Fluvial Hydrosystems

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Preface and acknowledgements

In 1986, the Large European Rivers Network was initiated with the support of the Council of Europe. Following a number of symposia, the first output of this network was a volume on *Historical Change of Large Alluvial Rivers: Western Europe* published by John Wiley in 1989. At the same time, staff exchanges as part of the ERASMUS Programme of the EU led to two research groups debating their different but complementary approaches to the analysis of change in fluvial systems. These two groups were from the universities of Lyon in France and Loughborough in the UK.

The University of Lyon was the centre of a Programme de Recherche Interdisciplinaire sur l'Environment (PIREN) of the CNRS. Their studies on the Rhône River had led to the introduction of the term 'fluvial hydrosystem' to provide an integrated multidisciplinary context for analyses of ecological change. The University of Loughborough had established a multidisciplinary team – the Freshwater Environments Group – with the objective of modelling the distribution of biota according to predictable environmental gradients, and to use these to evaluate impacts of river regulation. Fusion of the two sets of ideas and approaches into a single work was not only an exciting objective, but also an interesting academic challenge!

The original idea for the book was born during a conversation between G. E. Petts and M. T. Greenwood on a coach with 50 first-year students from Loughborough on the road to Scarborough. Joint authorship of each chapter would ensure that all contributors gained new insights into fluvial systems. This also required that colleagues adopted an open mind and showed a willingness to approach questions in ways that were often foreign.

In 1993, we published 'Hydrosystèmes Fluviaux' as a volume (no. 24) in the Collection d'Écologie series published by Masson of Paris. Publication of this French volume reflected the considerable enthusiasm of our colleagues at the University of Lyon, especially Claude Amoros, to whom I offer my gratitude for producing an excellent book.

Since embarking on a version suitable for the English-speaking market, the Loughborough Freshwater Environments Group has split up and colleagues have moved to new posts in other universities. This book is based on the original French version but has benefited from our experiences with different groups of students at our new universities, and from subsequent discussions with colleagues here and overseas, and it has been updated with new material.

We are grateful to colleagues for their help in the production of this volume, particularly to Peter Robinson (Loughborough) for producing most of the diagrams and Melanie Bickerton and Sue Lane (Birmingham) for last minute support in preparing the manuscript. A special note of thanks to Malcolm Greenwood without whose efforts this book may never have been completed.

Geoff Petts
April 1996

The fluvial hydrosystem

1

G. E. Petts and C. Amoros

1.1. THE BACKGROUND

Rivers are a popular source of fascination because of their changing moods from headwater stream to large lowland rivers and from quiet summer brooks to raging flood torrents. The character of a river changes continually, from day to night, from day to day, from season to season and from year to year. It is this dynamism that attracted the attention of naturalists and geologists in the 19th century, and that today provides a focus for research by biologists, fisheries scientists, geomorphologists and hydrologists. However, the interest in rivers is more than curiosity; most nations are dependent on sustainable river management.

Rivers have a vital role in the economies of most societies providing fundamental resources – water (domestic, industrial and irrigation supplies), power, navigation, food and recreation. Although agriculture is the single largest water user worldwide, accounting for nearly 70% of all use, hydroelectric power has a particularly important role in the economic development of many countries. One scenario (Goldemberg *et al.*, 1988) requires a tenfold increase of installed hydro-capacity if the per capita energy demand of the developing countries is to approach current levels in the United States and Western Europe.

Arguably, of all natural hazards rivers pose the greatest threat to the sustainability of human societies. Devastating floods are of obvious concern but drought remains the major threat today, as it was when early 'hydraulic civilizations' established, for example, along the Nile valley some 5000 years ago. Periods of economic growth, political power, and social stability in ancient Egypt coincided with wet phases of good river

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flows and a reliable annual flood; economic recession, depopulation and political instability resulted during periods of drought (Said, 1993). Little has changed over five millenia. Today, rapid population growth and increased per capita demands for water, especially within the developing nations, means that twenty countries are experiencing water scarcity and on the basis of population predictions by the United Nations (Engleman and LeRoy, 1993), by 2025 these are likely to be joined by twelve other countries.

In the past, river developments have caused dramatic ecological impacts: a loss of habitat diversity, the reduction of species richness, and a decline in productivity. However, the modern approach to river development is founded in the concept of environmental sustainability which incorporates the need to conserve biodiversity. Recent research has shown that river margins – the dynamic interfaces between terrestrial and aquatic environments – are locations where biological processes and biodiversity tend to be maximized (e.g. Petersen *et al.*, 1987; Gregory *et al.*, 1991). We now know that these environments are not only vital for sustaining river ecosystems but they also play a major role in sustaining biological diversity at the landscape scale. Yet it is these river margin environments that have been particularly severely impacted by past river developments, for example: along the Nile 2.7 million ha of diverse floodplain habitat was 'reclaimed' by 2000 years BP; in Europe, 12.5 million ha of floodplain was drained along the Tisza River in the mid 19th century; and throughout USA, more than 80% of natural river margin environments have been lost.

Sustainable river development – often requiring restoration measures to reverse the historic legacy of environmental degradation – must be based on a sound scientific understanding of river ecosystems. The *Fluvial Hydrosystem* concept provides a unifying approach to the study of running waters by viewing rivers as structured, four-dimensional systems. This chapter introduces the concept and the subsequent chapters elaborate on the primary features building an approach that, it is suggested in the final chapter, may provide the scientific basis for managing rivers in a sustainable way.

1.2 TRADITIONAL APPROACHES

Traditionally, running waters have been the focus of study by two different and distinct groups of disciplines. First, hydrologists and fluvial geomorphologists, with geographical, geological and engineering backgrounds, have investigated the ways in which streamflows, sediment loads, and channel forms vary along a river from headwaters to mouth and with time over periods ranging from hours (during individual floods), to one year (seasonal patterns), to 100 years (the main period of human impacts), and to 10 000 years (the Holocene).

Secondly, ecologists, biologists and fisheries scientists have examined downstream patterns in the structure and function of biological communities – algae, macrophytes, macroinvertebrates and fish – over scales ranging from microhabitats (e.g. the individual stone) to whole rivers, including the nature of food webs and nutrient fluxes. Reviews of these subjects are presented in Calow and Petts (1992). These classic approaches to the study of rivers emphasize the view of rivers as unidirectional systems.

1.2.1 THE LONGITUDINAL DIMENSION

Represented in their most simple form, rivers can be viewed as unidirectional systems that change progressively from headwaters to mouth. The physical gradient from a shallow, turbulent, mountain stream to a deep, meandering, lowland river results in sequences of biological communities that characterize rivers in different biogeographic regions. Studies of the downstream variation of physical and biological variables along a river followed the presentation of two approaches in fluvial geomorphology. First, the analysis of stream networks (Horton, 1945; as modified by Strahler, 1952) by defining 'stream orders', has been widely used as an objective and widely applicable classification system for the examination of rivers of different magnitudes (e.g. Barila *et al.*, 1981). Secondly, Leopold and Maddock (1953) demonstrated relationships to characterize variations of flow width, depth and velocity, relative to discharge (known as the hydraulic geometry approach; see Figure 2.8).

The upstream–downstream gradient in environmental conditions is associated with the progressive change in animal communities reflecting (a) the adaptive ability of the species in response to environmental constraints, and (b) the available trophic resources. The pioneer studies in river biology described river zones according to their habitat characteristics and related them to algae, benthic invertebrate and fish communities. The Illies and Botosaneanu (1963) classification distinguishes the springs (*crenon*) from the upper reaches of streams (*rhithron*) and from the lowland river (*potamon*). The rhithron corresponds to streams and rivers with steep gradients (greater than 0.15%), substratum of boulders, cobbles and pebbles, well oxygenated water and monthly average temperatures below 20°C supporting salmonid communities and cold-stenothermous and rheobiontic invertebrate communities dominated by insect larvae. In contrast, the potamon corresponds to large rivers with low gradients having bed sediments dominated by fine gravel, sands and silts with high organic content; the water is often turbid, temperatures can exceed 20°C and dissolved oxygen levels may be low; salmonids are rare in the fish community and the invertebrates are dominated by eurythermous species that have low oxygen requirements or are air breathers. Mollusca and oligochaetes are abundant on organic deposits and in submerged plant stands, and phytoplankton and zooplankton develop in open water.

1.2.2 THE RIVER AS A CONTINUUM

Following Vannote *et al.* (1980), the downstream gradient of physical factors is seen to exert a direct control on the biological strategies and dynamics of river systems. They described this gradient as the River Continuum Concept (see Figure 7.4). The physical structure of a stream, coupled with the hydrological regime and energy inputs, is seen to produce a series of responses within the constituent populations, resulting in a continuum of biotic adjustments, and common patterns of loading, transport, utilization and storage, of organic matter along the length of the river. Moreover, the concept emphasizes that river ecosystems are largely heterotrophic, being dependent on upstream sources for energy supplies (Hynes, 1970) – the most important fuel for running-water food webs being detritus from catchment sources.

The River Continuum concept advanced our understanding of river ecosystems by shifting attention away from system structure to system functioning, emphasizing the inputs and fluxes of matter and energy, but retained the unidirectional perspective. Thus, in headwater woodland streams that are heavily shaded, aquatic primary production is a minor component of food webs which are dominated by the input of particulate organic matter from riparian vegetation and hillslope sources, including excrement and corpses of terrestrial animals. Together these catchment sources are known as allochthonous inputs. As channel width increases along a river, the input of solar energy encourages the development of perilithic and periphytic algae fixed on stones or on the stems of macrophytes (vascular aquatic plants), respectively. Such 'autochthonous' production dominates the energy budgets of large streams. However, in the largest rivers, the depth and turbidity restrict light penetration to the bed to the shallow marginal zones and backwaters, but the decrease in autochthonous production by rooted plants and attached algae is compensated by large developments of planktonic algae.

Downstream invertebrate communities are sequenced to exploit the changing nature of food resources. Shredders exploit the coarse particulate organic matter in headwater streams; collectors feed on the fine particulate organic matter; and grazers utilize the attached algae. However, this theoretical scheme must be adapted to the geographical and climatic conditions (Statzner and Higler, 1985) and to take account of inputs from tributaries draining catchments of contrasting geology and landuse (e.g. Bruns *et al.*, 1984). Furthermore, human impacts can modify these downstream patterns and may 'reset' the continuum, as shown by

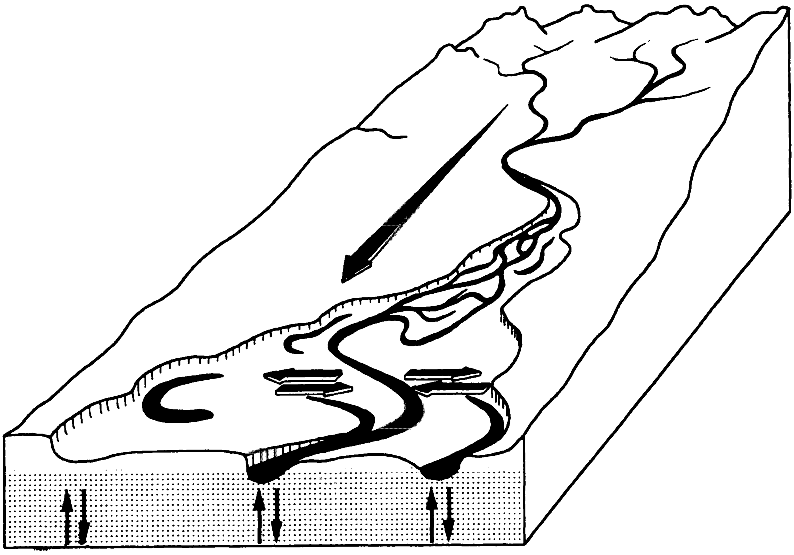

Figure 1.1 The fluvial hydrosystem as a three-dimensional system. The unidirectional, longitudinal dimension is supplemented by – and may be of minor importance in relation to – two-way lateral transfers between the channel(s) and the diverse range of patches on the alluvial plain, and two-way vertical exchanges with the underground environment of the alluvial aquifer.

the discontinuities in longitudinal profiles caused by many dams (e.g. Ward and Stanford, 1983).

1.3 THE FLUVIAL HYDROSYSTEM APPROACH

An approach based on the longitudinal and temporal dimensions focuses on the downstream variation of flow, temperature, channel form and biotic communities, and the unidirectional fluxes of energy and material from the watershed, through the hillslope system, and along the drainage network to the main river and then to the sea. Importantly, the temporal dimension emphasizes that the morphology and biological populations of rivers are dynamic over a range of time-scales. However, this approach has failed to provide the necessary scientific basis for advancing sustainable river management or effective river restoration which must integrate information from hydrology, geomorphology and ecology.

A river ecosystem must no longer be viewed as a simple linear feature delimited by the bed and banks of the main channel, and dominated by downstream transfers. Rivers should be viewed as three-dimensional systems (Figure 1.1) being dependent on longitudinal, lateral and vertical transfers of energy, material and biota. Upstream to downstream fluxes, lateral interactions with the river margin, and vertical exchanges with the groundwater of the alluvial aquifer are all important. The integrity of the *fluvial hydrosystem* depends on the dynamic interactions of hydrological, geomorphological and biological processes acting in these three dimensions over a range of time-scales. Fundamentally, fluvial hydrosystems relate to the variability of the fundamental hydrological and geomorphological processes that determine (a) the types of habitat patches present and (b) the strength, duration and frequency of their connectivity.

There are five key features of the fluvial hydrosystem approach to the study of rivers.

1. The concept focuses attention on the river corridor, comprising the river channel (or channels) and the adjacent floodplains with their diversity of aquatic, wetland and terrestrial habitats, and the underlying alluvial aquifer.
2. The spatial patterns of environmental variables and biological populations are described as longitudinal, lateral, vertical and temporal (successional) gradients, linked by fluxes of energy and materials. The lateral and vertical dimensions emphasize the importance of two-way fluxes and interactions between the river channel and the riparian and floodplain environments on the one hand, and between the river channel and the underlying alluvial aquifer on the other.
3. Biota are seen to be distributed according to predictable environmental gradients modified by biological processes (competition, predation, colonization, succession, extinction).
4. Over long time-scales (10–1000 years), the primary environmental variables are the discharge, sediment, and water-quality regimes, which relate to climate, vegetation and landuse, that is to the character of a river's catchment area.
5. The structure of a fluvial hydrosystem reflects the combination of fluvial dynamics and biological processes over a range of time-scales, but in most cases the structure and function of the fluvial hydrosystem today clearly shows the historical legacies of (a) climate change over Quaternary and Holocene timescales, and (b) of human impacts, especially over the past 200 years.

1.3.1 A HIERARCHY OF SCALES

Rivers are viewed as complex ecological systems made up of the biotopes and biocenoses of running water, standing water, temporary water, groundwater and terrestrial environments. Each one of these environments is dependent to a greater or lesser degree on connectivity with the active channel of the river and the ecological character of this main channel depends on interactions with those environments. Thus, the *fluvial hydrosystem* constitutes an 'eco-complex' as defined by Blandin and Lamotte (1985).

In order to simplify the analysis of fluvial hydrosystems they may be viewed as a nested hierarchy of subsystems. Different levels within the hierarchy are controlled by different rates and types of processes. Since the seminal work of Schumm and Lichty (1965) strong relationships have been demonstrated between effectiveness of different processes and the size or the area of the subsystem concerned (Legendre and Demers, 1984; O'Neill *et al.*, 1986; Urban *et al.*, 1987; Salo, 1990). The fluvial hydrosystem is viewed as comprising five distinct levels.

(a) The drainage basin

The primary unit for investigating rivers, is the drainage basin which is delineated by a topographic divide – the watershed (Figure 1.2). The structure of the basin results from geological processes (e.g. plate tectonics, eustatic uplift) and climatic changes which operate over time-scales of more than 10^4 years. Following Schumm (1977), within the drainage basin an 'ideal' river is seen to progress through three zones: the headwater or production zone where water, sediment, particulate organic matter and solutes pass from the hillslopes to stream channels; the transfer zone through which materials are transported or *routed*; and the storage zone, where materials are deposited and may be retained for a long period of time, in some cases thousands of year (Figure 2.1). Similarly, at this scale ecologists recognize the river as a continuum (Vannote *et al.*, 1980); the structure and function of the system changing through a series of weakly defined zones from source to mouth. The fluvial hydrosystem applies to the transfer and storage zones described by Schumm and recognizes the production zone as a 'black box' which controls the primary inputs to the hydrosystem.

(b) Functional sectors

The complex geological histories of most basins (e.g. Starkel, 1995) means that the development of the river continuum is interrupted by changes in valley width and gradient, and the confluence of tributaries with different flow, water-quality and sediment regimes* draining subbasins of different geological, climatic and biogeographical character. Thus, the fluvial hydrosystem may be divided into different *'functional sectors'* (Figure 1.2). Glacial troughs filled by outwash gravels having broad floodplains with braided channels, contrast with straight channel sectors

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*The term 'regime' is used to describe the pattern of process (e.g. flow or temperature) variation during a typical year, and is derived from long-term average data.

