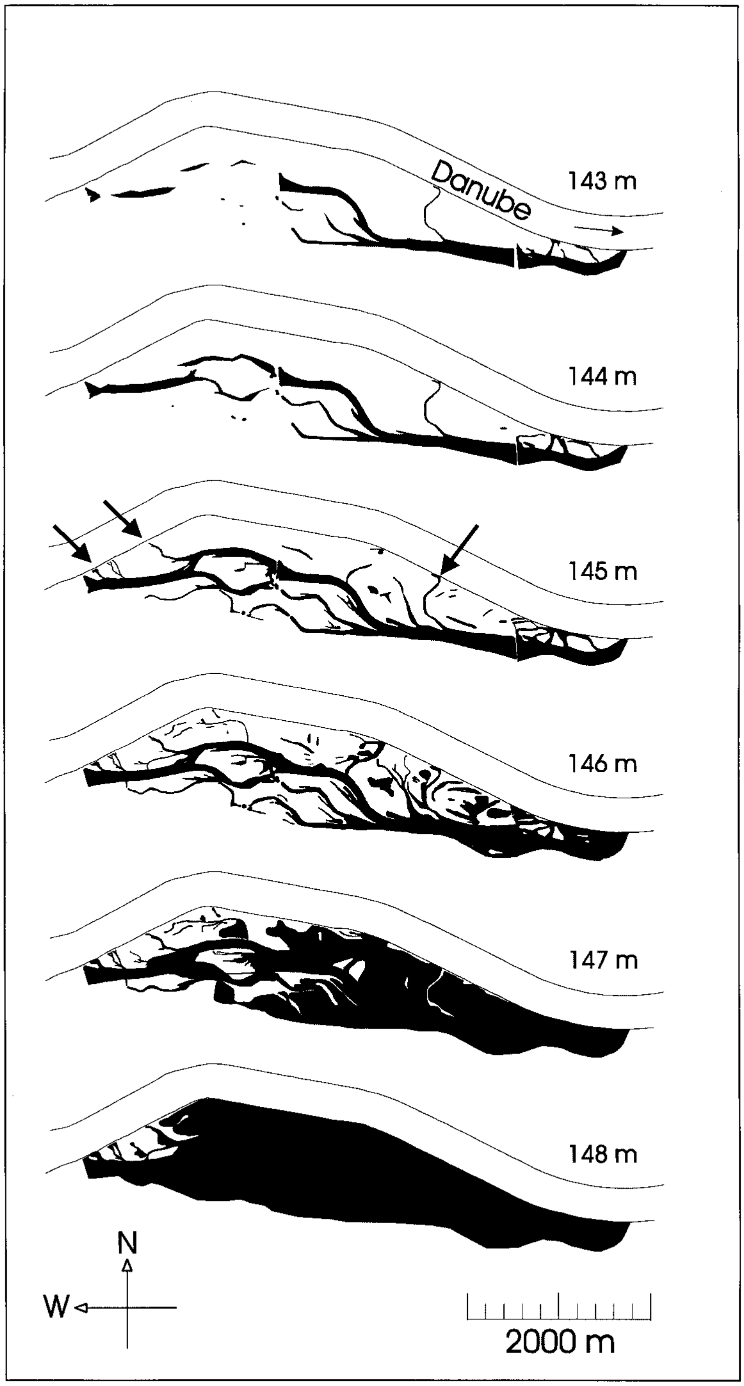

Figure 9. Inundation area (black) of the Danube floodplain (river-km 1896–1900·5) at different water levels (m a.s.l.); uncorrected for slope (slope 40 cm km^{-1}; modified after Tockner *et al.*, 2000. Reproduced by permission of Backhuys Publishers). Arrows mark major inflow channels

by semivariance, was observed in the reach where expansion occurred in response to a variety of flooding processes, including diffuse and channelled overbank flow of water.

A landscape approach, based on the dynamic spatiotemporal distribution patterns of physicochemical parameters, has been developed recently to quantify riverscape heterogeneity in the floodplains of the Danube and Roseg Rivers. The coefficient of variation (CV) was calculated as a compound index of habitat heterogeneity (Palmer *et al*., 1997). Indeed, variance rather than mean environmental values proved to be a valuable parameter for understanding how patterns and processes are linked in floodplain systems. In the following section, we demonstrate that expansion–contraction events had contrasting effects on habitat heterogeneity in a headwater floodplain (Val Roseg) compared with a large lowland river (Danube).

In the floodplain of the Roseg River, CVs of specific conductance and nitrate were positively related to discharge (Figure 10a). For a similar discharge, the CV for specific conductance was higher during the expansion phase than during the contraction phase. This observation clearly suggested that spatiotemporal heterogeneity depended more on the processes generating the expansion and contraction of the channel network than on the extent of the channel network. Malard *et al.* (in press) demonstrated that most physiochemical variables (e.g. Nitrate–N, Figure 10a) responded to the extent of expansion and contraction, as did specific conductance. Based on the correspondence between hydrological connectivity and physiochemical parameters, six major channel types were distinguished in the Val Roseg floodplain (Tockner *et al*., 1997; Ward *et al*., 1999b; Table I). In summer, each of these types contributed to the total channel network. In winter, however, tributaries, side channels and intermittently-connected channels disappeared almost completely. The remaining main-channel and mixed-channel segments were transformed into groundwater channels lacking upstream surface connectivity. Overall, the glacial floodplain shifted from a complex mosaic in summer to a simpler, more homogeneous physicochemical riverscape during winter. In this glacial floodplain, greater spatial habitat heterogeneity in summer is expected to mitigate the negative ecological effects of bed movement, shear stress, high turbidity and cold temperature caused by glacial meltwater. A 10-year erosional flood event in 1998 led to a decrease in floodplain heterogeneity by substantially increasing surface connectivity (F. Malard, unpublished data). Such resetting events are, however, of key importance for maintaining overall heterogeneity of alluvial floodplains.