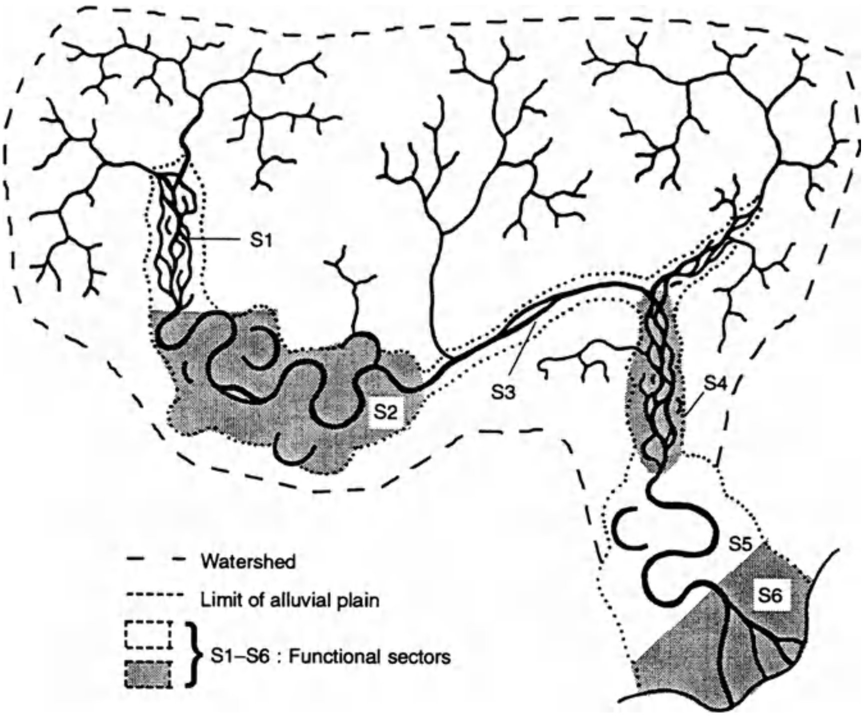

Figure 1.2 Schematic diagram illustrating the delimitation of functional sectors within a drainage basin. The 'fluvial hydrosystem' comprises the six functional sectors. The other areas of the basin are seen as comprising the 'production zone' which yields runoff, sediment, organic matter, nutrients and organisms, via the tributary stream network to the main river.

in confined valleys, and with low-gradient meandering channels. Channel pattern is the most obvious, but only one, manifestation of the differences that exist between functional sectors. Others relate to the contrasting process regimes (e.g. flow, sediment transport, temperature), and the different types of habitat and their relative stability over time. Subsequent chapters elucidate these differences in ecological functions. The scale of sectors reflects the size of river system: ranging from 10^{7-8} m^2 on a ninth order river such as the Upper Rhône, France to 10^{6-7} m^2 on the seventh order River Trent and to 10^{5-6} m^2 on the small, fifth order River Wissey, England.

(c) Functional sets

Each sector may be divided into *functional sets* of typical ecological units (Figure 1.3) associated with specific landforms such as a major cutoff

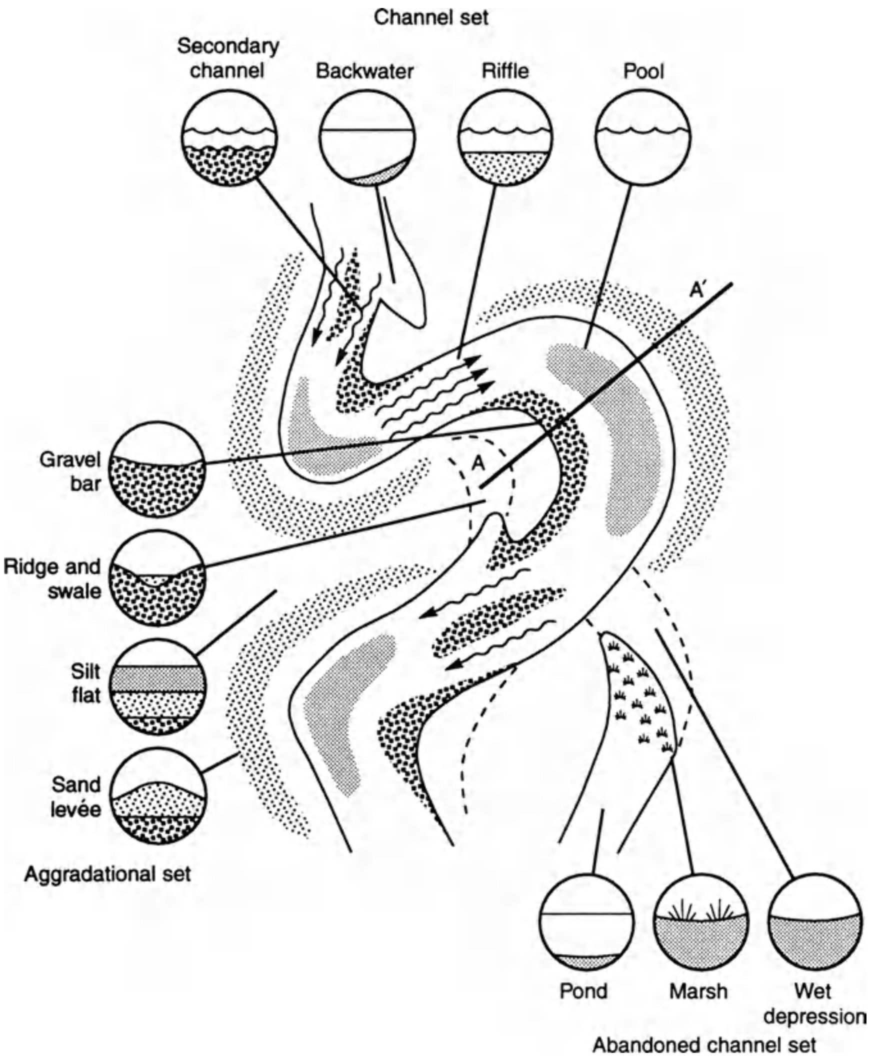

Figure 1.3 A schematic example of three functional sets (each of three or four units) within a meandering sector (e.g. sector S2 in Figure 1.2).

meander, or aggrading floodplain. The main channel is also seen as comprising a functional set. The appropriate time-scale for analysing functional sets is 10^{1-3} years and on the Upper Rhône, the area of a functional set ranges from 10^4 to 10^6 m^2. The character of each functional set within the river corridor is determined by the strength of lateral and vertical fluxes which relate to the morphology and sedimentary composition of each landform, and to its connectivity with the main channel. Thus, for example, a cutoff braided channel located near to the main river, on coarse sediment with high porosity, will be closely connected to the river whereas a former meander, remote from the main channel and underlain by sediments of low porosity may be dominated by rainfall inputs and groundwater seepage, and will be connected to the main channel only during major floods.

(d) Functional units

Each *functional unit* is characterized by a typical animal and plant community, that is indicative of the habitat conditions at the site (Figure 1.3). In the Upper Rhône, the area of individual functional units ranges from 10^2 to 10^4 m^2. The individual *functional units* are generally arranged in spatial successions along topographic gradients (or toposequences) defined, for example, by water depth, frequency of inundation or duration of periods of desiccation. These sequences also constitute chronosequences; ecological succession being described by changes in habitat conditions and their biotic communities. All units within a functional set evolve from a single origin by progressive changes over time-scales of 10^{-1} to 10^2 years. The processes involved include sedimentation, decrease in water depth and frequency of inundation, population development and species replacement, biomass production and organic matter accumulation. Considering the example of a newly formed gravel bar: one unit is the original deposit of gravel and sand which has a high permeability, is regularly scoured by high flows, and is colonized by pioneer annual herb communities; a second unit within the same functional set is the bar now overlain by silt with its surface at the level of the floodplain and inundated only during floods, and colonized by willow shrubs. Similarly, considering the cutoff meander: deep, standing open water constitutes one functional unit; the wetland communities (e.g. with *Phragmites australis* and *Carex elata*) that develop following siltation and 'terrestrialization' constitute another.

(e) Mesohabitats

Finally, each functional unit may be subdivided into a group of specific mesohabitats (such as gravel patch, sand bar, scour hole, submerged plant stand, tree roots). These mesohabitats are particularly sensitive to variations of the control variables and may change from year to year, and within years, reflecting the actual sequence of flows and sediment loads. However, in general terms, the level of sensitivity declines as succession progresses with older units being relatively isolated from the dynamic influence of the main channel and least sensitive to short-term variations in weather conditions. Thus, the appropriate time-scales for analyses at this level range from 10^{-2} to 10^{1} years. The areas of these meshabitats in the Upper Rhône, extend from 1 to 10^{3} m^{2}.

1.3.2 THE FLUVIAL HYDROSYSTEM: THE BOOK

This book uses the fluvial hydrosystem approach to explore the dynamic characteristics of river systems focusing on large floodplain rivers within which ecosystem functioning is determined by the interaction of longitudinal, lateral and vertical processes. The book is structured into three sections. First, Chapters 2–5 elaborate on the hydrological and geomorphological processes that create the physical environments along the river corridor within which biological communities develop. Chapter 2 places the fluvial hydrosystem in the drainage basin and long-term contexts, emphasizing the importance of water and sediment source–area characteristics, and introducing the ways in which fluvial hydrosystems respond to climatically induced changes of these variables. Chapter 3 focuses on the hydrological cycle and associated solute variations, emphasizing the role of the flow source and pathway through the hillslope system in determining the hydrochemical characteristics. Chapter 4 examines the processes of sediment transport and the adjustment of channel morphology to different conditions of sediment load and water discharge. Finally, Chapter 5 demonstrates the ways in which flow regime, sediment load and landform dynamics interact to determine the patch mosaic of functional sectors which provides the template for the development of biological communities.

The second section of the book focuses on the biological communities within the different aquatic environments and the ways in which they vary depending upon the physical setting. These processes are examined with regard to the primary producers (Chapter 6), invertebrates (Chapter 7) and fish (Chapter 8). Each chapter focuses on the spatial organization of communities and adaptive strategies of specific species at the scale of functional units and functional sets, i.e. in relation to the mosaic of habitats and the heterogeneity of biological resources.

The third section of the book explores the temporal dimension, particularly the ways in which the different functional units (surface water, groundwater and terrestrial) interact. Chapter 9 investigates the fluxes of energy, material and information between functional units within the hydrosystem developing the 'ecotone' – the transitional zones between units, sets and sectors – concept and giving particular attention to the importance of connectivity. Chapter 10 focuses on successional processes, examining the ways in which functional units are transformed by physical, chemical and biological processes. Finally, Chapter 11 examines the influence of human impacts on fluvial hydrosystems and applies the information presented in the previous chapters to explain the ecological changes that have taken place within fluvial hydrosystems especially over the past 200 years.

The book concludes (Chapter 12) with a brief consideration of how the fluvial hydrosystem approach might contribute to achieving the objective of river development within the context of sustainable environmental management, incorporating the conservation of biodiversity and the restoration of degraded environments. The fundamental message is that self-sustaining river systems require the maintenance not only of longitudinal connectivity but also of the two-way lateral and vertical exchanges between the river channel and its floodplain, and its alluvial aquifer, respectively. The chapter suggests that (a) water and land must be allocated to conserve river corridors, and (b) a range of flows and sediment-transporting events (to promote erosion and deposition) are required to sustain the local- and landscape-scale values of large rivers.

A drainage basin perspective

2

G. E. Petts and J.-P. Bravard

2.1 THE CONTEXT

Fluvial hydrosystems are the product of physical, chemical and biological processes operating throughout a river's drainage basin and over a range of time-scales from a year to tens of thousands of years. A drainage basin is the area that gathers water from precipitation and delivers it to the river (Figure 1.2). Defined by a topographic divide, the basin is occupied by a drainage network which collects the runoff from hillslopes, together with its load of sediment, particulate organic matter and solutes. Thus, a river may be seen as the artery of a drainage basin conveying water, minerals and organic matter to the sea. A drainage basin perspective is also important because the flow regime and sediment loads determine the morphology of the channel which has a strong influence on the structure and function of fluvial hydrosystems as first recognized by Hynes (1970, 1975). However, drainage basins are complex geomorphological systems with a history. This chapter describes the characteristics of drainage basins and examines the ways in which the basin influences fluvial hydrosystems over a range of time-scales.

2.1.1 THE RIVER BASIN AS THE BASIC UNIT

Horton (1945) first established the erosional drainage basin as the basic unit of landscape. The network of channels within a drainage basin focuses the delivery of water and material in transport from the hillslopes onto the main river and then downstream to the river mouth. As a result, rivers became viewed as dominated by longitudinal processes. 'Drainage

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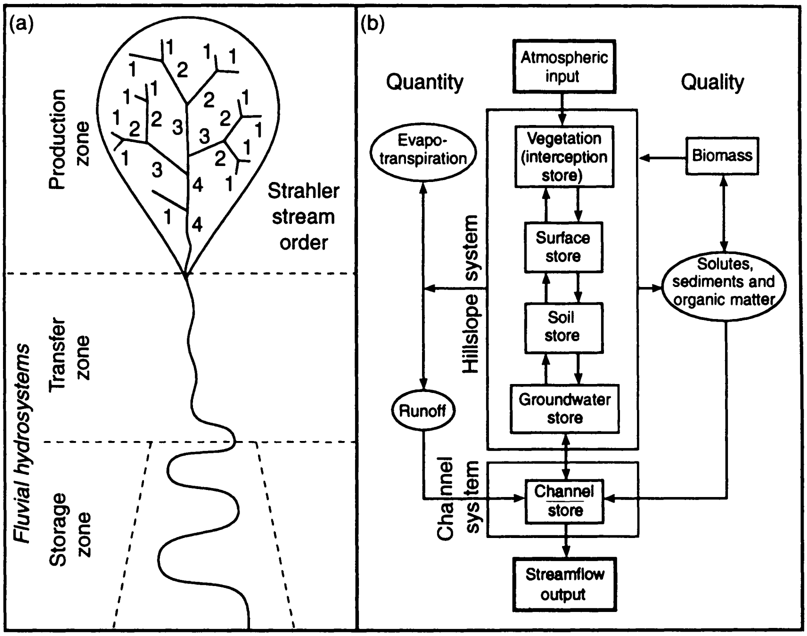

Figure 2.1 (a) The idealized fluvial system (based on Schumm, 1977) showing the Strahler (1952) method of stream ordering: (b) The basin hydrological cascade which influences both quantity and quality characteristics of streamflow (this is developed in Figure 3.1).

area' and 'distance from source' have been used as scale variables for studies of river systems, but measures of drainage network composition have particular significance. The number of headwater, finger-tip, tributaries (the stream magnitude, Shreve, 1967) and the number of confluences (the stream frequency, NERC, 1975) in a basin relate closely to streamflow characteristics, but most ecological studies have employed stream ordering techniques as an objective, and widely applicable, classification system. The most commonly used system is that proposed by Strahler (1952) modified after Horton (1945). This convention (Figure 2.1a) designates all headwater streams, terminated by the first confluence, as first-order streams. Two first-order streams join to form a second-order stream, the confluence of two second-order streams produce a third-order river, and so on.

2.1.2 THE BASIN SYSTEM

For any point along a river, stream ordering provides an index of scale and a measure of position within the drainage network. However, an analysis of the characteristics of a river at any point along its course requires a more dynamic perspective. To achieve this perspective a systems approach (Chorley and Kennedy, 1971) may be employed.

The drainage basin comprises a set of structural units – landforms – which function both as storages and sites of material and energy conversion and transformation. Together, a set of structural units can be described as a *morphologic system* and the strength and direction of the connectivity between the units can be revealed by correlation analysis. In a short reach of river, for example (Figure 2.2a), the morphological properties might include such parameters as local slope, bed material size and cross-sectional form (depth:width ratio). The interrelationships between the parameters often indicate the degree to which their dynamic properties are related. Thus, an increase in bed material size is associated with an increase in local slope and a reduction of the depth:width ratio.

The different structural units are linked by a range of processes. Drainage basins are open systems dependent on *inputs, transfers* and *outputs* of mass and energy. The processes – the mass and energy flows through the basin – that link the different structural units can be seen as a *cascading system*. Within the drainage basin, the most important of these systems is the hydrological cascade (Figure 2.1b). Solar energy and precipitation form the inputs to the basin hydrological cascade and the outputs, streamflow and evapotranspiration losses, are generated by the transfer of water through a sequence of storages within the hillslope and channel subsystems. The most important regulator is the soil store. The hydrological cascade not only describes the amount of rain that becomes runoff and the rate of runoff, but also the quality of runoff, that is, the concentration of ions, released from weathering and biological processes, and particulate material (organic and inorganic).

A complete explanation of a fluvial hydrosystem requires integration of the morphologic and cascading systems, known as a *process–response system*. Thus, in Figure 2.2(b) channel morphology is seen to be determined by the discharge of water (Q) and sediment (L). These systems rarely attain exact equilibria and generally the river channel tends toward a mean form, defined as quasi-equilibrium. With a system in equilibrium, the outputs will equal the inputs. If the inputs change, the morphologic system will adjust to a new equilibrium condition. For example, an increase in sediment load, with no change of discharge, will induce an increase in channel slope and bed material size, and a reduction of the depth:width ratio.