In the Danube floodplain between 35 and 49 sites were sampled at different water levels and seasons. The CV for specific conductance remained constant irrespective of the water level, river water being the predominant source in most floodplain water bodies (Figure 10b). In contrast, spatial heterogeneity of nitrate decreased significantly with increasing water level. Expansion created uniformity (low CV); during contraction phases floodplain water bodies diverged and ‘individuality’ of water bodies was re-established (high CV). The CV of chlorophyll-a peaked around mean water level. At this water level, different rates of nutrient input, water resistence times and primary production led to a high spatial heterogeneity of sestonic

Table I. Val Roseg floodplain: relative proportion (%) of individual channel types during high summer and low winter flow conditions. Channel typology from Tockner *et al.* (1997)

	Relative proportion (%)	
	10 July 1997 ($7{\cdot}8$ m^3 s^{-1})	26 January 1998 ($0{\cdot}1$ m^3 s^{-1})
Main channel	16·3	27·4
Side channel	15·0	3·4
Intermittently-connected channel	14·4	0·4
Mixed channel	15·3	24·1
Groundwater channel	25·9	43·0
Tributary	13·1	1·5
Total channel length (km)	20·9	5·9

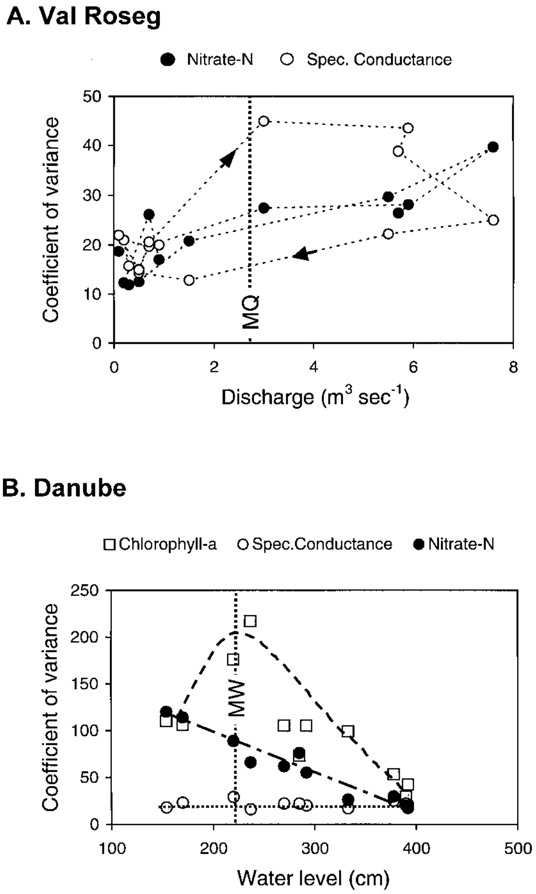

Figure 10. (a) Val Roseg: relationship between river discharge ($m^3 s^{-1}$) and habitat heterogeneity measured as the coefficient of variance (CV) of specific conductance and nitrate–N. Number of replicates per sampling date: 9–27. Arrows indicate expansion–contraction phases. MQ = mean annual discharge. Sampling period: January 1997 to February 1998. (b) Danube: relationship between water level and habitat heterogeneity measured as the coefficient of variance (CV) of specific conductance, nitrate–N and sestonic chlorophyll. Number of replicates per sampling date: 35–49. Curves are fitted by eye. Sampling period: 1 November 1998 to 4 September 1999 (data: K. Tockner and C. Baumgartner, unpublished). MW = mean water level

algal biomass (i.e. 'primary productivity phase', see Table II). Hamilton and Lewis (1990), who investigated floodplain lakes along the Orinoco River reported similar results. The lakes diverged in their physical, chemical and biological characteristics as the water receded after flooding. Overall, heterogeneity was much higher in the Danube floodplain compared with the Val Roseg glacial floodplain.

In the Danube floodplain, nitrate-N was also used as an indicator of hydrological connectivity (between the nutrient-rich main channel and individual floodplain waters). At low water conditions (LW), nitrate concentrations were uniformly low in most floodplain water bodies, except in the main river channel and in a few sites influenced by seepage inflow from the Danube (Figure 11). A concentration gradient formed as discharge approached mean water level (MW), but disappeared at high water level when nitrate concentrations were uniformly distributed across the entire floodplain. During HW, MW and LW, nitrate concentrations in 97, 41 and 18% of all sampling sites, respectively, were controlled primarily by river water input (cf. arrows in Figure 11).

The above examples showed that changes in spatial heterogeneity during expansion and contraction events were controlled by regional processes operating at the catchment scale and by local processes occurring at the

Table II. Functional processes in a Danubian floodplain (Austria) during a 15-month sampling period in 1995–96 (modified from Tockner *et al.*, 1999b)

Process/Property	Disconnected phase	Seepage phase	Connected phase
Phase duration (%)	67·5	29·3	3·2
Retention time	Very high	High	Low
Nutrient dynamics	Closed system cycling	Open system cycling	Open system spiralling
Nutrient uptake	Autogenic	Autogenic	Allogenic
Primary productivity	Medium	High	Low
P/R	±1	> 1	< 1
Sink or source	Sink (autochthonous)	Source (DOC,Chl-a)	Sink (particulates)
DOC:POC ratio	1·27	0·22	0·07
Ecological state	Biotic interactions	Primary productivity	Transport

floodplain scale. Regional processes include the shifting contribution of different hydrological reservoirs and their linkages with landscape elements of river–floodplain systems. Local processes include hydrological exchange processes across the river–floodplain and autogenic processes within individual water bodies. In the Val Roseg floodplain, increase in riverscape heterogeneity was attributed to the diversification of water sources (i.e. groundwater, snow pack, ice) and flow paths (surface, shallow and deep subsurface pathways) (Malard *et al.*, in press). Autogenic processes within the floodplain played an insignificant role. In the Danubian floodplain, however, the balance between autogenic and allogenic processes was observed to mainly control habitat heterogeneity.