The drainage basin of large rivers comprises a large number of small basins and Schumm (1977) divided the drainage basin system into three distinct parts (Figure 2.1a) representing different types of process–response system. Small headwater catchments represent the production zone where runoff generation and sediment yields are determined mainly

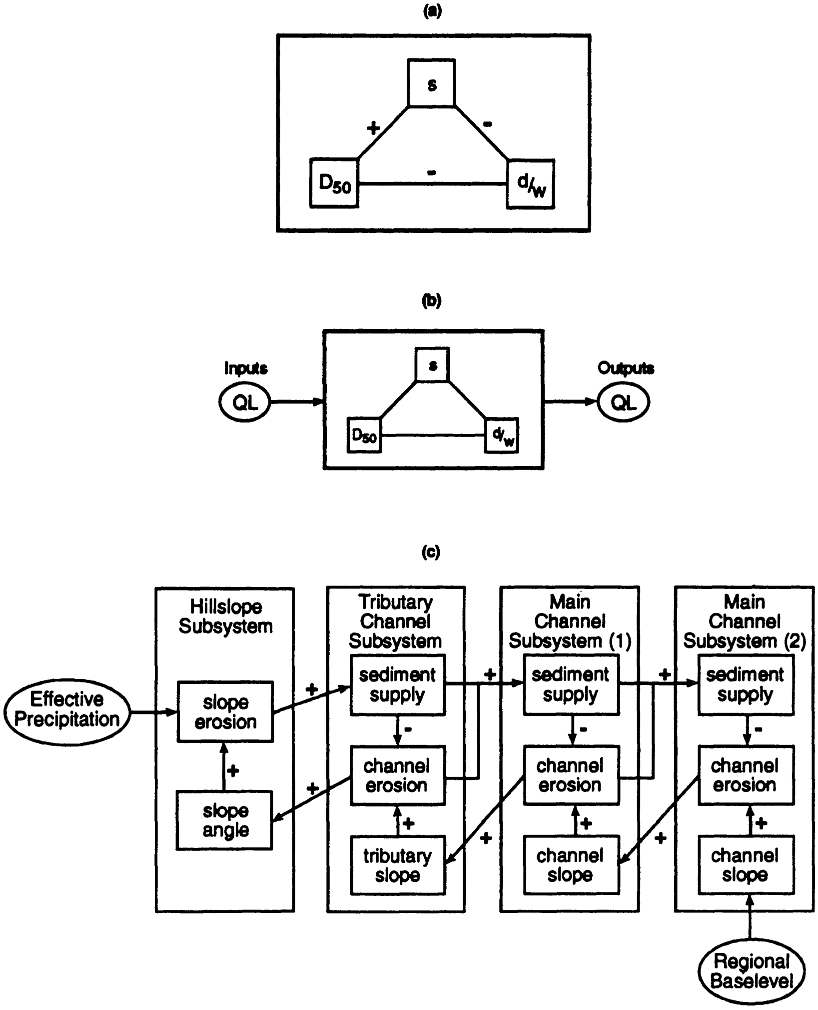

Figure 2.2 Relationships within the river channel and basin systems. An example of a simple morphologic system is given in (a) showing positive (+) and negative (−) relationships between reach slope (s), sediment size (the 50th percentile) of the channel bed (D_{50}) and cross-sectional form expressed as the depth (d) to width (w) ratio. (b) shows this system as part of a process–response system within which the morphologic variables are adjusted to changes of discharge (Q) and sediment load (L). In (c) negative feedback loops are shown connecting cascading and morphologic systems, illustrating the complex sequence of interactions between main channel sectors, tributaries and hillslopes that result from a change of effective precipitation or regional baselevel. The resulting changes to channel morphology (S, D_{50}, and d/w) can be interpreted by reference to (a).

by hillslope processes. Strong lateral linkages between hillslope and channel make this zone, which can extend to include fourth-order streams, distinct. Water, with its particulate and dissolved load, is then transferred downstream through the channel network (the transfer zone) to the major alluvial river which is characterized by its storage properties. Within the storage zone the flow regime is strongly influenced by water retention on the floodplain during high flows and within the alluvial aquifer during low flows; sediments and organic matter are stored within the floodplain and nutrient cycling is highly dependent on interactions between the alluvial aquifer, the floodplain and the main river. These processes are examined in later chapters.

The fluvial hydrosystem of each river sector may be described as a process–response system with point inputs (from the upstream basin) and outputs. Within each sector strong functional relationships exist between the physical, chemical and biotic components such that a quasi-equilibrium state may be defined over time-scales of 10–100 years.

An important characteristic of process–response systems is the role of *feedback* loops, particularly negative ones. The operation of these loops introduces processes which tend to oppose continued change within the system caused by variation of the cascade input. For example, the sediment load is a function of both hillslope and channel erosion at the base of the slope, increasing slope angle. The increase in sediment supply reduces channel erosion and may induce aggradation. This stabilizes the slope subsystem and reduces hillslope sediment supply. Self-regulation operates to maintain the quasi-equilibrium and to establish a new quasi-equilibrium condition if a change of the external controls (here effective precipitation or baselevel) occurs.

In reality, the controls within each loop are only partial. Change is associated with many loops linking the variables involved, so that responses to changes of the external controls are usually complex, involving interactions between the different tributaries and interrelated sectors (Figure 2.2c). Within each sector of channel the morphological dynamics reflect the sediment supply from the sector immediately upstream (comprising sediment transported through, and eroded from, this sector) and the influence of local baselevel changes determined by the next downstream sector.

2.1.3 INFLUENCE OF SCALE

Rivers can be viewed in many different ways and not only as systems in quasi-equilibrium over an historical time-scale (10–100 years). Over short time-scales, from a day to one year, they may be seen as rather stable systems. Over geological time-scales they are viewed as systems undergoing continual change, known as a state of dynamic equilibrium.

The importance of these three different perspectives, first defined by Schumm and Lichty (1965), is in the definition of cause and effect because the status of variables and the nature of their interrelationships vary according to the scale adopted.

The status of variables influencing the hydrogeomorphological characteristics of rivers over different time-scales is given in Table 2.1. At a single point in time, the spatial variation of flow velocities and depths (variable 10) within a short reach are determined by channel morphology (variable 9). Similarly, day to day variations of river flow result in variations of hydraulic parameters as the discharge adjusts within a cross-section. Over such short time-scales channel morphology is determined and independent but over the historical time-scale, channel forms are viewed as dependent on the mean discharge of water and sediment (variable 8). The channel form is considered to be in equilibrium with the discharges and sediment loads produced by the interaction of climate (variable 6) and vegetation (variable 7) within the drainage basin upstream. However, the equilibrium channel dimensions will also reflect the valley characteristics (variable 5) which have developed over the longer (geological) time-scale. The valley gradient and the sedimentology of valley fill deposits, inherited from palaeoclimatological conditions (variable 3), are particularly important.

Table 2.1 The status of river variables during time spans of decreasing duration (after Schumm and Lichty, 1965)

	Status of variables during designated time		
Variables	Geologic	Historical	Present
1. Geology (lithology, structure)	Independent	Independent	Independent
2. Palaeoclimate	Independent	Independent	Independent
3. Palaeohydrology	Independent	Independent	Independent
4. Relief or volume of system above baselevel	Dependent	Independent	Independent
5. Valley dimensions (width, depth, slope)	Dependent	Independent	Independent
6. Climate (precipitation, temp., seasonality)		Independent	Independent
7. Vegetation (type and density)		Independent	Independent
8. Hydrology (mean discharge of water and sediment)		Independent	Independent
9. Channel morphology		Dependent	Independent
10. Hydraulics of flow (at-a-section)			Dependent

In the same way, the status of variables changes with spatial scale. *Between-basin* differences are explained by variations in climate, vegetation and relief, or by comparison of hydrological regimes, water balances or water-quality which have particular significance for fluvial hydrosystems. These are discussed in the next section. Differences *between sectors* reflect the declining gradient and reducing altitude; progressive changes occur in discharge and channel morphology with increasing catchment area. Large rivers also tend to be characterized by more regular and predictable variations of the abiotic variables than headwater streams and this change is particularly important for the functioning of fluvial hydrosystems. However, important differences between sectors – between fluvial hydrosystems – also reflect the different histories of each sector. This will be discussed in Section 2.4.

2.2 SOURCE AREA CHARACTERISTICS

Hydrology, channel morphology and temperature form the principal components of the abiotic milieu of river ecosystems. Their complex interactions determine, to varying degrees, species distributions and abundances of biota. In low-order headwater streams the variation of river flows, water quality and sediment transport is closely related to hillslope processes.

Discharges, water quality and sediment loads vary over a range of time-scales from hours to years according to the relative contributions from the different source areas within the headwater catchments. The source areas are defined by rock/soil type, vegetation/landuse, altitude and topographic setting; drainage basin characteristics fundamentally determined by geology, climate and the way the basin has evolved over time.

2.2.1 HYDROLOGICAL REGIMES

A river's flow regime may be defined as the seasonal variation in its discharge, usually described by a graph of monthly mean flow. Beckinsale (1969) described the global variation of hydrological regimes in relation to climate and relief, and noted that within large areas of the world the hydrological regime of rivers draining small and moderately sized basins closely reflects the regional climatic rhythm (Figure 2.3a). Five major types of regime were defined: tropical rainy climates having a mean temperature over 18°C in all months; dry climates with an excess of evaporation over precipitation; warm, temperate climates; seasonally cold, snowy climates with a mean temperature of the coldest month being below −3°C; and snow and ice environments of high mountains. Variations of each type have also been defined (Figure 2.3b), reflecting the magnitude and timing of seasonal variations of flow and temperature.

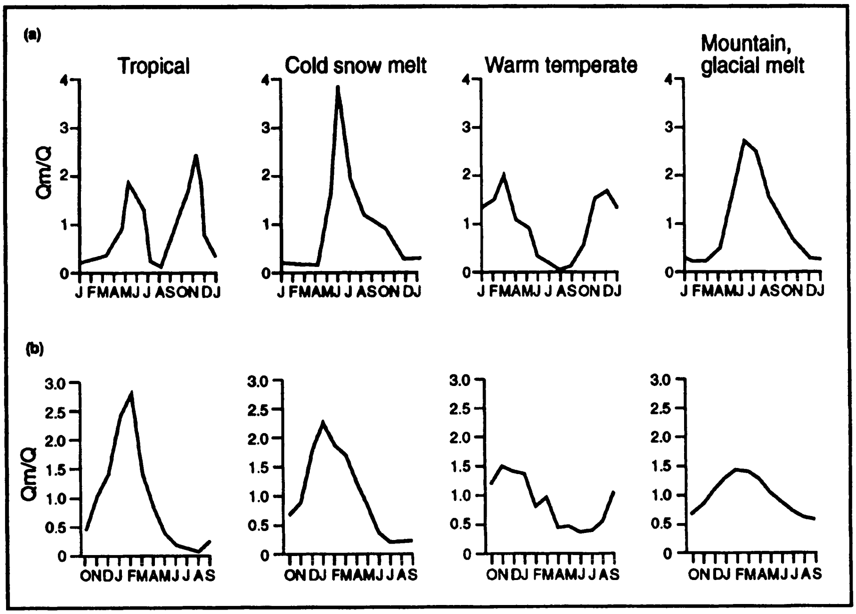

Figure 2.3 Typical flow regimes. (a) Regional types of flow regime (after Beckinsale, 1969) and (b) variations within the warm temperate type illustrated for selected headwater catchments in Britain (after Burt, 1992). Each diagram shows the daily mean flow for each month (Qm) in relation to the annual mean flow (Q). Note that in (b) the *hydrological year* is seen to begin on 1 October, the point in time when, on average for the warm temperate regime, basin storage begins to recharge following depletion during the summer evapotranspiration-dominated 'dry' season.

2.2.2 THE WATER BALANCE

Over a selected time period, the water balance of a drainage basin can be evaluated as:

$$P - (E + Q) = 0$$

where, P is precipitation; E is evaporation plus transpiration; and Q is stream discharge.

In humid temperature regions, annual precipitation increases with altitude and proximity to the sea. Thus, across Europe annual precipitation ranges from above 2000 mm to below 600 mm. Actual evapotranspiration across most of humid temperate Europe is between 500 and 600 mm. As the scale of observation decreases, the physical characteristics of the drainage basin become increasingly important in explaining variations in catchment hydrology. In particular, variable losses by evapotranspiration occur as a result of land-use differences. Thus, in comparing small forested and grassland catchments in Wales with an annual precipitation of over 2000 mm, Calder and Newson (1979) found that in the forested catchments evapotranspiration losses were doubled. In deforested catchments, reduced interception storage capacity and evapotranspiration rates lead to an increase in the proportion of rainfall becoming runoff. In one example from the Hubbard Brook experimental catchment in New Hampshire, USA, in the first year after felling runoff increased by 40% (Hornbeck *et al.*, 1970). Similarly, urban development can reduce evapotranspiration losses. Lvovitch and Chernogaeva (1977), for example, presented a water balance for Moscow suggesting that urban development reduced evapotranspiration by 62% (310 mm).

2.2.3 WATER QUALITY

The dissolved content of rivers is dominated by solutes released by weathering processes and reflecting catchment geology. Dominant solutes are bicarbonate (HCO_3), sulphate (SO_4), calcium (Ca) and silicate (SiO_2). The load-weighted average total dissolved solids content of world river water has been calculated as 120 mg l^{-1} (Webb and Walling, 1992). However, total dissolved solids concentrations range over five orders of magnitude from less than 10 mg l^{-1} in some Amazon tributaries to over 10 000 mg l^{-1} in some arid areas. Thus, at the global scale, Gibbs (1970) emphasized the influence of climate and geology on the variability of river water quality, separating Ca-HCO_3 (rock-dominated) rivers from those dominated by Na-Cl with low (precipitation-dominated) or high (evaporation-dominated) conductivity. The influence of climate acting through high rainfall to dilute river water gives a typical inverse relationship between discharge-weighted solute concentration and mean annual runoff. Meybeck (1982) also described global variations of dissolved organic carbon concentrations with median values of 10 mg l^{-1} for taiga rivers (in high latitude areas with marshy coniferous forest), 6 mg l^{-1} for tropical rivers, and 3 mg l^{-1} for temperate rivers. Although indicating a general climatic control, these values probably relate to the different organic contents of the soils in the different climatic regions.

The role of geology and land use again becomes clearer at a smaller scale. In a review of water quality in British rivers (Walling and Webb, 1981) specific electrical conductance was found to vary from 35 to 1200 $\mu S\ cm^{-1}$ in small and unpolluted catchments. Within one medium-sized basin, the River Exe in south-west England, conductivity under low flows ranged from less than 50 $\mu S\ cm^{-1}$ to over 1000 $\mu S\ cm^{-1}$ being dominated by geological variability within the catchment: lowest levels are associated with resistant slates and grits and highest levels with the younger, and more easily weathered, marls (Walling and Webb, 1975).

2.3 LARGE BASINS

The drainage basin of a large river can be viewed as a nested hierarchy of basins of different size. With increasing distance downstream and increasing catchment area, the influence of a particular headwater basin is diminished, and the influence of particular geologies and land uses decline. For example, the hydrological regime of the lower Rhine integrates the runoff pattern from the Alpine region where 50% of the precipitation falls as snow, and where snowmelt produces a high summer flow, with runoff from the maritime climatic region which produces high flows in winter. In such large basins, flow and water quality reflect not only the mixing of water from the different headwater catchments but also the routing of flows through the channel network, and the influence of channel, floodplain and groundwater storage.

In many ways the longitudinal 'continuum' is simply a reflection of increasing scale: increasing discharge, increasing channel size and the progressive downstream regulation of the spatial and temporal variations that characterize small basins. The different transfers may be expressed over a range of time-scales and incorporate important storages with different transport rates, retention times, and turnover rates. Consequently, the changing nature of the different storages along a river and the complex interactions of these storages are important factors in determining the functional dynamics of fluvial hydrosystems. There are many different storages, both physical and biological, but three brief examples illustrate their significance.

2.3.1 DEAD ZONES

At flows below bankfull, variations of channel shape and vegetation characteristics create hydraulic boundaries within the channel which separate the main flow from backwaters. Such 'dead-zones' with near zero flow velocity (Figure 2.4a) are separated from the main flow by localized lines of lateral shear. During storage, water-quality changes take place by interactions between water, sediment, detritus and biota. Tracer experiments undertaken on the lower Severn, UK (Bevan and Carling, 1992) show typical distributions (Figure 2.4a) which suggest the existence of large-scale storage areas – dead zones – within the reach.

2.3.2 FLOOD ROUTING

The passage of water from the production zone (Figure 2.1a) to the mouth of the river during a flood involves lags over short time-scales. As discharge rises, water enters each successive reach of channel, part enters storage within that reach such that there is a net reduction in the rate of increase of discharge downstream. The resulting 'attenuation' of flood peaks is illustrated in Figure 2.4(b). Attenuation is at a minimum and nearly zero at about 375 $m^3 s^{-1}$ (at just above bankfull), and increases for lower discharges contained within the channel and also very considerably at higher, floodplain, flows (Archer, 1989). Through floodplain sectors, this attenuation is exacerbated by overbank storage and by losses through the channel bed into the alluvial aquifer. Thus, along a 220 km reach of the River Allier, France, losses to the alluvial aquifer during the 1968 flood reduced the flood volume by 13% (Dacharry, 1974).

2.3.3 SEDIMENT DELIVERY

The downstream transport of sediment is markedly influenced by storages operating over a range of temporal scales. Sediment yield to the oceans is but a small fraction of that eroded from hillslopes. That part of the gross erosion or sediment mobilization within a catchment represented by the sediment yield at the catchment outlet is defined by the sediment delivery ratio (Walling, 1983). Values of the delivery ratio below 10% are common and an example of a catchment sediment budget is shown in Figure 2.4(c).

Some of the eroded material will be deposited within the production zone, further down the slope or at the foot of the slope. Woody debris jams, macrophyte beds, the roots and overhanging branches of riparian vegetation are important retention features for leaf litter and sediment storage. Although instream deposits are periodically flushed from the system following decomposition of debris jams and/or by high floods, debris jams can retain a substantial proportion of the organic matter in channels. Typical residence times vary from a few years to a few hundred years (Gregory, 1992).

Depositional landforms represent particularly important storages: bars, fans, floodplains, terraces and deltas. There are many different sedimentary environments (Happ, 1971), some retaining large amounts of organic material, such as cutoff channels and backswamps. Some floodplain sediments together with their organic deposits can remain stable for tens of thousands of years. Throughout the temperate zone, for example, the long-term storage of thicknesses of sands, gravels, alluvium and organic material has resulted from valley aggradation during the period of Holocene sea-level rise (Gregory and Maizels, 1991).