The relationship between riverscape heterogeneity and discharge (or river stage) is a functional characteristic of any river–floodplain system that is likely to exert a major influence on biodiversity patterns. Using this relationship to classify river floodplains is suggested as a way in which the flood pulse concept could be expanded to encompass a wide range of river systems. Although the choice of variables and indices to calculate riverine landscape heterogeneity remains problematic, it should not be restricted in any way. Environmental variables may include surface features (e.g. gravel bars, vegetated islands, flooded areas, etc.), sediment and soil characteristics, or physicochemical parameters of floodplain waters. Ward *et al.* (1999c) used shoreline length to evaluate the strength of aquatic–terrestrial linkages in the island-braided reach of the Tagliamento River. Shoreline length was maximum (up to 22 km per river-km) around mean water level and decreased only slightly during further contraction or expansion of flooded areas. In the Danube floodplain, maximum shoreline length occurred well above mean water level, and decreased rapidly as individual floodplain water bodies merged (cf. Figure 9).

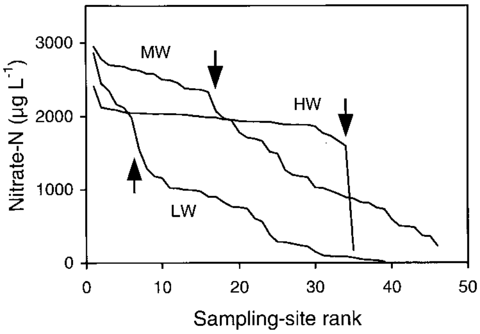

Figure 11. Danube floodplain: sampling sites are arranged from highest to lowest nitrate-N concentrations. Arrows indicate the transition from primarily hydrological to biological controlled sampling sites. LW, low water level (n = 45); MW, mean water level (n = 47); HW, high water level (n = 35)

Numerous statistical methods including indices of overall variability (Cooper *et al.*, 1997), geostatistical methods (Rossi *et al.*, 1992), and indices of landscape patterns (Gustafson, 1998) may be used to quantitatively describe the different aspects of riverine landscape heterogeneity. For example, Malard *et al.* (in press) used categorical maps of turbidity and specific conductance and calculated various indices of landscape patterns (e.g. total channel length, richness, number of patches, contrast) to evaluate the extent, composition and configuration of the physicochemical riverscape in the glacial floodplain of the Roseg River.

EXPANSION/CONTRACTION, ECOSYSTEM PROCESSES AND BIODIVERSITY

The understanding of (natural) functional processes in river–floodplain ecosystems is in a primitive state (e.g. Bayley, 1995). Anderson *et al.* (1996) stated that 'floodplain processes can be considered as a four-dimensional jigsaw (*x*–*y*–*z* through time) in which most of the pieces (data) are missing'. A possible way to investigate functional river–floodplain interactions is to measure the balance between transport and biological transformation processes (Lewis *et al.*, 1990; Walker *et al.*, 1995). For example, three phases of hydrological connectivity between the Danube channel and its floodplain (Alluvial Zone National Park, Austria) were distinguished: (1) a disconnection phase, (2) a seepage connection phase and (3) a surface connection phase (Tockner *et al.*, 1999b; Table II). These hydrological phases were tightly linked with ecological processes. Generally, the floodplain shifted from a mainly biologically controlled system during phase 1 ('biological interaction phase') to an increasingly open and more hydrologically controlled system during phases 2 and 3 (see also Figure 11). Corresponding oscillations between heterotrophy (phase 3) and autotrophy (phase 2, less during phase 1) were regarded as a general phenomenon of many large rivers (cf. Admiraal and Zanten, 1988). Highest algal biomass and primary production were observed during phase 2. During this phase large amounts of nutrient-rich groundwater entered the floodplain, yet water residence times were high. Phase 2 was classified as the 'primary production phase'. Additionally, there is some evidence that frequent shifts between individual phases fostered primary production (Tockner *et al.*, 1999b; Hein *et al.*, 1999a,b). Thus, water-level fluctuations well below 'bankfull' may considerably enhance floodplain productivity. Finally, transport of matter was restricted mainly to the short periods with an upstream surface connection ('transport phase'). Mass balance calculations revealed that the floodplain was alternately a 'sink' and a 'source' of material (Table II; Tockner *et al.*, 2000). Knowlton and Jones (1997) also found that some intermediate level of connectivity between the Missouri River and floodplain lakes was optimal for autochthonous primary production. In contrast to many lowland rivers, the Val Roseg floodplain was not a major source for material. The floodplain served primarily as a transit area, transporting matter from different reservoirs downstream (Malard *et al.*, 1999). Transport patterns of a range of given materials were associated with expansion–contraction phases (Tockner *et al.*, 1997; Malard *et al.*, 1999; Figure 12). Transport of snowmelt water via subsurface pathways produced a pulse of nitrate in all floodplain water bodies, although different peaks in individual floodplain channels reflected the spatial heterogeneity of snow melt within the catchment. Runoff of glacial water resulted in a peak of suspended solids only in channels having an upstream connection with the river (M15, X2; Figure 12). Dissolved organic carbon (DOC) was spatially more homogeneous and unrelated to discharge despite highest concentrations in winter.