2.4 BASIN HISTORY

Many rivers of the temperate zone have a history extending for millions of years, complicated by major climatic and tectonic changes. For example, the proto-Thames had established a concordant drainage

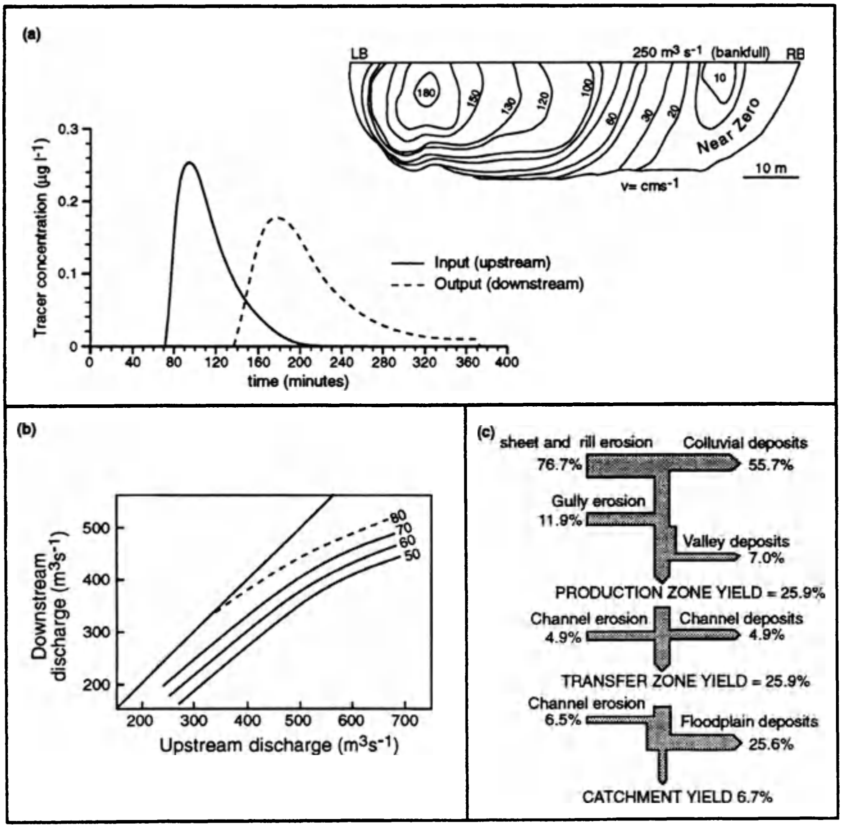

Figure 2.4 Examples of retention characteristics in fluvial systems. (a) The effect of dead zones on flow and transport processes is exemplified by Rhodamine WT tracer data for a 1 km pool-riffle reach of the River Severn, UK (after Bevan and Carling, 1992). The insert shows cross-sectional velocity variations close to bankfull discharge at a riffle within the reach. Note the region of slow flow with a high residence time near the right bank (RB). In (b) floodpeak attenuation along a 35 km reach of the River Tees, UK is shown by the relationship between upstream and downstream discharges (after Archer, 1989). The parameter used is the ratio of 12-hour mean flow to the peak flow. (c) shows the sediment budget for Coon Creek, Wisconsin for the period 1938–1975 (after Trimble, 1981). Note that within the transfer zone, a balance between erosion and deposition has been assumed.

pattern in response to mid-Tertiary orogenic movements by about 20 million years ago. Its present lower course was established during the early Pleistocene when it was diverted southwards by a complex sequence of ice advances and retreats.

Major efforts have been made to elucidate the response of fluvial systems to climatic change over the past 15 000 years (Gregory, 1983;

Gregory *et al.*, 1987; Starkel *et al.*, 1991). At the change from cold to warm climate at the beginning of the Holocene the general trend of middle river courses throughout the temperate zone has been from braided to meandering channel patterns. This change, manifested by a reduction in channel width and an increase in sinuosity, was caused by a decrease in flood frequency and sediment load following the establishment of the temperate forest. Many rivers today are flowing directly within coarse-grained gravels that have been inherited from deglaciation outwash and valley-fill deposits. However, these general trends mask a complexity of responses, both along and between rivers.

2.4.1 DRAINAGE MODIFICATION DURING THE PLEISTOCENE

Throughout much of the temperate zone, drainage patterns were modified by glaciation during the Pleistocene by:

1. Diversion of drainage lines, a characteristic of the former glacial zone, by which many rivers had their courses markedly altered by ice advances during the Pleistocene;
2. Intensification of the pre-existing drainage by valley erosion, sometimes forming flat-floored and steep-sided glacial troughs;
3. Deposition, especially by ice-sheets, which resulted in till sheets mantling large areas of low-lying landscapes upon which new stream networks have formed;
4. Glacio-isostasy, which describes the deformation of the earth's crust beneath the load of ice. Given the average densities of ice and rock a 1000 m thick ice sheet would depress the earth's crust by 267 m;
5. Glacio-eustasy, which describes the influence on sea-level of water periodically stored in, and discharged from, ice sheets.

Thus, differences between rivers and between sectors along rivers may reflect their situation during the Pleistocene. Four general situations can be defined:

1. Rivers draining young valleys formed after the retreat of the ice sheet and characterized by complex valley profiles including lakes and bedrock sections;
2. Rivers draining areas of former valley glaciers;
3. River valleys dominated by former glacial meltwaters, being characterized by rivers flowing in obviously much larger valleys (known as underfit streams) and often with extensive dry-valley networks, indicating a formerly more extensive drainage system;
4. Aggraded lower valleys where the bedrock valley floor relates to low sea level during the maximum glaciation.

2.4.2 CLIMATE CHANGE AND DRAINAGE-NETWORK RESPONSE

Changes of a fluvial hydrosystem can result from changes in upstream or downstream variables. Climatic changes influence fluvial hydrosystems by changing discharge and sediment yields in two ways: (1) by changing precipitation and solar energy inputs, and by the resulting vegetation changes; and (2) by changing baselevel. For example, one measure of drainage structure within river basins is the drainage density (D), the total channel length (L) divided by basin area (A):

$$D = L/A$$

Another measure of drainage character is stream frequency (F):

$$F = N/A$$

where N is the number of stream segments of all Strahler orders.

Studies of relationships between drainage density and stream frequency for mature basins (Melton, 1958) demonstrate a high coefficient of correlation. The derived function $F = 0.694D^2$ shows that as drainage density increases within a constant area, it does so by an accompanying increase in stream frequency.

Drainage networks develop on new land surfaces over time-scales of 10^4+ years. For a study of drainage development on tills of different age, Ruhe (1952) suggested that rapid initial network expansion was followed by stabilization after about 20 000 years. Experimental studies (Schumm, 1977) confirmed a third phase, first noted by Glock (1931), of drainage integration and channel loss. During the period of constant drainage density there is a progressive change of drainage pattern, characterized by the loss of low-order tributaries in the centre of the basin and the addition of first-order tributaries at the periphery. Thus, as the 'older' interior segments enter Glock's phase of integration and channel loss, network growth continues in those areas of steeper slope towards the margins of the basin. Sediment yield is high during the first phase of network expansion, but then declines rapidly over time (Figure 2.6c). In part, the decreasing sediment yield reflects the falling rate of network growth but it also relates to the progressive widening of the valleys and declining main valley slopes which increase opportunities for sediment storage within the drainage basin.

Climate exerts a strong influence on drainage density (e.g. Gardiner, 1987). Under constant climatic conditions, the drainage density adjusts to an equilibrium conditioned by channel head steam erosion and depositional infill by slope processes (Calver, 1978). The primary controls on drainage density are surface geology, relief, climate and vegetation (Table 2.1). The influence of vegetation on runoff and sediment yields (Figure

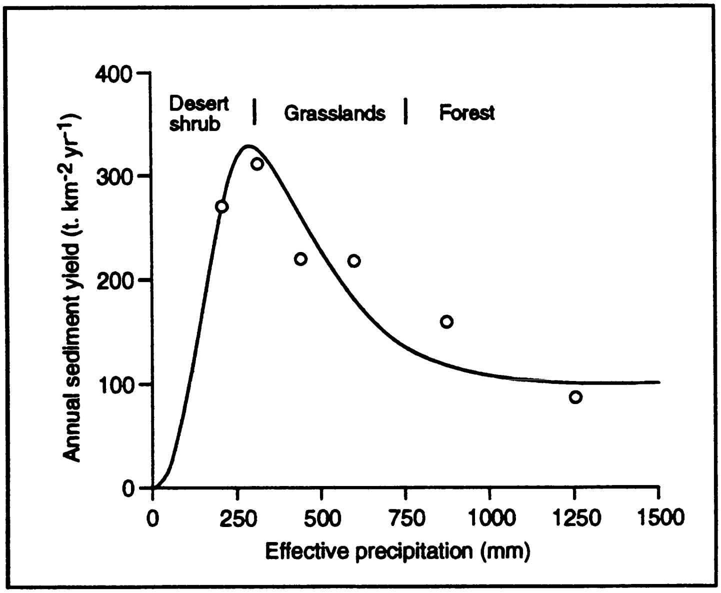

Figure 2.5 Variation of sediment yield with climate for 4000 km² basins in the United States (after Langbein and Schumm, 1958) illustrating the effect of vegetation on runoff and soil erosion. Effective precipitation is defined here as the annual precipitation required to produce the known runoff in a region having a mean annual temperature of 50 °C.

2.5) is particularly important. With high runoff rates, channel headward extension and bifurcation increase channel density; a small catchment area is required to sustain a stream, and drainage density is high. Thus, in semiarid environments where high-intensity storms combine with thin soils and poor vegetation cover to generate high runoff rates and high sediment yields, drainage densities can exceed 100 km^{-1}. In contrast, humid temperate environments with well-rounded slopes, dense vegetation cover and deep soils have low drainage densities, often less than 5 km^{-1}.

2.4.3 EPISODES OF CHANGE.

Changes of the external controls induce adjustments to new equilibrium states but because time lags occur in the system, drainage basin evolution can be characterized by episodes of high rates of geomorphic work, evidenced by high sediment yields. With climatic change, vegetation response is relatively slow and a short period of landscape instability may be triggered (Figure 2.6a). For example, with a change from arid to humid climates, drainage density, runoff rates and sediment yields are seen to increase rapidly to a maximum before declining to a relatively low level. Similar episodes of change occur following glaciation. Church and Ryder (1972) defined the term paraglacial to cover non-glacial processes that are directly conditioned by glaciation. This concept focuses on the instability of the exposed glacial sediments with respect to the fluvial environment which succeeds the glacier spatially and temporally. The sediment yield of postglacial rivers is far in excess of the 'normal' material supply to be expected in the non-glacial environment (Figure 2.6b). Following deglaciation, vegetation succession, changes in runoff and sediment exhaustion return the sediment yield to levels conditioned by concurrent rates of debris production by primary weathering.

Another important external change is baselevel lowering. Declining sea-level increases relief leading to an extension of the drainage network. Initially, there will be an episode of very high sediment yield (Figure 2.6c) as main channel incision moves progressively upstream from the basin mouth, scouring alluvium previously deposited in the valley. Tributaries will be rejuvenated successively as incision progresses upstream, and drainage density will increase. A new 'normal' sediment yield will be established reflecting the increased basin relief and extended drainage network.

2.4.4 COMPLEX RESPONSES

Field studies of alluvial chronologies in relation to regional climatic changes during the Holocene (Schumm, 1977; Starkel *et al.*, 1991) demonstrate that the number, magnitude, and duration of erosional and depositional events varied between valleys and along the same valley. Geomorphic histories are complicated: first, because changes of the external controls varied at the regional scale; secondly, because large basins comprise a hierarchy of process–response systems (subbasins and main channel sectors); and thirdly, because the morphological systems are also complex.

With regard to regional variations of the external controls, baselevel changes, for example, have varied markedly around the North Atlantic. Following the maximum of the last glaciation, eustatic rise was complete by about 5000 years BP but isostatic movements have continued and are still continuing in some areas. About 28 000 years BP, the channel of the River Thames in what is today the outer estuary, was about 50 m below present sea level. Clark *et al.*, (1978) predicted changes of sea-level relative to the 16 000 years BP shoreline which indicated a rise of sea-level by over 75 m along the Portuguese coast to a relative fall of 900 m around the Baltic, here reflecting the dominance of isostatic movements.

Within a single, large drainage basin a complex response is indicated

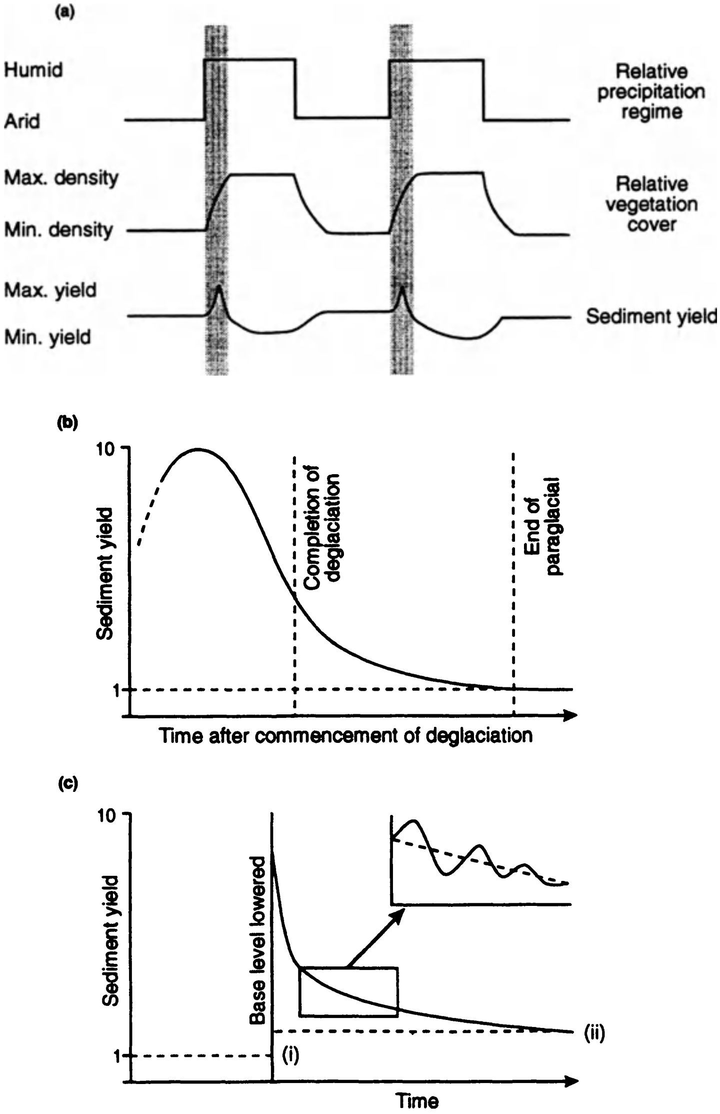

Figure 2.6 Episodic changes of fluvial systems. Episodes of high sediment yield may be associated with (a) a change of precipitation regime (after Knox, 1972), (b) glacier retreat (after Church and Ryder, 1972), and (c) base level lowering (from data in Schumm, 1977). In (b) and (c), sediment yield is expressed in relation to the geological 'norm'. In (c) the 'norm' (i) is seen to increase following baselevel lowering (ii) due to the resulting increase in basin relief. In all cases basin response will be complex (e.g. (c) insert) reflecting the adjustment of main channel sectors, tributary streams and hillslopes (see Figure 2.2c) and at any point in the river system sediment yields will vary about a general trend.

by studies of sediment-yield variations during drainage basin development following baselevel lowering (Figure 2.6c). Typically, the decrease in sediment yield over time is punctuated by secondary sediment pulses. The morphological interactions involved in such a complex sequence of sediment-yield variations are indicated in Figure 2.2c. Tributary erosion follows main channel incision, the main channel becomes a conveyor of upstream sediment in increasing quantities, and the inevitable result is deposition and formation of a braided stream. As tributaries adjust to the new baselevels, sediment loads decrease, and a new phase of main channel erosion occurs. The channel form changes to a single channel with low width/depth ratio reflecting the decreased sediment loads.

The speed with which morphological changes establish a new equilibrium or recover to the former equilibrium dimensions is known as the *relaxation time* (Figure 2.7a). A change of input may be a short-lived disturbance (e.g. a rare high-magnitude flood) or a sustained impact such as climate change or human interference (e.g. dam construction). Nevertheless, different components of the system respond at different rates (Figure 2.7b). An increase in runoff, for example, will lead relatively quickly to a change of the cross-sectional width and depth of alluvial channels, but the increase of drainage density, requiring the development of new fingertip channels, will occur more slowly. Thus, different landforms have different *sensitivities* to change (Brunsden and Thornes, 1979).

The *recovery* of morphologic equilibrium will also vary (Figure 2.7c). Systems with low sensitivity have long relaxation times and slow recovery, such that they reflect the characteristics of relatively frequent disturbance and demonstrate progressive change (Figure 2.7cc). Those with high recovery rates tend to exhibit considerable temporal adjustment to the general magnitude of frequent processes (Figure 2.7ca). However, even within these systems, at any given point in time each part of the landscape may exhibit varying degrees of adjustment to present processes.