In river–floodplain ecosystems, the relative importance of allochthonous and autochthonous organic matter has to be re-examined. In both large temperate (Thorp *et al.*, 1998) and tropical rivers (Lewis *et al.*, 1990), it was shown that autochthonous primary production was the predominant energy basis rather than terrestrial organic matter as suggested by the FPC (Junk *et al.*, 1989). Thorp and Delong (1994) hypothesized that riparian and instream shoreline habitats are of crucial importance for ecosystem processes in large rivers ('riverine productivity model', RPM). Thorp *et al.* (1998) showed that the RPM rather than the FPC more adequately addressed food-web structure in constrained and floodplain sections of the regulated Ohio River (USA). In forested mid-order floodplains, however, inputs of allochthonous organic matter from the

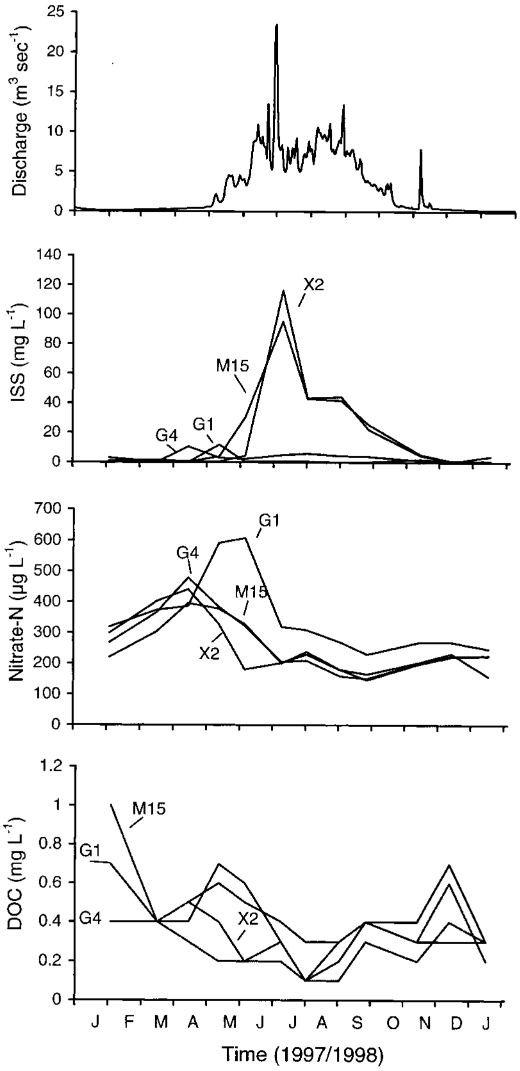

Figure 12. Val Roseg: seasonal patterns of discharge, and concentrations of nitrate–N, inorganic suspended solids (ISS) and dissolved organic carbon (DOC) in different floodplain channels (Tockner and Malard, unpublished data): G1, hillslope groundwater channel; G4, alluvial groundwater channel; X2, mixed-channel type; M15, main channel at the downstream end of the floodplain (channel typology and location of sampling sites from Tockner *et al.*, 1997)

floodplains were the primary source of carbon (e.g. Cuffney, 1988). In glacial floodplains, terrestrial plants contributed virtually nothing to the food web; therefore, the food base presumably was limited to benthic algal production. The availability of the algae food base, however, was restricted mainly to low water periods in spring and autumn (Uehlinger *et al.*, 1998). During high flow in summer, turbidity and bedload transport hindered algal development, except in groundwater-fed channels. In bar-braided floodplains (cf. Figure 1) devoid of perennial vegetation, instream primary production in pools, backwaters and secondary channels is expected to drive metabolic processes, in particular during low water and expansion periods. Vegetated islands (cf. Figure 5), however, may substantially contribute to instream riparian ecotone development in island-braided rivers, thereby enhancing the input of terrestrial organic matter. In the island-braided section of the Tagliamento River, riparian ecotone length is up to 20 km per river-km (Ward *et al.*, in press).

Generally, we expect spatial and temporal shifts in the relative importance of autochthonous/allochthonous matter corresponding to the location of the floodplain in the drainage system and the degree of expansion and contraction. Similarly, the spatial position of source, retention, transformation and sink areas for organic matter and nutrients is also expected to shift with variations in discharge. For example, the main channel of the Danube River is a major source for nutrients, which are either deposited together with fine sediments on the floodplain (during high water), transformed into algae biomass in floodplain waters (during mean water level), or released again (after extended low water conditions) into the main channel.

Recent investigations of biodiversity in floodplains emphasize the importance of different degrees of connectivity and habitat heterogeneity for a high biodiversity (Van den Brink *et al.*, 1996; Naiman and Décamps, 1997; Bornette *et al.*, 1998; Ward *et al.*, 1999a). In a Danubian floodplain, for example, species diversity of individual groups (molluscs, fish, amphibians, macrophytes and benthic invertebrates), reached their maxima at different points along the river–floodplain connectivity gradient (Figure 13). Total species diversity of all faunal and floral groups peaked in floodplain water bodies with an intermediate degree of connectivity (Tockner *et al.*, 1999a). Similar results were found in other types of expanding–contracting ecosystems. For example, Desender and Maelfait (1999) sampled terrestrial arthropods in a large number of tidal marshes (Belgium) and found no relationship between diversity and marsh area. However, diversity peaked in habitats with an intermediate degree of connectivity between marine and fresh waters. In a glacial floodplain, however, habitats with the highest 'environmental stability' (spring brooks, alluvial groundwater-channels) contained the highest species diversity. Diversity decreased with increasing surface connectivity to the main channel (Klein and Tockner, in press; P. Burgherr, personal communication). Glacial floodplains are defined as harsh ecosystems with low biodiversity. Forested floodplains, however, with relatively stable channels are also characterized by a lower biodiversity. Island-braided floodplains, however, are somewhere between these two extremes and, based on the intermediate disturbance hypothesis (cf. Connell, 1978), may contain a higher diversity. Habitats associated with islands such as backwaters or ephemeral and permanent pools lead to a non-linear increase in the length of water–floodplain ecotones. Within its geographical location, however, each individual floodplain is regarded as a 'hot spot' of biodiversity, significantly contributing to overall regional biodiversity (e.g. Stanford *et al.*, 1996). Unfortunately no data are yet available to directly compare biodiversity patterns in different floodplain systems.

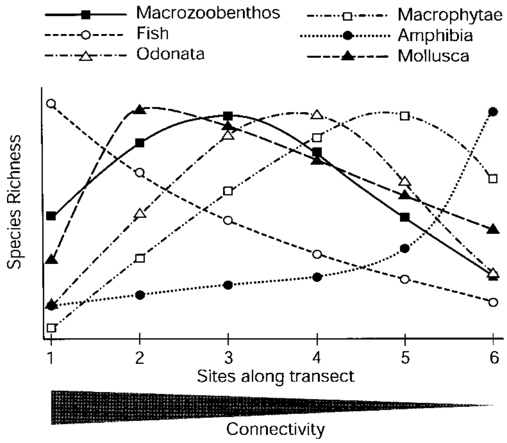

Figure 13. Danube river–floodplain system: idealized species diversity patterns of different biota across a river–floodplain transect (modified after Tockner *et al.*, 1998. Reproduced by permission of John Wiley & Sons, Ltd.)

According to the FPC, expansion–contraction events of short duration and low predictability correspond more to catastrophic events for the biota. More recent investigations clearly demonstrated that 'stochastic events' are fundamental phenomena responsible for maintaining biodiversity in temperate floodplains (e.g. Plachter and Reich, 1998). Species traits of organisms in temperate rivers with short and unpredictable floods differ to some extent from those in large tropical rivers with predictable flood pulses. In the tropics, the formation of large numbers of flood and drought resistant seeds and resting eggs is one of the most common adaptations to flow variation (Junk, 1997). In addition, life cycles of many species are synchronized with the flood pulse. Predictable flood pulses with long terrestrial and aquatic phases allow a greater exploitation of available resources. In both temperate and tropical floodplains, mobility is a strategy for coping with fluctuating water levels (reviewed in Ward, 1992). In temperate floodplains, flexible life cycles (e.g. the amphibian *Bufo bufo*; Kuhn, 1993), retreat to floodplain refugia, or the formation of metapopulations (e.g. the endangered grasshopper *Bryodema tuberculata*; Stelter *et al.*, 1997) are common strategies to survive in highly fluctuating systems. Relatively little is known, however, about the ecological consequences of rapid expansion–contraction events. Mosley (1982), for example, has shown that with increasing discharge some channels in a braided river became larger and deeper, and frequently merged, while other channels were created with similar characteristics as the former channels at low discharge. One ecological consequence was that total area available for spawning salmon remained constant despite great changes in inundated area. Holcik and Bastl (1976) documented that a seasonal increase in river discharge favoured productivity and diversity of fish in floodplain waters along the Danube. Vanhara (1994) reported that a unique fauna colonizes areas subjected to frequent inundation in floodplain forests along the River Morava. At a smaller spatial scale, species diversity of benthic invertebrates within the main channel of the Danube River peaked in bank areas that exhibited an intermediate level of flooding and drying (Reckendorfer *et al.*, 1996).

General predictions on the ecological 'benefit' of episodic expansion–contraction events are not yet possible. In both tropical and temperate floodplains, however, many species depend on expansion–contraction events or erosional floods that create open space and new habitats. We may expect that aquatic and terrestrial communities react differently on short-termed expansion–contraction events yet data are not available at present. Simultaneous investigations of aquatic and terrestrial communities are required in order to understand diversity patterns in alluvial floodplains and how they are linked to each other (Tockner and Ward, 1999).

CONCLUSION

The flood pulse concept (Junk *et al.*, 1989) has greatly contributed to our understanding of riverine floodplain interactions and has become an important paradigm in lotic ecology. In the present paper we expand the FPC to more fully integrate temperate river–floodplain systems. There, the interaction between temperature and flow plays a major role in structuring habitat conditions and biotic communities. In addition, we stress the ecological significance of expansion–contraction events below bankfull flooding, thereby adding 'flow pulses' to the 'flood pulse' concept. Furthermore, headwater floodplains differ substantially from lowland floodplains in their functioning, with different processes controlling environmental heterogeneity and biodiversity patterns. There are urgent needs for more empirical data that address the dynamic nature of different riverine floodplains. River–floodplain restoration projects, for example, can be used as large-scale manipulation experiments to better understand river–floodplain interactions. Most current restoration schemes of river corridors are based on a re-establishment of the flood pulse (Molles *et al.*, 1998; Tockner *et al.*, 1998; Toth *et al.*, 1998). Their success will depend not only on their capacity to reproduce the flow variability (e.g. magnitude, frequency, duration, timing and predictability of floods) but also on their ability to recreate the diversity of flooding processes. A landscape approach is required in order:

(1) to document spatial patterns and processes of flooding (patterns of expansion and contraction and the processes generating them);
(2) to quantify the relationship between fluvial dynamics and landscape heterogeneity;
(3) to identify the numerous flow characteristics that are important for the maintenance of habitat diversity and biological diversity.

Such a landscape approach also can be applied to evaluate the effectiveness of river–floodplain restoration schemes.

ACKNOWLEDGEMENTS

Research on the Val Roseg floodplain was supported by the Swiss National Science Foundation (SNF grant 21-49243·96); work on the Tagliamento was supported by a grant from the ETH-Forschungskommission (Project: 0-20572-98); research on the Danube was funded in part by the Austrian Federal Waterway Agency (WSD Wien). Thoughtful suggestions by Urs Uehlinger, Mark Gessner and two anonymous reviewers improved the manuscript. We are especially grateful to Dave Arscott, Christian Baumgartner and Urs Uehlinger who kindly provided unpublished data.

REFERENCES

Admiraal W, von Zanten B. 1988. Impact of biological activity on detritus transport in the lower river Rhine: an exercise in ecosystem analysis. *Freshwater Biology* **20**: 215–225.

Amoros C, Rostan J-C, Pautou G, Bravard J-P. 1987. The reversible process concept applied to the environmental management of large river systems. *Environment Management* **11**: 607–617.

Anderson MG, Bates PD, Walling DE. 1996. The general context of floodplain process research. In *Floodplain Processes*, Anderson MG, Bates PD, Walling DE (eds). Wiley: Chichester; 1–13.