To understand the evolutionary behaviour of river channels Schumm (1973, 1977, 1979) introduced the concepts of 'complex response' and 'geomorphic thresholds'. 'Complex response' explains many of the peculiarities of river channel evolution and recent alluvial and terrace sequences, by recognizing that a single event can trigger a complex reaction as the components of the basin morphologic system respond to change. Part of this complexity relates to a change of an external variable (climate, baselevel, isostatic response to denudation, vegetation cover); an external threshold is crossed causing changes within the affected system. However, part also relates to internal adjustments between the components of the drainage basin system. Thresholds can also be exceeded when the external variables remain constant; progressive change of the system itself renders it unstable. For example, progressive channel aggradation causes an increase of channel slope; deposition

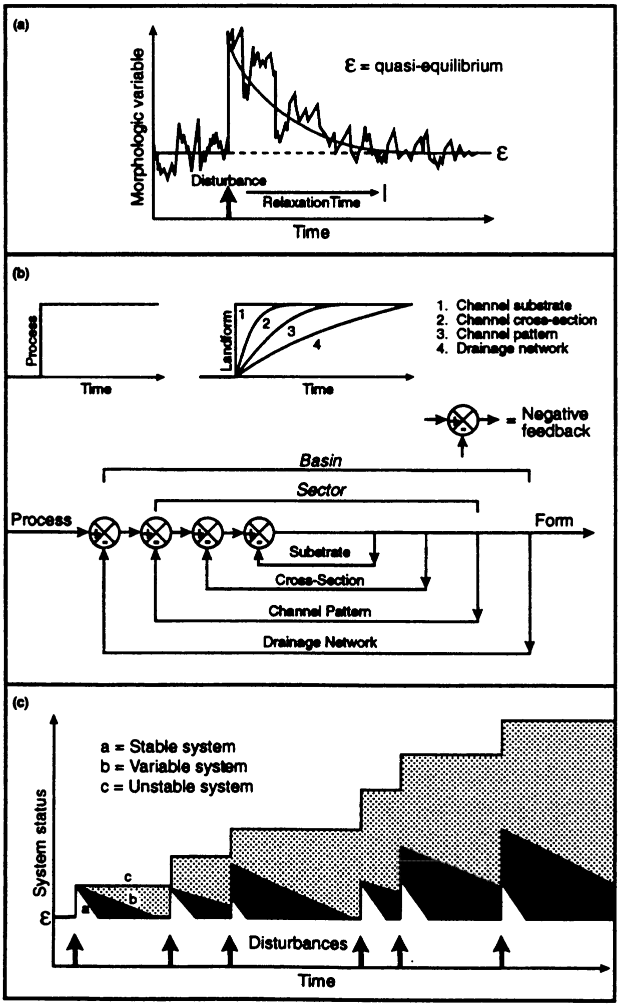

Figure 2.7 Channel response to disturbance (after Petts, 1994). (a) A morphologic variable in quasi-equilibrium is seen to vary about some long-term average condition; when disturbed the system recovers by negative feedback processes. During the relaxation period a complex sequence of *transient states* may be defined by different combinations of morphologic variables. In part the complexity of response relates to the sequence of changes of discharge and sediment load induced by the disturbance (see Figure 2.6b) but it also relates to the different rates of change of the morphological variables (b). At any point in time a channel sector can include a set of differentially adjusted landforms reflecting their different sensitivities to process changes and the nested negative feedback loops which effect mutual adjustments within the morphologic system. In (c) a series of disturbances is seen to have different effects on channels, depending on the effectiveness of *recovery processes*: contrasting systems can have (a) highly effective, (b) intermediate or (c) weak recovery processes.

– sediment storage – continues until a threshold slope is reached at which point a phase of channel incision and sediment removal is initiated. The nature of such geomorphic thresholds, determined by the control of slope on sediment transport processes, can be particularly important in explaining the different histories of valley sectors.

2.5 BIOLOGICAL RESPONSES

For biota, rivers and streams are hazardous environments characterized by stresses (the velocity or shear stress of the flowing water) and disturbances: erosion, abrasion, siltation and burial, and desiccation as well as extremes of water quality (temperature, dissolved oxygen, pH, toxic metals). Early biological research on rivers attempted to define zones on the basis of site-specific, or biotope-specific, characteristics and related these to the longitudinal succession of fish species, benthic invertebrate taxa and algae (see Hawkes, 1975 for a review). The stream classifications (see Table 8.1) used various physical parameters such as the types of stream bed, channel slope, valley cross-sectional form, and annual temperature profiles. However, rivers were viewed merely as canals isolated from drainage basin processes.

Hynes' (1970) pioneering approach to running-water ecology led to the rapid development of interactions between biologists, hydrologists and geomorphologists. Subsequently, the 'catchment ecosystem approach' (Bormann and Likens, 1979) has become accepted for a variety of studies. Thus, Lotspeich (1980, p. 585) concluded:

> The problem of classifying natural areas, especially aquatic systems, would be greatly simplified if the watershed (=drainage basin) were the base for classifying, since it is the watershed, functioning in response to external forces, that controls aquatic systems.

Biological communities became viewed as deterministic systems having evolved toward the most probable conditions of channel morphology and flow, and the drainage basin became the basic unit in lotic (running water) ecology (Cummins, 1992).

2.5.1 HYDRAULIC STRESS

The structure and function of most aquatic communities, and many river-margin ones, is related to hydraulic conditions (Gore 1994): to flow patterns at scales ranging from the whole river to the individual bedform (Chapters 5, 6, 7 and 8). Variations of hydraulic variables at a point or averaged for a cross-section are particularly important in studies of fluvial hydrosystems and can usefully be described in relation to changes

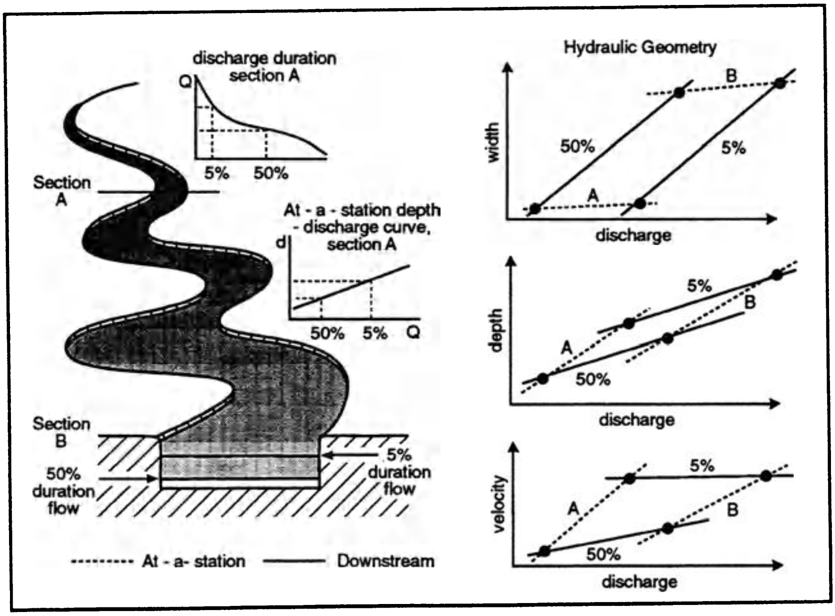

Figure 2.8 The hydraulic geometry approach to describing at-a-station and downstream changes of width, depth and velocity in relation to discharge (after Leopold and Maddock, 1953). At-a-station relationships describe the variation of hydraulic parameters over the range of discharges experienced at a site. Downstream relationships can be derived from measurements of the hydraulic parameters for a standard discharge at each site, which may be defined by a frequency or duration statistic. Here, following Richards (1982), the 5% and 50% duration flows are shown. The top insert shows the form of the *flow duration curve* where discharge (*y* axis) is related to the percentage of time that each specified discharge is equalled or exceeded (*x* axis).

of discharge (Figure 2.8) – the 'hydraulic geometry' approach (Leopold and Maddock, 1953). This approach may also be used to describe the variation of hydraulic variables along a river (the downstream hydraulic geometry) in relation to a standard flow, such as the median (50th percentile), the bankfull, or some intermediate, reference flow (such as the 5th percentile flow).

At a local scale (0.1–100 m^2) hydraulic conditions, especially flow velocity, are seen as having the dominant influence on the pattern of species distributions within a site or sector. This has been stressed especially for benthic macroinvertebrates (Statzner and Higler, 1986; Statzner *et al.*, 1988) but it is also implicit in studies of habitat suitability for fish (Stalnaker *et al.*, 1989). Velocity is particularly important because it influences metabolism and a large variety of behavioural characteristics in animals living in running waters.

2.5.2 DISTURBANCES

Those concerned with riparian zones and floodplains also recognize the role of hydraulics in determining the patchy distributions of species, even though the patch dimensions are larger than the aquatic ones, typically varying from 10 to 1000 m^2 (Naiman and Décamps, 1990; Petts, 1990). Physical disturbance plays a key role in structuring these systems. For example, rivers maintain vegetation typical of early succession due to periodic scouring and disturbance influences competition by creating gaps for exploitation by less competitive species. However, in order to understand the long-term influence of such disturbances, the nature of recovery mechanisms (or negative feedback processes) must also be considered.

Pickett and White (1985) define disturbances as any relatively discrete event in time that disrupts ecosystem, community, or population structure and that changes resources, availability of substratum, or the physical environment. The roles of disturbance in stream ecology have been discussed by Resh *et al.*, (1988) and specifically with regard to land-water ecotones, by Naiman and Décamps (1990). However, a disturbance, such as a flood, can not be defined solely in terms of the event magnitude and frequency. The severity of impact will also relate (a) to the timing of the disturbance in relation to stability thresholds, physical and biological, and (b) to the effectiveness of recovery processes (Milner, 1994).

Two groups of disturbances should be distinguished: relatively frequent and low magnitude events that are part of the 'normal' regime and more or less predictable; and relatively rare disturbances that are outside the predictable range. In reality, these two groups are the end members of a continuum because the frequency of low magnitude disturbances influences the rate of system recovery to unpredictable disturbance by extreme events (Figure 2.7c).

Over medium timescales (10–100 years) most river systems may be viewed as quasi-equilibrium states. The long-term effectiveness of an event in disturbing this quasi-equilibrium condition varies widely, depending on the system component under consideration (such as benthic invertebrates or channel morphology) and the effectiveness of the recovery processes (Figure 2.7c). For example, the insect species of semiarid streams recover quickly to catastrophic wash-out by floods because they have short life cycles and continuous emergence, ensuring rapid recolonization by adults from adjacent riparian areas (Fisher *et al.*, 1982). In contrast, the morphology of these streams may experience progressive change because of the weak physical recovery processes to flood-induced erosion (Wolman and Gerson, 1978). Most river ecosystems are characterized by strong recovery processes and this is important when considering river management (Chapter 12).

2.6 THE FLUVIAL HYDROSYSTEM APPROACH

Chorley *et al.*, (1984, p. 7) describe 'The palimpsest view of the landform system . . . composed of a nested hierarchy of subsystems each having different levels of sensitivity and recovery, the whole being subject to a temporal stream of input (i.e. process) changes'. This view may be extended to consider the fluvial hydrosystem and is complicated further by biological processes, especially succession. Whereas functional explanations of fluvial hydrosystems can be developed for short time-scales, short-term functional relationships must be seen as superimposed on the longer-term character of the dynamic drainage basin system.

Inter-adjustments of the different structural units within a fluvial hydrosystem involve directional changes, thresholds, feedback effects and time-lags. Within the drainage basin, different landforms evolve in different ways and at different rates and the basin may be viewed as a patchwork of morphological units each bearing the imprint of processes of different antiquity. Time lags within the fluvial system operate at two levels: lags in the upstream and downstream transmission of perturbations, and lags between changes of physical habitat and biological responses. As illustrated in Figure 2.2(c), such responses are made complex by interactive adjustments between adjacent sectors along the main river and between the main river and its tributaries.

Superimposed on the overall downstream gradient of ecological conditions, the fluvial hydrosystem approach recognizes discrete reaches (channel sectors), differentiated by discontinuities, within which a quasi-equilibrium condition may be defined and functional relationships established over time-scales of 10–100 years. The discontinuities between sectors reflect the heterogeneous character of large basins:

1. The complex geologies, spatially variable climates and different vegetation zones which cause different headwater basins to produce different discharges, water qualities and sediment loads;
2. The complex geologic history of large basins which produces sectors with different valley dimensions and alluvial fills that vary in thickness and sedimentology; and
3. The variable rates of change of the different components of the morphologic system and of biological succession.

Thus, fluvial hydrosystems reflect the interaction of hydrological, geomorphological and biological processes. They are characterized by a patchwork of aquatic and semiaquatic habitats, the arrangement of which continually changes as a result of disturbance (Chapter 5) and succession (Chapter 10). In summary, the fluvial hydrosystem approach views the ecological characteristics of any site on a river (a) as part of the larger drainage basin system, modified by (b) the historical legacy of environmental change that may have affected the whole catchment or have been specific to each sector, and (c) as determined not only by longitudinal fluxes but also by lateral and vertical exchanges between the channel and its floodplains and alluvial aquifer, respectively (Chapter 9).

Hydrological and hydrochemical dynamics

3

R. Wilby and J. Gibert

3.1 INTRODUCTION

The terms *hydrological and hydrochemical dynamics* imply the motion of water and associated solutes under the influence of external forces and mass exchanges. They are also suggestive of process operations and of energy exchange within a defined systems framework. This chapter examines such concepts from two distinct but complementary perspectives. The first section examines in greater detail the fundamental dependency of upland water quality on dynamic hydrological pathways, chemical budgets and catchment characteristics. Here emphasis is placed on micro- to mesoscale processes, and on the role of heterogeneity within basins. The second section considers the aggregate effect of multiple headwater systems routed and mixed via the channel network and the significance of channel-floodplain interactions. This will underline the importance of considering macroscale controls versus anthropogenic impacts from both a spatial and temporal perspective. Throughout the discussion a twofold division into headwater streams and large rivers provides a useful vehicle for examining the significance of scale and connectivity.

3.2 HEADWATER STREAMS

3.2.1 HYDROLOGICAL DYNAMICS

Analyses of data sets incorporating rainfall, streamflow and catchment characteristics have led to the formulation of simple hydrological models.

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The 'Rational Method' was an early technique (attributed to Mulvaney in 1850) used to predict river discharge from rainfall. This fundamental equation relates the peak discharge (Qp) at the catchment outlet, to a coefficient (c) representing the proportion of rainfall becoming runoff, the catchment area (A), and the mean intensity (i) of the rainfall during the time taken for water to move from the most distant part of the basin to the outlet:

$$Qp = cAi$$

More recently, the NERC Flood Studies (1975) and Low Flow Reports (1980) subsequently applied regional analyses of flow data and catchment properties to develop regression equations of flow from mapped variables. An important achievement of such regionalization techniques has been to facilitate flow estimation for ungauged catchments (Pirt, 1983).

For example:

$$MAM_{10} = 11.2BFI + 0.0982SAAR - 6.81$$

where MAM_{10} is minimum daily mean flow in a 10-year period, BFI is the baseflow index related to geology and $SAAR$ is annual average rainfall (mm).

$$AMAF = aA^{0.94}STMFRQ^{0.27}\ S1085^{0.16}RSMD^{1.03}\ SOIL^{1.23}(1+LAKE)^{-0.85}$$

where a is a constant that varies from 0.0172 for Ireland to 0.053 for East Anglia, A is the catchment area (km^2), $STMFRQ$ is the number of stream junctions per km^2, $S1085$ is the slope from 10 to 85% of the mainstream length (m km^{-1}), $RSMD$ is the five-year return period one-day rainfall minus the 'effective' soil moisture deficit (c.30 mm for lowland central UK) and $LAKE$ is the proportion of the catchment area draining through lakes or reservoirs.

Although such analyses of regional data sets can yield valuable flow statistics (such as flood frequencies or minimum flows) the approach is limited in its ability to describe the finer details of the hydrograph and does not readily accommodate *dynamic* rainfall and/or catchment conditions. Thus, conceptual models have been developed to utilize simplified representations of the interconnected stores and flows involved. Two of the earliest conceptual models were the Stanford Watershed Model (Crawford and Linsley, 1966) and the General Catchment Model (Douglas, 1974).