Bayley PB. 1991. The flood pulse advantage and the restoration of river–floodplain systems. *Regulated Rivers* **6**: 75–86.

Bayley PB. 1995. Understanding large river–floodplain ecosystems. *BioScience* **45**: 153–158.

Bornette G, Amoros C, Lamouroux N. 1998. Aquatic plant diversity in riverine wetlands: the role of connectivity. *Freshwater Biology* **39**: 267–283.

Clausen B, Biggs BJF. 1997. Relationship between benthic biota and hydrological indices in New Zealand streams. *Freshwater Biology* **38**: 327–342.

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

Cooper SD, Barmuta L, Sarnelle O, Kratz K, Diel S. 1997. Quantifying spatial heterogeneity in streams. *J. N. Am. Benthol. Soc*. **16**: 174–188.

Cuffney TF. 1988. Input, movement and exchange of organic matter within a subtropical coastal blackwater river–floodplain system. *Freshwater Biology* **19**: 305–320.

De Vries JJ. 1995. Seasonal expansion and contraction of stream networks in shallow groundwater systems. *Journal of Hydrology* **170**: 15–26.

Desender K, Maelfait J-P. 1999. Diversity and conservation of terrestrial arthropods in tidal marshes along the River Schelde: a gradient analysis. *Biological Conservation* **87**: 221–229.

Dynesius M, Nilsson C. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science* **266**: 753–762.

Fisher SG, Grimm NB, Martí E, Holmes RM, Jones JB. 1998. Material spiraling in stream corridors: a telescoping ecosystem model. *Ecosystems* **1**: 19–34.

Galat DL, Kubisiak JK, Hooker JB, Sowa LM. 1997. Geomorphology, distribution and connectivity of lower Missouri River floodplain waterbodies scoured by the flood 1993. *Verh. Internat. Verein. Limnol*. **26**: 869–878.

Galat DL, Fredrikson LH, Humburg DD, Bataille KJ, Bodie JR, Dohrenwend J, Gelwicks GT, Havel JE, Helmers DL, Hooker JB, Jones JR, Knowlton MF, Kubisiak J, Mazourek J, McCoplin AC, Renken RB, Semlitsch RD. 1998. Flooding to restore connectivity of regulated, large-river wetlands. *BioScience* **48**: 721–733.

Gustafson EJ. 1998. Quantifying landscape spatial pattern: what is the state of art? *Ecosystems* **1**: 143–156.

Hamilton SK, Lewis WM Jr. 1990. Basin morphology in relation to chemical and ecological characteristics of lakes on the Orinoco River floodplain, Venezuela. *Archiv fuer Hydrobiologie* **119**: 393–425.

Harper D, Mekotova J, Hulme S, White J, Hall J. 1997. Habitat heterogeneity and aquatic invertebrate diversity in floodplain forests. *Glob. Ecol. Biog. Lett*. **6**: 275–285.

Heiler H, Hein T, Schiemer F, Bornette G. 1995. Hydrological connectivity and flood pulses as the central aspects for the integrity of a river–floodplain system. *Regulated Rivers* **11**: 351–361.

Hein T, Heiler G, Riedler P, Schaggerl M, Schiemer F, Pennetzdorfer D. 1999a. The Danube restoration project: functional aspects and planktonic productivity in the floodplain system. *Regulated Rivers* **15**: 259–270.

Hein T, Baranyi C, Heiler G, Holarek C, Riedler P, Schiemer F. 1999b. Hydrology as a major factor determining plankton development in two floodplain segments and the Danube River, Austria. *Archiv fuer Hydrobiologie Supplementband* **115**: 439–452.

Holcik J, Bastl I. 1976. Ecological effects of water level fluctuations upon fish populations in the Danube river floodplain in Czechoslovakia. *Acta Sc. Nat. Brno*. **10**: 1–46.

Hughes DA. 1980. Floodplain inundation: processes and relationships with channel discharges. *Earth Surface Processes* **5**: 297–304.

Irion G, Junk WJ, de Mello JASN. 1997. The large central Amazonian river floodplains near Manaus: geological, climatological, hydrological and geomorphological aspects. In *The Central Amazon Floodplain*, Junk WJ (eds). Springer-Verlag: New York; 23–46.

Junk WJ (eds). 1997. *The Central Amazon Floodplain*. Springer-Verlag: New York.

Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river–floodplain systems. *Can. Spec. Publ. Fish. Aquat. Sci.* **106**: 110–127.

Klein B, Tockner K. In press. Biodiversity in springbrooks of a glacial flood plain (Val Roseg, Switzerland). *Verh. Internat. Verein. Limnol.* **27**.

Knowlton MF, Jones JR. 1997. Trophic status of Missouri River floodplain lakes in relation to basin type and connectivity. *Wetlands* **17**: 468–475.

Kollmann J, Vieli M, Edwards PJ, Tockner K, Ward JV. 1999. Interactions between vegetation development and island formation in the Alpine river Tagliamento. *Appl. Veg. Sci.* **2**: 25–36.

Kuhn J. 1993. Fordpflanzungsbiologie der Erkdröte *Bufo bufo* (L.) in einer Wildflussaue. *Z. Ökol. u. Natursch.* **2**: 1–10.

Lewin J, Hughes DA. 1980. Welsh floodplain studies, II. Application of a qualitative inundation model. *Journal of Hydrology* **46**: 35–49.

Lewis WM, Weibezahn FH, Saunders III JF, Hamilton SK. 1990. The Orinoco river as an ecological system. *Interciencia* **15**: 346–357.

Löffler H. 1993. Anostraca, Notostraca, Laevicaudata and Spinicaudata of the Pannonian region and in its Austrian area. *Hydrobiology* **264**: 169–174.

Lorenz CM, Van Dijk GM, Van Hattum AGM, Cofino WP. 1997. Concepts in river ecology: implications for indicator development. *Regulated Rivers* **13**: 501–516.