Walling (1980) has provided a useful representation of the key hydrological and chemical processes operating in a pristine catchment ecosystem. As Figure 3.1 suggests, the input–output of the individual conceptual stores is driven by water which 'cascades' through the system under the influence of gravity to emerge from the catchment outlet as streamflow. Precipitation is first intercepted by the vegetation canopy, and a certain

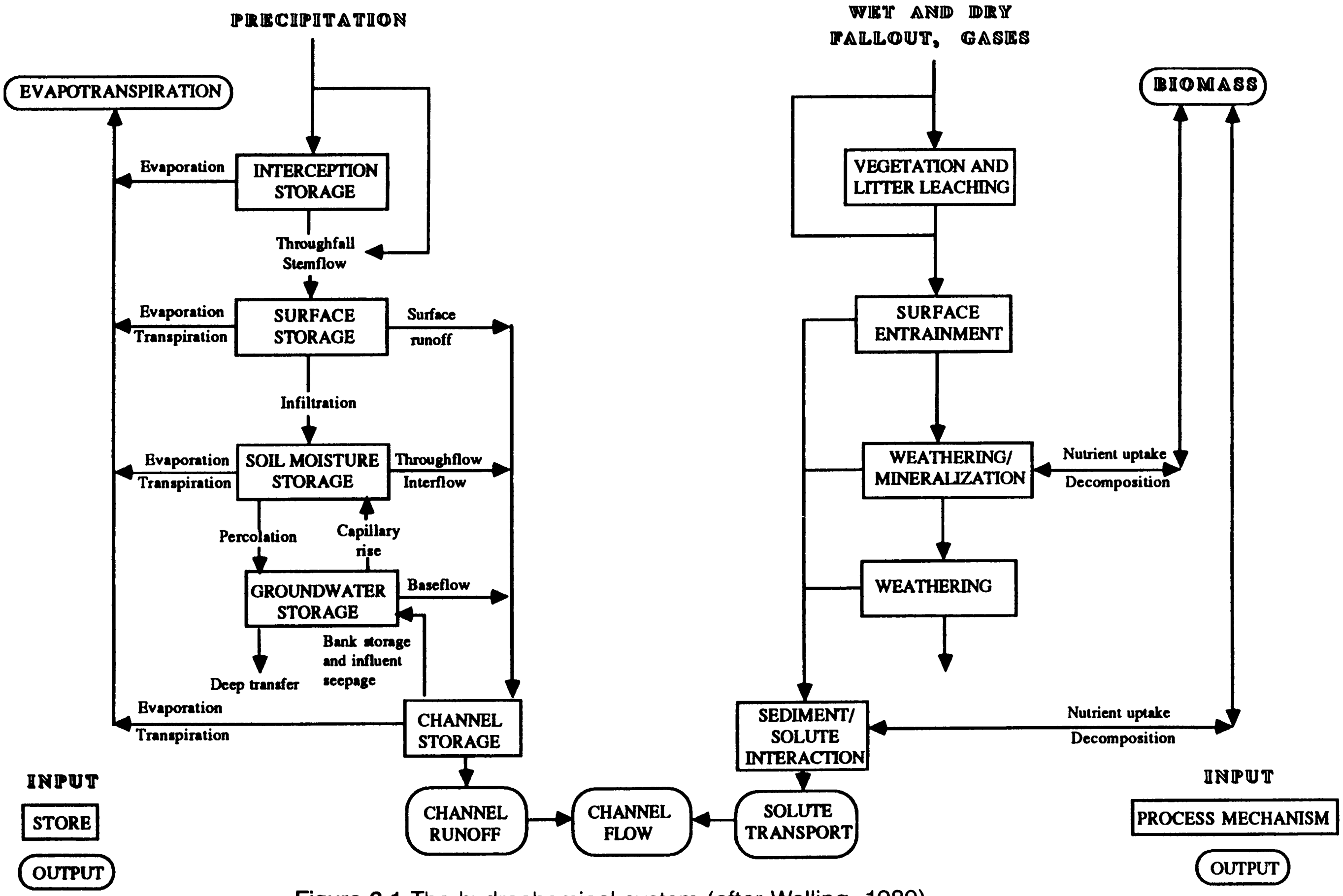


Figure 3.1 The hydrochemical system (after Walling, 1980).

volume is lost via evaporation. This amount is a function of the vegetation type, meteorological factors (such as wind speed, precipitation type, intensity and frequency of storms) and season. Regional variations in the magnitude of interception losses correspond to the dominant characteristics of the canopy store and the proportion of the time that it remains saturated (Gash *et al.*, 1980). For example, Calder and Newson (1979) found that the interception loss from a forest canopy in Wales receiving 2000 mm yr^{-1} was 43%, whereas the loss from grassland was 22%. Rowe (1983) found seasonal differences of interception loss were also significant with 22% in winter and 35% in summer, reflecting changes in the canopy storage capacity and variable evaporation rates from a wet canopy.

The throughfall or stemflow component may be subjected to further interception losses of up to 0.1 mm day^{-1} due to a leaf litter store (Calder *et al.*, 1986). According to the nature of the ground surface a proportion of the residual throughfall will generate surface runoff; the remainder infiltrates the soil and is lost via evaporation. In urbanized catchments or over frozen soil the amount of incident precipitation that becomes surface runoff may approach 100% due to the impervious nature of the ground surface. However, experimental studies have demonstrated that surface runoff may be produced over only a small percentage of a rural catchment area, and that this arises due to a saturation excess as opposed infiltration excess mechanism (Beven *et al.*, 1988). In the former case, areas immediately adjacent to the stream channel, lower value slopes and hillslope hollows become saturated as the water table rises to the ground surface (Figure 3.2). As rainfall continues the water table rises and intersects the ground surface further upslope whilst the contributing area adjacent to the channel simultaneously expands laterally. Subsequent rainfall (P) is then unable to infiltrate the soil and the saturated area acts as a source of quickflow (S) as well as throughflow (T). Throughout, a small fraction of the total rainfall enters the channel directly (Q) and the groundwater component (G) is proportional to the height of the water table.

The infiltration excess mechanism occurs when the rainfall intensity exceeds the rate at which the soil can absorb it, resulting in overland flow. In vegetated temperate areas these conditions seldom occur despite the fact that the infiltration capacity of a soil decreases rapidly during a storm, and may be reduced in the longer term by soil compaction during cultivation. Furthermore, oxygen-18 isotope studies have challenged the traditional concept of surface-runoff by revealing the 'old' or stored soil water can contribute 40–95% of the observed stormflow in forested watersheds possessing high infiltration capacities (Dewalle *et al.*, 1988). Under these circumstances, the hydrograph will be dominated by subsurface stormflows, generated by rapid throughflows, which are in turn

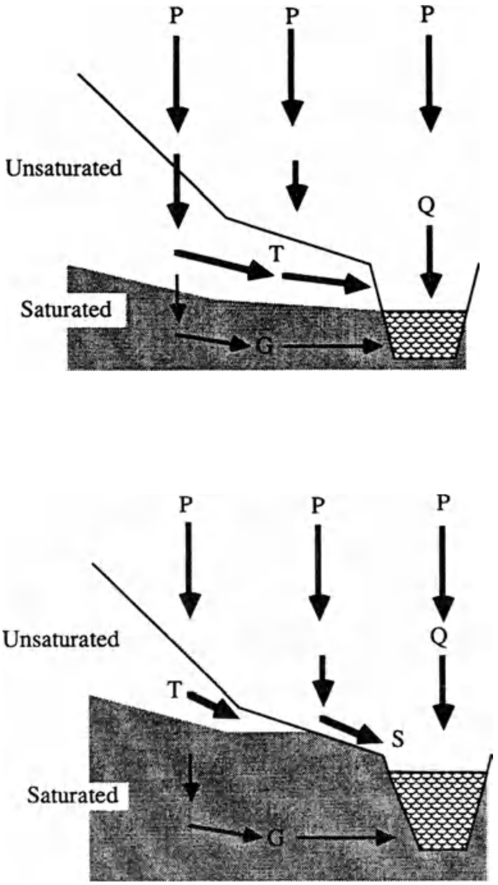


Figure 3.2 The saturation excess mechanism.

governed by catchment morphology, soil depth and hydraulic characteristics.

The infiltration of water into unsaturated soil horizons is therefore characterized by marked complexity and heterogeneity at the hillslope scale. Surface litter and vegetation may effect input intensities or restrict water penetration at the soil surface. According to the land-use and soil structure, variable quantities of water can by-pass the bulk soil matrix via preferential flow pathways associated with soil macropores, drains or localized zones of higher hydraulic conductivity. Once within the soil, moisture is redistributed according to the heterogeneous patterns of infiltration and under the influence of the plant root-zone requirement of water for evapotranspiration (Beven *et al.*, 1988). In terms of the transport of solutes within the soil matrix it is essential to recognize that the myriad flow pathways will afford wide-ranging contact times for soil-water interactions (Bache, 1984). For example, Dunne (1978) found that rates of surface runoff were two orders of magnitude greater than subsurface throughflow for areas in excess of 0.02 km^2. Elsewhere, ephemeral soil pipe networks have been shown to contribute up to 50% of stormflow 'very rapidly' at the start of the flood hydrograph (Welsh Water Authority, 1987). Flow of water in the unsaturated zone is therefore a highly complex phenomenon. It involves transfers of not only water and solutes but also gases through dynamic pathways under the influence of hydraulic, temperature, density and osmotic gradients within the soil which acts as a compressible, porous media (Beven, 1988).

In alpine environments rapid snow melt may represent a key source of surface runoff or flood water, particularly where permafrost inhibits infiltration. Under isothermal conditions at 0°C the snowpack may be viewed as an open system consisting of a series of energy inputs and outputs (Dunne *et al.*, 1976):

$$Q_m = Q_s(1-a) + Q_{lw} + Q_h + Q_e + Q_p$$

where Q_s is the incoming solar radiation, $(1-a)$ is the albedo of the snowpack (a measure of its reflectivity), Q_{lw} is the incoming long-wave radiation, Q_h is the sensible heat exchanged by turbulent transfers, Q_e is the latent heat of vaporization, Q_p is the energy advected to the snowpack from rainfall, and Q_m is the energy required to melt snow. Q_s is influenced by the gradient and orientation of the hillslope in addition to vegetation cover which may reduce the penetration of solar radiation. $(1-a)$ is largely controlled by the age of the snowpack and the local rates of atmospheric deposition. Q_{lw} is a function of the temperature of the surrounding vegetation, hillslope and air, whereas Q_h depends on the level of exposure and surface roughness of the snowpack. Q_e refers to the energy released by moist air condensing on the surface of snowpack (590 calories g^{-1} of condensate, or the equivalent of 7.5 g potential runoff). Although the energy supplied by Q_p is not negligible for large, warm rainstorms, the water contributed directly from the rainfall far exceeds the amount of meltwater generated by any energy exchange.

Problems associated with predicting streamflow hydrographs from snow-covered catchments include: (a) estimating the water equivalent of a snowfall or sequential falls particularly under high wind velocities; (b) calculating the amount of meltwater generated by changes to the equilibrium of the energy balance equation; (c) the effects of microclimates which may not necessarily be in phase: (d) variable travel times for percolating meltwater with changing snowpack volumes; and (e) infiltration losses to the underlying (partially) frozen soil surface. Indeed, Morris (1991) has suggested that the inherent problem of energy feedback mechanisms between meteorological inputs and snowpack processes can only be adequately modelled via a physics-based approach.

The movement of water in response to transpiration by vegetation is also recognized as a highly complex process given that it is influenced by site-specific meteorological conditions, vegetation age, species, soil structure and soil moisture status. Nonetheless, Roberts (1983) has shown that for European forests these factors tend to equalize annual losses to around 300 mm, such that transpiration may be regarded as a conservative hydrological process. Furthermore, annual totals were found to be far below the potential rate due to the buffering effect of forest understoreys, feedback response mechanisms between insolation and humidity deficits, stomatal behaviour and temperature losses and the fact that variations in soil water content, except under severe drought conditions, have a negligible effect on transpiration rates.

In addition to evapotranspiration and downslope movements via throughflow, a fraction of the moisture held within the soil is subject to downward percolation to the water table. The main components of groundwater recharge have been defined by Ward and Robinson (1990) as: infiltration of part of the total precipitation at the ground surface; influent seepage through the banks and beds of surface water bodies; groundwater leakage and inflow from adjacent aquifers; and finally, artificial recharge from irrigation, reservoirs, spreading operations, mains leakage and injection wells. Conversely, the main components of groundwater discharge are: evapotranspiration from areas where the water table is close to the ground surface; natural losses through springflow and seepage; groundwater leakage into adjacent aquifers; and artificial abstraction. Groundwater recharge and discharge interact by varying the elevation of the water table, which in turn dictates the magnitude of both short-term and seasonal fluctuations in base-flow.

Compared with surface runoff, groundwater movements are relatively slow and highly variable. Darcy's Law approximates the mean velocity (v) for saturated groundwater flow as a function of the hydraulic conductivity of a porous media (k) and the gradient of total potential ($\Delta\phi$) in the direction of high to low head (or the mean gradient of the water table surface):

$$v = -k\Delta\phi$$

The hydraulic conductivity describes the ability of a rock to transmit water of a given temperature, and typical values are: 0.0002 m day^{-1} for clay; 2 m day^{-1} for medium sand; and 270 m day^{-1} for medium gravel (Petts and Foster, 1985). However, tracer experiments have revealed that the macroscopic velocities predicted by Darcy's equation underestimate true velocities in fractured, faulted or jointed rocks. The effects of lithology and geological structure are particularly apparent at times of low

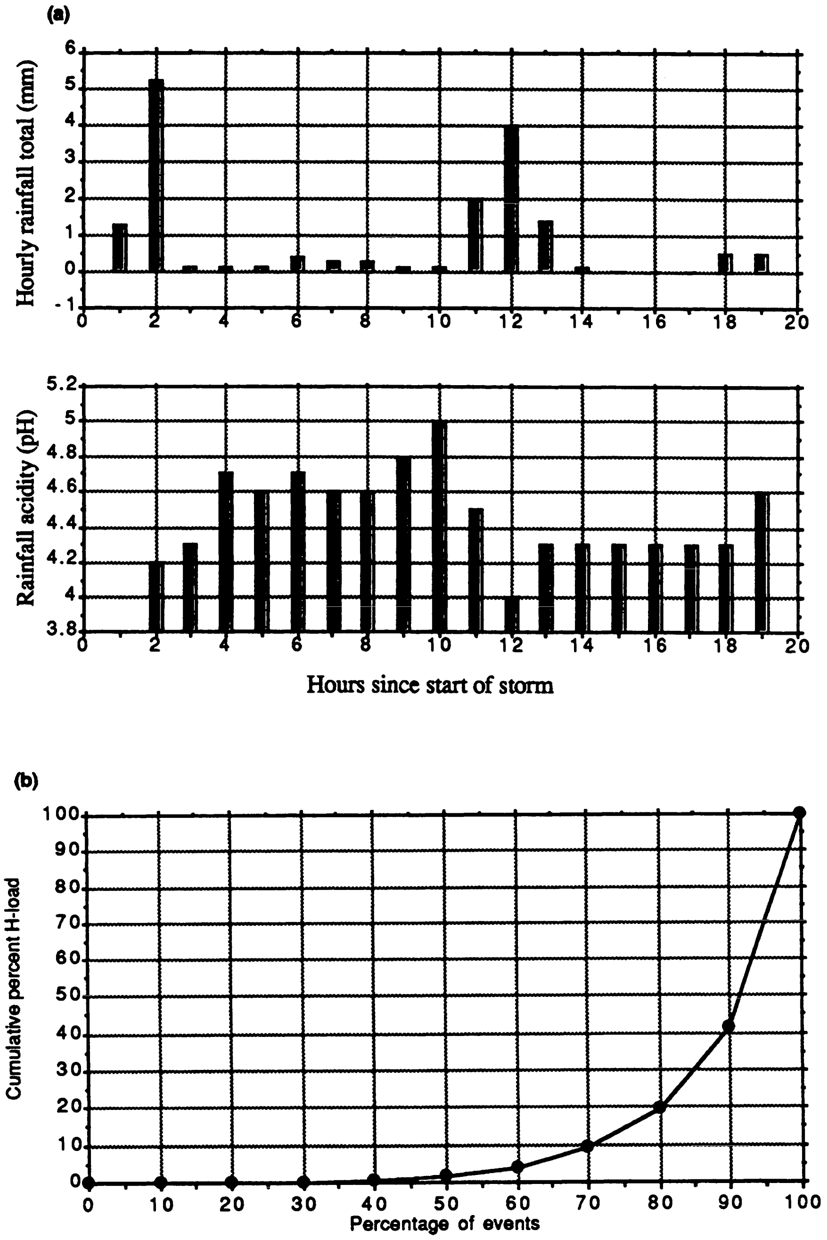


Figure 3.3 (a) An example of within storm variations of acidity, Loughborough; the rainfall event of 3 July 1988. (b) The cumulative percentage H-ion load against the proportion of precipitating events at Loughborough (March 1988–June 1989).

flow when the entire discharge of a stream may be sustained by releases from groundwater storage. According to Wright's (1970) arbitrary geological index, chalk (with its system of relatively fine fractures and high porosity) tends to sustain the highest base-flows.

3.2.2 HYDROCHEMICAL DYNAMICS

The use of rating relationships between solute concentrations and discharge provides a fundamental approach to examining water-quality variations. The rating equation is typically expressed in the form:

$$C = aQ^b$$

where C is the concentration of a given parameter, Q is the discharge, a is the regression constant and b is the regression exponent. The method assumes a linear relationship (given a log transformation) that is time invariant, i.e. identical flows will yield the same concentrations at a point. In practice, the simple dilution of constituents by increased flow is often distorted by flushing at the onset of a storm hydrograph (when sources of rapid runoff generate increased channel flow) leading to hysteretic effects (Figure 3.4b). Furthermore, the export of assimilated organics may be reliant upon secondary flow-related processes such as sediment transport. Seasonal or secular changes to the biological uptake of nutrients such as phosphate or nitrate, and periodic soil disturbances (such as ploughing and ditching) will further distort simple linear relationships to flow. Rating relationships are also chemically specific, reflecting the variable sources of runoff and the solubility of the dissolved material. For example, Edwards (1973) found that, in Norfolk, UK rivers, nitrate had a highly significant positive correlation with discharge due to its high solubility and the leaching of nitrogenous fertilizers from upper soil horizons by storm runoff. By contrast magnesium, bicarbonate and calcium were usually diluted, whereas the pattern for silicon was obscured by biological uptake.

As water moves from and between the stores shown in Figure 3.1, its quality will be modified by contact made with both the abiotic and biotic components of the catchment hydrosystem. Whereas the dynamic processes involving water transfer tend to govern the complex pattern of water quality variation in time, spatial variations in water chemistry arise from the heterogeneity of broad land-use, soil, geological and climatic variables. Nowhere are these observations more relevant than within the context of catchment acidification which involves both the atmospheric and terrestrial phases of water quality. Due to the wealth of experimental data and international nature of the problem, surface water acidification provides a unique opportunity for exemplifying the hydrochemical dynamics of headwater streams. The following examples will

Table 3.1 The Beacon catchment, Charnwood Forest, Leicestershire; UK: basic hydrometric and hydrochemical information (based on DOE, 1991 and Wilby, 1991)

Hydrometeorology		**Land use** (% area)	
Catchment area (ha)	66.2	Bracken heathland	39
Maximum altitude (m)	248	Deciduous woodland	28
Mean annual precipitation (mm)	693	Open grassland	23
Maximum annual precipitation (mm)	963	Coniferous plantation	6
Minimum annual precipitation (mm)	503	Other	4
Mean annual runoff (mm)	124		
% days with zero flow	24		

Mean annual water chemistry

	Bulk deposition	Runoff	Multiplier
Aluminium (mg l^{-1})	—	1.7	—
Alkalinity (meq l^{-1})	0.03	0.13	4.3
Conductivity (μS cm^{-1})	65.8	276.3	4.2
Hydrogen (μeq l^{-1})	60.9	19.5	0.3
Sulphate (mg l^{-1})	7.8	50.1	6.4
Chloride (mg l^{-1})	6.1	40.9	6.7
Ammonia (mg l^{-1})	1.2	0.03	0.025
Nitrite (μg l^{-1})	10.6	2.0	0.2
Nitrate (mg l^{-1})	3.7	10.3	2.8
Calcium (mg l^{-1})	1.4	9.4	6.7
Magnesium (mg l^{-1})	0.4	8.2	20.5
Sodium (mg l^{-1})	3.4	20.2	5.9
Potassium (mg l^{-1})	0.9	3.0	3.3

Geology

Pre-Cambrian outcrops of the Charnian system consisting of Archaen granites, pyroclastics, quartzites and syenites.

Soils

Hill top 'tors' which are largely devoid of soil; upper hillsides consisting of brown rankers and acid brown soils of low base status; lower hillsides which are mainly leached brown soils of higher base status and gleying.

illustrate the significance of variable precipitation chemistries, the modifying effect of biotic processes, scales of analysis, and hydrological pathways on hydrochemical dynamics.

Acidic deposition, conifer afforestation and land management practices have all been implicated in the elevated aluminium and hydrogen-ion concentrations of upland streams in Scandinavia, Europe, North America and the Tropics (UKAWRG, 1989; Drablos and Tollan, 1980; Rodhe and Herrera, 1988; Schindler *et al.*, 1989; Reuss *et al.*, 1987; Hornung, 1988). However, the extent of the acidification depends on the complex interplay between acid loads, the structure and chemical composition of receiving soils, rates of weathering, soil thickness, geological substrata, vegetation type and dominant hydrological pathways (Mason, 1985). Detailed scientific studies have figured extensively in the elucidation and quantification of the responsible processes to the extent that entire basins have been artificially acidified and/or manipulated (e.g. Wright *et al.*, 1986). Against this background the Beacon Hill, East Midlands, UK study was initiated in 1984 to examine the chemical input–output budget of a catchment that has been subjected to significant levels of atmospheric deposition past and present, yet also possesses the characteristic combination of geology, pedology, topography and vegetation of more remote upland sites in Britain (DOE, 1991; Wilby, 1991). A summary of the catchment characteristics is presented in Table 3.1

In the following discussion two measures of acidity are used. The pH is the negative base-10 logarithm of the hydrogen-ion *concentration* expressed in moles per litre. A decrease in the pH therefore indicates an increase in the acidity of the water sample. The solute or acid load is the product of a given chemical ion concentration with the water volume, yielding a measure of the total ionic *mass*.

Although the main volume-weighted precipitation acidity for the Beacon Hill was pH 4.1 in 1988/89, considerable variation was observed within and between individual events. For example, Figure 3.3(a) shows the changing rainfall acidity for a single storm on 3 July 1988 which demonstrates the effect of variable scavenging rates of atmospheric pollution on precipitation chemistry. This arises from microscale changes in the rainfall intensity, the evaporation of raindrops at the beginning and end of the storm, ventilation effects and, the depletion of available aerosols from the atmospheric boundary layer during the event. By contrast, differences between storms (Table 3.2) and the episodic nature of total wet-deposited acid load have been attributed to macroscale meteorological processes and synoptic weather patterns (Fowler and Cape, 1984: Farmer *et al.*, 1989). As indicated in Figure 3.3.(b) 90% of the total wet-deposited acid load between 1988 and 1989 occurred on just 30% of the rain days, with one event alone accounting for 15% of the period total. For time periods of a month or more, 64% of the total acid load was determined by the relative prevalence of four dominant weather types, namely: the westerly, cyclonic, northerly and anticyclonic classes (Table 3.2). As each synoptic group possesses characteristic precipitation probabilities, event magnitudes and acidities (Figure 3.3c) secular changes to atmospheric circulation will have major consequences for the spatial and temporal patterns of acidic deposition (Davies *et al.*, 1986; Wilby, 1989).

In addition to temporal patterns of precipitation chemistry, significant spatial variations arise due to dry-, mist-, and occult-deposition fields which are known to be sensitive to the nature of the underlying surface (Dasch, 1983). For vegetated surfaces the rate of SO_2 interception depends

Table 3.2 Daily weather type characteristics observed between March 1988 and June 1989 (Wilby, 1991)

Weather pattern	Frequency (days)	% Rain	24 h rain (mm)	pH	H-load (μg m^{-2})	Conductivity (μS cm^{-1})	Temperature (°C)	Fetch (km day^{-1})
Westerly	67	52.2	2.6	5.07	107	69	10.3	393
Anticyclonic	111	10.8	2.9	4.31	380	114	10.0	185
Cyclonic	76	67.1	4.4	4.78	358	73	10.9	307
Northerly	19	52.6	4.2	3.52	1864	152	7.2	196
Northwesterly	6	50.0	1.6	4.67	259	96	9.3	361
Southerly	23	43.5	3.6	4.87	142	63	11.4	262
Easterly	19	63.2	4.8	4.72	453	109	8.4	233
All types	476	43.9	3.8	4.74	357	82	10.3	295

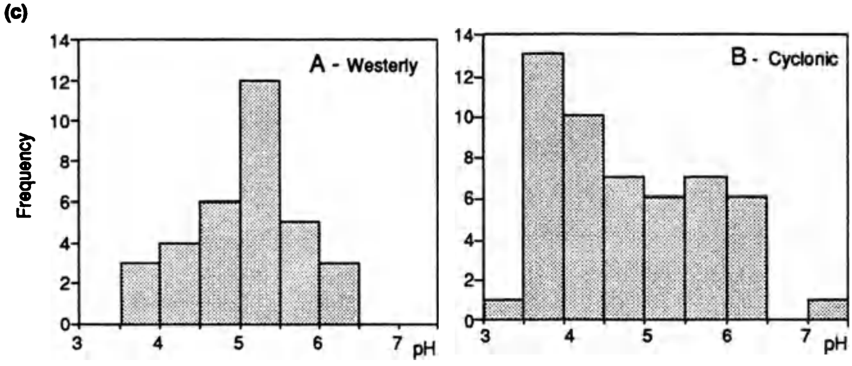


Figure 3.3 (c) Frequency distributions of precipitation acidity by weather type for Beacon Hill (Leicestershire, UK) 1988–1989.

on the scavenging efficiency of stomata and cuticles, and according to whether or not the canopy is wet (Fowler and Cape, 1983). Vegetation may also modify the concentration and ionic loads of throughfall chemistry by acting as a source of organic acidity, or as a proton sink and net exporter of calcium, magnesium and potassium ions. For example, Foster (1987) found that oak throughfall had a pH of 4.1 compared with 5.2 for bulk precipitation, whereas paired catchment studies have suggested that a forest canopy may increase local sulphate and chloride loads by 50–100% (UKAWRG, 1989). High interception and evapotranspiration rates under forest canopies result in the concentration of soil-water solutes, and the drying of organic rich soil horizons can lead to the oxidation of organic sulphur or mineralization of organic nitrogen. Modern forestry practices further promote water-quality changes through the addition of nitrogenous fertilizers to peats and podzols, the net removal of base cations by cropping and improved drainage leading to reduced soil water residence times and a higher proportion of acidic, near-surface runoff (Hornung, 1988). Annual differences of up to 1.5 pH units have been observed within the Beacon catchment for water draining contrasting land uses separated by as little as 10 m.

In addition to land use, other spatial factors have been shown to influence streamflow acidity. Upland soils typically exhibit a clear vertical progression from the highly acidic, organic-rich upper horizons to the lower-acidic, base-rich parent material beneath. Similarly, lateral trends in the stream Al- and H-ion chemistries of experimental catchments such as the Hubbard Brook, New Hampshire (Lawrence *et al.*, 1986, 1988) or the Birkenes site, Norway (Christophersen *et al.*, 1990) have been related to variations in vegetation type, soil depth, solute pathways and variable source areas. At the highest elevations maximum densities of spruce and fir combine with lowest soil depths to favour the mobilization of aluminium via transformations involving organic matter. Conversely, at the lowest elevations, the relatively thick soil provides greater opportunities for the neutralization of acidity through mineral weathering and exchange reactions. Under low-flow conditions the upper reaches of the stream network become dry, so that there is little contribution to the total flow from this part of the watershed and the stream chemistry then tends to reflect the soil solution of the lower mineral horizons. Experiments with the variable source area TOPMODEL have also confirmed the importance of topography to spatial variations in the production of near-surface runoff and hence acidity (Wolock *et al.*, 1990). Model results obtained for the Llyn Brianne, Wales catchments revealed that the average stream acidity and the magnitude of storm fluctuations were highest where the saturated conductivity of the soil was lowest, and where large upslope areas were drained by relatively low slope angles. In other words, the sites which were most prone to the generation of near-surface runoff (and hence the lowest soil contact times) tended to exhibit the most acidic streamflows.

An appreciation of the role of variable contributing areas and of hydrological pathways has led to a greater understanding of the short-term response of acidic catchments. These processes were clearly borne out by the hourly variations of stream acidity observed during the rising and falling limbs of the Beacon chemographs. Figure 3.4(a) shows the hourly stream stage (discharge), pH and conductivity for a storm event of 21.2 mm which fell on 24 February 1989. Four characteristic stages were identified; *Phase A* represents the stable, pre-event conditions which in this instance were relatively low flow but relatively moist soil conditions following a week of intermittent showers and light snowfalls. During *Phase B* there was a rapid rise in discharge, marked dilution of stream solutes (as indicated by the falling conductivity) and a slight reduction in the streamflow acidity. These changes were attributed to the displacement of pre-event soil water and to a surface runoff component derived from an impermeable area close to the catchment outlet. During *Phase* C as discharge continues to increase (albeit at a reduced rate) the streamflow acidity begins to climb, and the conductivity rises accordingly. At this point the discharge comprises water from surface runoff and a significant contribution from soil-pipe or macropore flow. However, the maximum acidity was not attained until more than 10 hours after the peak flow due to the time required for water to infiltrate through the upper acidic soil layers and into the stream. The time delay between both the onset of the storm and the maximum discharge, as well as between the peak flow and highest stream acidities are functions of the antecedent soil moisture status. As shown in Figure 3.4(b), these lag

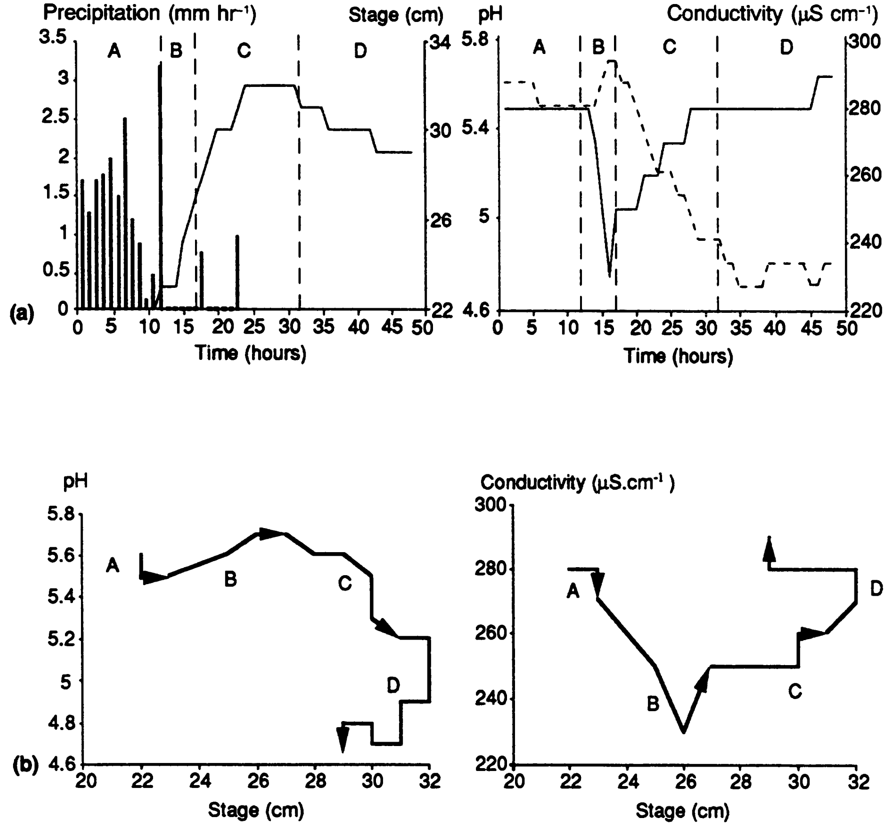


Figure 3.4 (a) Hourly variations in stream water acidity and conductivity for an event on the Beacon Hill (Leicestershire, UK) during and after a storm on 24 February 1989. (b) Examples of clockwise and anticlockwise hysteresis for the storm of 24 February 1989; hourly variations of pH and conductivity with stage.

effects characteristically produce anticlockwise hysteresis patterns when the chemical concentration (in this case the H-ion) is plotted against discharge. During *Phase D*, the discharge recession commences but stream acidities remain high. Under these conditions the soil-water buffer store had been depleted by infiltrating moisture whereas the contributions of the most distant slopes of the catchment begin to supply highly acidic throughflow to the basin outlet. Depending on the subsequent meteorological conditions and time of year, the final return to Phase A conditions may take more than 50 days.

Whereas short-term acidic episodes may result from individual storms, rapid snow-melt or seasonal variations in the dominant hydrological pathways, long-term acidification reflects the relative balance between soil weathering and acidic deposition rates. The distinction between these two time-scales broadly corresponds to what Reuss *et al.* (1987) have termed ***equilibrium*** and ***flux*** relationships. According to the MAGIC model formulation (Cosby *et al.*, 1985b) long-term acidification and recovery is believed to progress through seven distinct chemical stages or flux balances.

1. The preacidification phase is the steady state prior to increases in atmospheric deposition;
2. The soil is undersaturated with respect to sulphur resulting in a lag in the increase in the strong acid anion concentrations as the soils adsorb the sulphur. Continued acid depositions increase the external input of strong acid anions such as SO_4^{2-} and NO_3^- and their accompanying cations (largely H^+ and NH_4^+). The H-ion then exchanges place with cations such as Ca^{2+}, Mg^{2+} and K^+ at sites on the surface of clay–humus complexes. These cations are in turn leached from the soil profile by the strong, mobile, acid anions (SO_4^{2-}) such that there is a progressive increase in the soil and soil-solution acidities. At $pH<5.5$ the rate of loss of basic cations is further accelerated by the dissolution of clay minerals and the subsequent release of Al into solution. If the external acid load continues unabated, the exchangeable base cations in the soil become so depleted by this process that further Al can not be exchanged and the surplus begins to increase soil water and runoff Al-ion concentrations;
3. The soil sulphate absorption sites are filled and a new dissolved-adsorbed sulphate equilibrium is established;
4. The flux of high concentrations of anions through the soil continues to deplete the store of exchangeable cations until a new steady state at the higher levels of atmospheric deposition is reached by the end of phase four;
5. This stage is initiated when the deposition rate is reduced to its original low level and the accumulated sulphur begins to be desorbed. As the anion concentration declines, so too do the base cation, hydrogen and aluminium concentrations required to maintain the ionic balance;
6. After the anions have returned to their preacidification levels, a gradual recovery of the soil base saturation occurs accompanied by a rise in alkalinity;
7. Finally, the return to the preacidification steady state, may not be achieved until over 200 years after the initial onset of acidification!

3.3 LARGE RIVERS

The previous section described the principal hydrological and hydrochemical processes of headwater catchments where the regimes are closely related to distinct physicochemical processes. Research at this scale has tended to focus on small upland, impermeable, experimental catchments (<100 km^2) or highly instrumented hillslope systems. At this scale it is often assumed that rainfall inputs are constant in space, but that soil, vegetation and topographic characteristics (and hence the processes of runoff generation) exhibit marked variability. However, as the catchment scale increases, the basin area will embrace an even wider sample of hillslope forms and surface types, and rainfall patterns may display distinct heterogeneity, particularly during convective storms, in coastal areas and mountainous regions (Beven, 1988). The catchment may also be capable of sustaining a floodplain, so the channel then becomes separated both physically, hydrologically and chemically from its adjacent hillslopes. The perennial channel network and channel flow processes also begin to exert increasing control over the magnitude and timing of the flood hydrograph whereas the diverse effects of catchment management on water quantity and quality become increasingly apparent. Within this context it is convenient first to define a large river as one in which a floodplain is present and, secondly to examine the dynamics of these hydrosystems from a spatial (upstream–downstream or transverse) dimension and temporal perspective (that embraces both natural variations and anthropogenic impacts).

3.3.1 SPATIAL VARIATIONS IN HYDROLOGY

The concept of the river as a linear continuum has been usefully employed in temperate latitudes to describe natural changes in the physical properties of a river from headwater to mouth. This continuum may relate to a progressive increase in discharge and channel dimensions arising from the greater drainage area and manifested in the hydraulic geometry (Leopold and Maddock, 1953); to geomorphological zones of sediment production, transfer and deposition (Schumm, 1977); or to downstream changes in the lotic communities due to variable habitat availability (Vannote *et al.*, 1980). The concept is equally valid for describing longitudinal variations in water quality as the river network increasingly aggregates an ever-widening array of catchment properties, source areas and tributary inputs.