Malard F, Tockner K, Ward JV. 1999. Shifting dominance of subcatchment water sources and flow paths in a glacial floodplain, Val Roseg, Switzerland. *Arctic, Antarctic and Alpine Research* **31**: 114–129.

Malard F, Tockner K, Ward JV. In press. A landscape-level analysis of physico-chemical heterogeneity in a glacial flood plain. *Landscape Ecology*.

Mertes LAK. 1997. Documentation and significance of the perirheic zone on inundated floodplains. *Water Resources Research* **33**: 1749–1762.

Mertes LAK, Daniel DL, Melack JM, Nelson B, Martinelli LA, Forsberg BR. 1995. Spatial patterns of hydrology, geomorphology, and vegetation on the floodplain of the Amazon River in Brazil from a remote sensing perspective. *Geomorphology* **13**: 215–232.

Metzger J-P, Décamps H. 1997. The structural connectivity threshold: an hypothesis in conservation biology at the landscape scale. *Acta Oec.* **18**: 1–12.

Michener WK, Haeuber RA. 1998. Flooding: natural and managed disturbances. *BioScience* **48**: 677–680.

Molles MC, Crawford CS, Ellis LM, Valett HM, Dahm CN. 1998. Managed flooding for riparian ecosystem restoration. *BioScience* **48**: 749–756.

Mosley MP. 1982. Analysis of the effect of changing discharge on channel morphology and instream uses in braided river, Ohau River, New Zealand. *Water Resources Research* **18**: 800–812.

Mosley MP. 1983. Variability of water temperature in the braided Ashley and Rakaia rivers. *New Zealand Journal of Marine and Freshwater Research* **17**: 331–342.

Naiman RJ, Décamps H. 1997. The ecology of interfaces: riparian zones. *Annu. Rev. Ecol. Syst.* **28**: 621–658.

Neiff JJ. 1996. Large rivers in South America: toward the new approach. *Verh. Internat. Verein. Limnol.* **26**: 167–180.

Newbold JD, Elwood JW, O'Neill RV, Van Winkle W. 1981. Measuring nutrient spiralling in streams. *Can. J. Fish. Aquat. Sci.* **38**: 860–863.

Palmer MA, Hakenkamp CC, Nelson-Baker K. 1997. Ecological heterogeneity in streams: why variance matters. *J. N. Am. Benthol. Soc.* **16**: 189–202.

Prach K, Jenik J, Large ARG (eds). 1996. *Floodplain Ecology and Management, the Luznice River in the Trebon Biosphere Reserve, Central Europe*. SPB Academic Publishing: Amsterdam.

Petts GE. 1996. Sustaining the ecological integrity of large floodplain rivers. In *Floodplain Processes*, Anderson MG, Bates PD, Walling DE (eds). Wiley: Chichester; 535–551.

Petts GE, Amoros C (eds). 1996. *Fluvial Hydrosystems*. Chapman & Hall: London.

Plachter H, Reich M. 1999. The significance of disturbance for populations and ecosystems in natural floodplains. In *Proceeding of the International Symposium on River Restoration*, Tokyo; 29–38.

Poff NL, Ward JV. 1989. Implications of streamflow variability and predictability for lotic community structure: an analysis of streamflow patterns. *Can. J. Fish. Aquat. Sci.* **46**: 1805–1818.

Poff NL, Allan JD, Main MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC. 1997. The natural flow regime. *BioScience* **47**: 769–784.

Puckridge JT, Sheldon F, Walker KF, Boulton AJ. 1988. Flow variability and the ecology of large rivers. *Marine and Freshwater Research* **49**: 55–72.

Reckendorfer W, Keckeis H, Winkler G, Schiemer F. 1996. Water level fluctuations as a major determinant of chironomid community structure in the inshore zone of a large temperate river. *Archiv fuer Hydrobiologie Supplementband* **115**: 3–9.

Richter BD, Baumgartner JV, Wigington R, Braun DP. 1997. How much water does a river need? *Freshwater Biology* **37**: 231–249.

Rossi RE, Mulla DJ, Journel AG, Franz EH. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecological Monographs* **62**: 277–314.

Roux AL (eds). 1982. *Cartographie polythématique appliquée à la gestion écologique des eaux. Etude d'un hydrosystème fluvial: le Haut-Rhône français*. Centre National de la Recherche Scientifique: Paris.

Schiemer F, Baumgartner C, Tockner K. 1999. Restoration of floodplain rivers: the 'Danube restoration project'. *Regulated Rivers* **15**: 231–244.

Sedell JR, Richey JE, Swanson FJ. 1989. The river continuum concept: a basis for the expected ecosystem behavior of very large rivers?. *Can. Spec. Publ. Fish. Aquat. Sci.* **106**: 49–55.

Sparks RE, Nelson JC, Yin Y. 1998. Naturalization of the flood regime in regulated rivers. *BioScience* **48**: 706–720.

Spink A, Sparks RE, van Oorschot M, Verhoeven JTA. 1998. Nutrient dynamics of large river floodplains. *Regulated Rivers* **14**: 203–216.

Stanford JA, Ward JV, Liss WJ, Frissell CA, Williams RN, Lichatowich JA, Coutant CC. 1996. A general protocol for restoration of regulated rivers. *Regulated Rivers* **12**: 391–413.

Stanley EH, Fisher SG, Grimm NB. 1997. Ecosystem expansion and contraction in streams. *BioScience* **47**: 427–435.

Stelter C, Reich M, Grimm V, Wissel C. 1997. Modelling persistence in dynamic landscapes: lessons from a metapopulation of the grasshopper *Bryoderma tuberculata*. *Journal of Animal Ecology* **66**: 508–518.

Taylor PD, Hafrig L, Henein K, Merriam G. 1993. Connectivity as a vital element of landscape structure. *Oikos* **68**: 571–573.

Thorp JH, Delong MD. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos* **70**: 305–308.

Thorp JH, Delong MD, Greenwood KS, Casper AF. 1998. Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. *Oecologia* **117**: 551–563.

Tockner K, Ward JV. 1999. Biodiversity along riparian corridors. *Archiv fuer Hydrobiologie Supplementband* **115**: 293–310.

Tockner K, Malard F, Burgherr P, Robinson CT, Uehlinger U, Zah R, Ward JV. 1997. Physico-chemical characterization of channel types in a glacial floodplain ecosystem (Val Roseg, Switzerland). *Archiv fuer Hydrobiologie* **140**: 433–463.

Tockner K, Schiemer F, Ward JV. 1998. Conservation by restoration: the management concept for a river–floodplain system on the Danube River in Austria. *Aquatic Conservation* **8**: 71–86.

Tockner K, Schiemer F, Baumgartner C, Kum G, Weigand E, Zweimüller I, Ward JV. 1999a. The Danube Restoration Project: species diversity patterns across habitat gradients in the floodplain system. *Regulated Rivers* **15**: 245–258.

Tockner K, Pennetzdorfer D, Reiner N, Schiemer F, Ward JV. 1999b. Hydrological connectivity and the exchange of organic matter and nutrients in a dynamic river–floodplain system (Danube, Austria). *Freshwater Biology* **41**: 521–535.

Tockner K, Ward JV, Arscott DB, Edwards PJ, Kollmann J, Gurnell AM, Petts GE, Maiolini B. In press. The Tagliamento River: a model ecosystem for Alpine gravel-bed rivers. In *Ecology and Conservation of Gravel Bed Rivers and Alluvial Floodplains in the Alps*, Plachter H, Reich M (eds). Springer-Verlag: Berlin.

Tockner K, Baumgartner C, Schiemer F, Ward JV. 2000. Biodiversity of a Danubian flood plain: structural, functional and compositional aspects. In *Biodiversity in Wetlands: Assessment, Function and Conservation*, Gopal B, Junk WS, Davis JA (eds). Backhuys: Leiden; 141–159.

Toth LA, Melvin SL, Arrington DA, Chamberlain J. 1998. Hydrologic manipulations of the channelized Kissimmee River. *BioScience* **48**: 757–764.

Townsend CR. 1996. Concepts in river ecology: pattern and process in the catchment hierarchy. *Archiv fuer Hydrobiologie Supplementband* **113**: 3–21.

Turner MG, Gardner RH. (eds). 1991. *Quantitative Methods in Landscape Ecology*. Springer-Verlag: New York.

Uehlinger U, Zah R, Bürgi H-R. 1998. The Val Roseg project: temporal and spatial patterns of benthic algae in an Alpine stream ecosystem influenced by glacial runoff. *International Association of Hydrological Sciences Publication* **248**: 419–434.

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.* **37**: 130–137.

Vanhara J. 1994. Long-term ecological studies of terrestrial arthropods in the floodplain area along the lower reaches of the Morava and Dyje river, with regard to floodplain forest Diptera. *Quad. Staz. Ecol. civ. Mus. St. nat. Ferrara*. **6**: 185–204.

Van den Brink FWB, de Leeuw JPHM, van der Velde G, Verheggen GM. 1993. Impact of hydrology on the chemistry and phytoplankton development in floodplain lakes along the Lower Rhine and Meuse. *Biogeochemistry* **19**: 103–128.

Van den Brink FWB, Van der Velde G, Buijse AD, Klink AG. 1996. Biodiversity of the Lower Rhine and Meuse river–floodplains: its significance for ecological management. *Netherlands Journal of Ecology* **30**: 129–149.

Walker KF, Sheldon F, Puckridge JT. 1995. A perspective on dryland river ecosystems. *Regulated Rivers* **11**: 85–104.

Ward JV. 1985. Thermal characteristics of running waters. *Hydrobiologia* **125**: 31–46.

Ward JV. 1992. *Aquatic Insect Ecology*. Wiley: New York.

Ward JV. 1994. Ecology of alpine streams. *Freshwater Biology* **32**: 277–294.

Ward JV, Stanford JA. 1983. The serial discontinuity concept of lotic ecosystems. In *Dynamic of Lotic Ecosystems*, Fontaine TD, Bartell SM (eds). Ann Arbor Science: Ann Arbor, MI; 347–356.

Ward JV, Stanford JA. 1995a. The serial discontinuity concept: extending the model to floodplain rivers. *Regulated Rivers* **10**: 159–168.

Ward JV, Stanford JA. 1995b. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers* **11**: 105–119.

Ward JV, Tockner K, Schiemer F. 1999a. Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated Rivers* **15**: 125–139.

Ward JV, Malard F, Tockner K, Uehlinger U. 1999b. Influence of ground water on surface water conditions in a glacial flood plain of the Swiss Alps. *Hydrological Processes* **13**: 277–293.

Ward JV, Tockner K, Edwards PJ, Kollmann J, Bretschko G, Gurnell AM, Petts GE, Rossaro B. 1999c. A reference river system for the Alps: the Fiume Tagliamento. *Regulated Rivers* **15**: 63–75.

Ward JV, Tockner K, Edwards PJ, Kollmann J, Bretschko G, Gurnell AM, Petts GE, Rossaro B. In press. Potential role of island dynamics in river ecosystems. *Verh. Internat. Verein. Limn.* **27**.

Ward JV, Malard F, Tockner K. Submitted. Landscape ecology integrates pattern and process in river corridors. *Landscape Ecology*

Webb BW, Nobilis F. 1994. Water temperature behaviour in the River Danube during the twentieth century. *Hydrobiologia* **291**: 105–113.

Wiens JA. 1995. Landscape mosaics and ecological theory. In *Mosaic Landscapes and Ecological Processes*, Hansson L, Fahrig L, Merriam G (eds). Chapman & Hall: London; 1–26.

Wright R. 1982. Seasonal variations of water quality of a West African river (R. Jong in Sierra Leone). *Rev. Hydrobiol. Trop.* **15**: 193–199.