Despite the problems of defining topologically distinct networks from maps and field surveys, stream-ordering techniques have been widely applied as an objective means of classifying rivers regardless of scale. Models such as the Geomorphological Unit Hydrograph (Rodriguez-

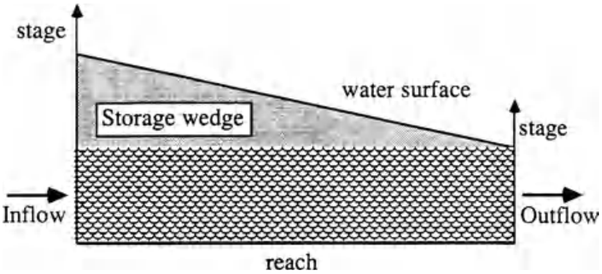


Figure 3.5 Simplified view of flood routing at the reach scale.

Iturbe and Valdes, 1979) have even used network parameters to derive equations for the time to peak and maximum discharge given an instantaneous, uniform input of 'excess' rainfall. This is possible because there are close relationships between catchment geology, channel network densities, channel geometry and thence runoff routing. For example, the peak flow Q_{pk} is defined as:

$$Q_{pk} = \frac{1.31\, R_L^{0.43} v}{L\Omega}$$

where R_L is the length ratio (calculated from the expected channel length given its order and the order of the whole network), $L\Omega$ is the length (in km) of the highest order stream, and v is the peak streamflow velocity (in m s^{-1}) which is assumed constant through the network.

For the purpose of runoff routing it is convenient to view the river channel as a linear storage such that the rate of outflow from a reach (O) relates to the inflow rate (I) and the change in storage (dS/dt):

$$dS/dt = I - O$$

For conditions of uniform flow, the change in storage is effectively zero since the reach inflow and outflows are equal. Under these conditions a direct (rating) relationship exists between the water depth and discharge at a given cross-section. For unsteady flow, the Muskingum method envisages changing reach storage as a dynamic wedge (Figure 3.5). During the advance of a flood wave inflow to the reach will temporarily exceed outflow resulting in higher stages at the upstream end. (Similar 'backing-up' effects occur whenever a floodwave passes from a confined channel to a zone of floodplain storage.) Due to hysteresis, the local maximum flood wave velocity occurs before the maximum discharge which in turn precedes the maximum water depth (Price, 1973). In other words, velocity tends to increase more rapidly on the rising limb of the hydrograph, and declines more rapidly during flood recession.

Channel storage and flood hydrograph propagation are both functions of the length, cross-sectional area, shape, boundary roughness and slope of the reach. Since these properties vary in longitudinal direction so too does the flood wave speed. The wave speed will generally increase with discharge up to about 0.4 times bankfull discharge where upon the flow encounters increasing boundary roughness due to bankside vegetation. Further reductions in wave speed will occur due to localized floodplain storage at or below the general bank level.

The kinematic (or flood wave) speed should not be confused with the mean water velocities under steady flow conditions. Using tracer dispersion techniques on the River Severn, UK at Montford and Leighton, Beven and Carling (1992) found that reach-scale velocities were generally lower than cross-sectional mean velocities. This was attributed to large-scale flow structures within the reach resulting in the retardation of the tracer by exchanges across internal shear zones into volumes of slow-moving water. These 'dead zones' were also reflected in the calculated effective roughness coefficients which were higher for the reaches than the cross-sections. Dead zones, therefore complement grain roughness, form roughness and internal distortion as factors governing the total resistance to channel flow. They can also represent significant in-channel sources of nutrients under certain flow conditions.

Transmission losses through a permeable channel bed or banks may attenuate flow volume as it is routed downstream. Such losses occur especially in semiarid systems but can also arise where the channel is in contact with a dewatered aquifier. For example, detailed gauging of the River Glen, UK between Shillingthorpe and Kates Bridge (prior to the operation of the Gwash–Glen transfer scheme) revealed that up to 20% of the daily discharge could be lost to groundwater at flows of less than 25000 m^3 day^{-1}.

For large river networks the mixing and routing of runoff contributions from numerous tributaries may produce a quantity and quality response that is more to do with network and floodplain effects than to processes occurring within the upstream drainage basins (Walling, 1980). The importance of the basin network is probably at its most extreme in the case of the River Amazon. This classic river system has a mean annual precipitation total of 2500 mm across an area of 6×10^6 km^2 yielding a discharge of 175 000 m^3 s^{-1} (or 20% of the world's runoff to the oceans). Owing to the contrasting regimes of the tributaries (which drain areas of Andean mountain, tropical forest, savannah and swamp land), the hydrograph of the main artery of the Amazon is relatively uniform ranging from 20 000 to 60 000 m^3 s^{-1} upstream at Vargeun Grande and 100 000 to 220 000 m^3 s^{-1} down river at Óbidos. This is in part due to seasonal differences in precipitation inputs of the north- and south-draining tributaries which are typically three months out of phase. The damped hydrograph of the river at Óbidos also reflects the storage of water on the floodplain which contributes up to 20% of the total flow in the area of Rio Japurá (Richey *et al.*, 1991).

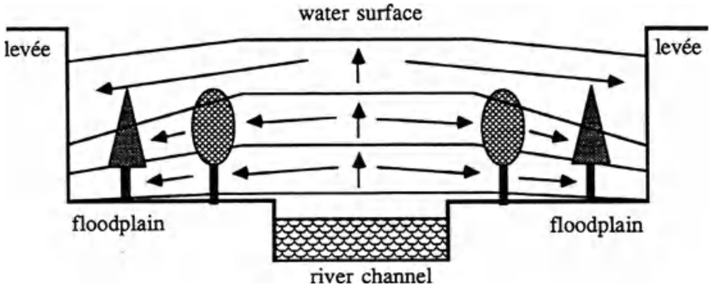
From the preceding example it is apparent that the floodplain performs two hydrological functions. First, as a temporary storage for part of the total, overbank flood volume and second, as a contributor to the main channel discharge. The extent to which a passing flood wave is damped depends on the ratio between the floodplain storage and the conveyance width, both of which may be modified by human activities such as levée construction, infilling and drainage. Local constrictions in the floodplain due to outcrops may further reduce the available storage and/or discharge capacity leading to locally elevated stages.

There is an important distinction between uniform and non-uniform floodplain storage. In the former case, limited resistance to overbank flow results in an almost horizontal water surface across the floodplain such that the storage capacity is simply proportional to the floodplain width and the rate of change of stage. Conversely, under non-uniform storage, obstructions to channel outflow and inflow (during flood recession) establish hydraulic gradients centred on the channel (Figure 3.6). The resistance offered by hedges, small dykes and other objects diminish as the stage increases so that at very high flood levels there may even be a return to uniform storage. For example, in November 1951 a discharge with a return period of over 50 years on the River Po, Italy caused disastrous downstream flooding when the non-uniform storage of the river defences was exceeded, followed by a dramatic rise in water levels associated with the remaining, limited, uniform storage (Price, 1973). Although floodplains may be engineered to control channel processes it is imperative that due regard should be given to the potential consequences in both lateral and longitudinal directions.

3.3.2 SPATIAL VARIATIONS IN WATER CHEMISTRY

The division of lowland hydrological processes into network and floodplain controls provides an equally appropriate framework for the examination of lowland hydrochemistry. Anthropogenic impacts aside, the fundamental controls of background water quality are climate, geology, soils, topography and biota. In a classic study of the River Exe, UK, Walling and Webb (1975) demonstrated that streams draining different geological strata and land-use types were associated with statistically distinct water qualities. The lowest conductivities corresponded to resistant slates and grits (<40–150 μS cm^{-1}), intermediate values with Upper Carboniferous shales (110–470 μS cm^{-1}), and the highest levels to the more easily weathered marls, sandstones and conglomerates (230–1070 μS cm^{-1}). Although geology determines the minerals available

Rising stage



Falling stage

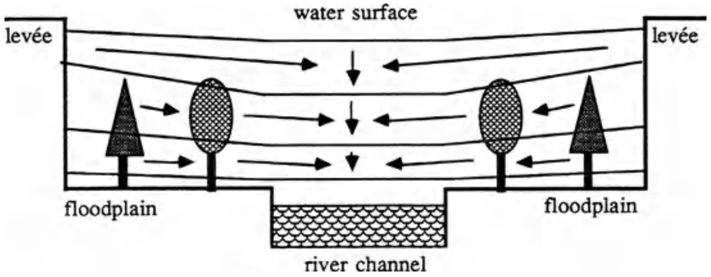


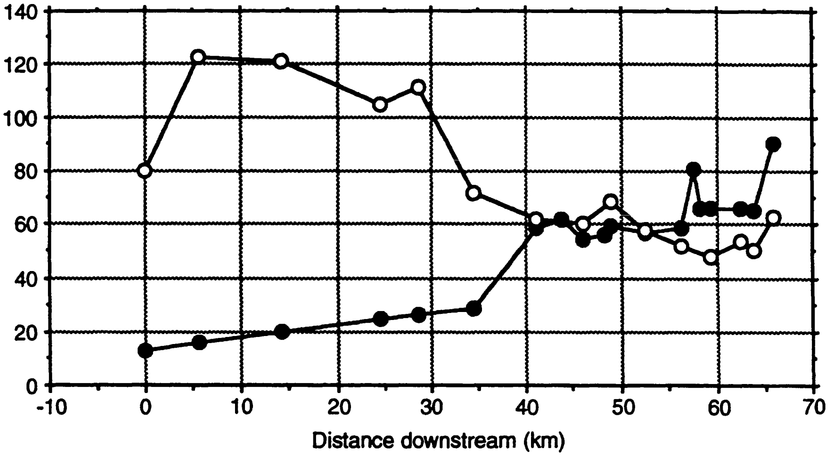
Figure 3.6 The principle of non-uniform floodplain storage.

for chemical reactions, climate remains an important regulator of the rate of weathering by constraining the supply of water. Over catchments as large as the Amazon, climatic differences may be sufficiently great to yield spatial variations in water quality through changing biota and soil associations.

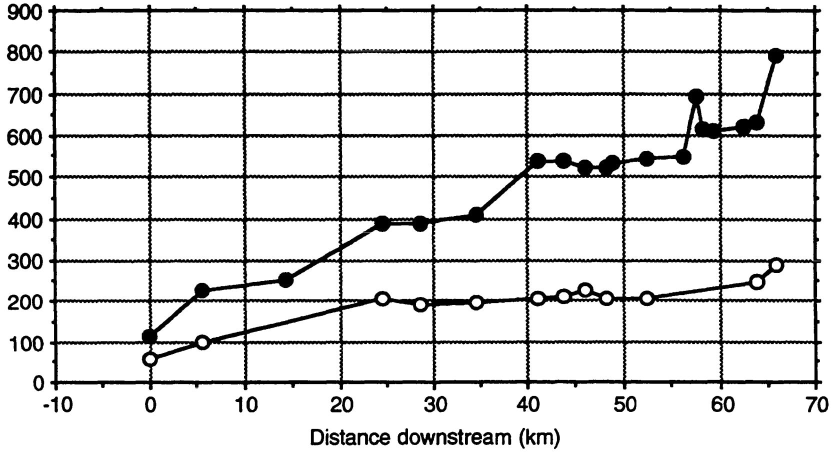
Superimposed upon spatial patterns of background water quality are the aggregated effects of chemical inputs from a multitude of diffuse and point sources. Simple river quality models use a mass-balance mixing approach which combines mean annual flow and quality to predict chemical changes at tributary confluences or at other 'point' discharges. In their simplest form the mixing models may be expressed as:

$$C_3(Q_1 + Q_2) = C_1Q_1 + C_2Q_2$$

where C_3 is the resulting concentration at the point of mixing, C_1 and C_2 represent the chemical concentrations in the separate reaches, and $Q_{1/2}$


0
20
40
60
80
100
120
140
-10
0
10
20
30
40
50
60
70
Distance downstream (km)

(a)


0
100
200
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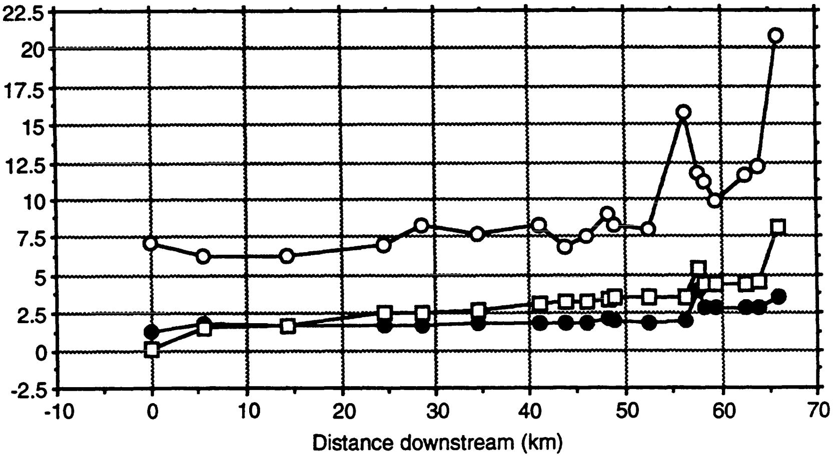
Distance downstream (km)

(b)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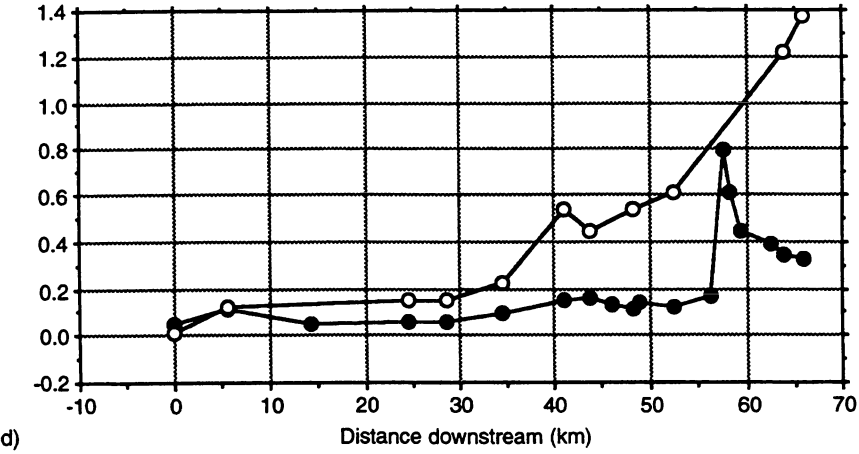
Distance downstream (km)

(c)



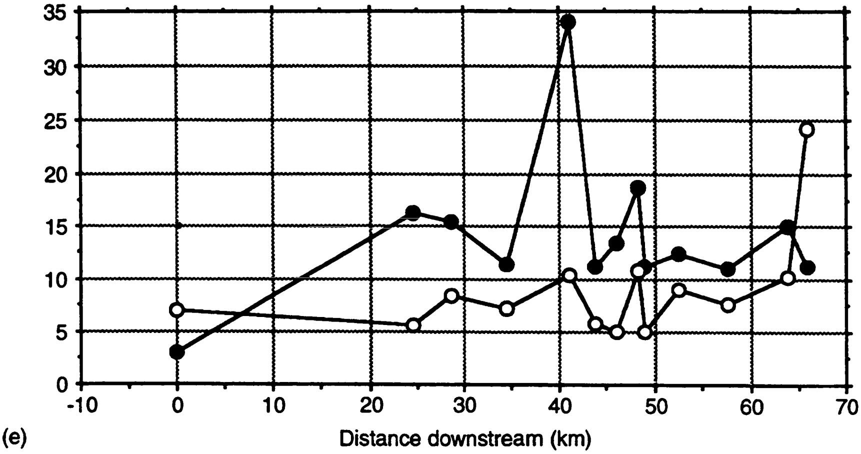


Figure 3.7 Downstream changes in selected water quality parameters for the River Derwent, UK. (a) National Water Council Score (NWC,o) and chloride (•,mg/ml); (b) electrical conductivity (•,μS/cm) and hardness (o,mg/l); (c) biological oxygen demand (•, mg/l), suspended solids concentration (o,mg/l) and total organic nitrogen (,mg/l); (d) ammonia (NH_4,•,mg/l) and orthophosphate (PO_4,o,mg/l); (e) lead (•,πl) and copper (o,πg/l). All values are long-term averages.

are their respective discharges. The approach is equally valid for effluent discharges assuming that the pollutant mixes completely and is conservative (i.e. chemically inert). For non-conservative substances (such as ammoniacal nitrogen) the equation must also incorporate simple first order coefficients to describe the quality changes along river reaches arising from the biological and/or chemical processes that alter the concentration of the substance concerned (Elliot and James, 1984).

Thus the effects of localized inputs of pollution (Table 3.3) may be evident for considerable distances downstream or until the processes of dilution, aeration, reaction, deposition and degradation have lowered the ambient concentration.

Table 3.3 Selected sources of water quality deterioration (after Farrimond, 1980)

Effluent	Factors affecting water quality
Domestic sewage	BOD, suspended solids, ammonia, nitrate, phosphate, bacteria
Vegetable processing	BOD, suspended solids, colour
Chemical industry	BOD, ammonia, phenols, non-biodegradable organics, heat
Iron and steel	Cyanide, phenols, thiocyanate, pH, ammonia, sulphides
Coal mining	Suspended solids, iron, pH, dissolved solids
Paint industry	Titanium, silicon dioxide, solvents
Textiles	Dyes, surfactants, organochlorines, pesticides
Metal finishing	Cyanide, copper, cadmium, nickel, pH
Brewing	Suspended solids, BOD, pH
Dairy products	BOD, pH
Agriculture	Nitrate, phosphate, suspended solids, pesticides, bacteria
Oil refining	Heat, ammonia, phenols, oil, sulphide
Quarrying	Suspended solids, oil
Power generation	Heat

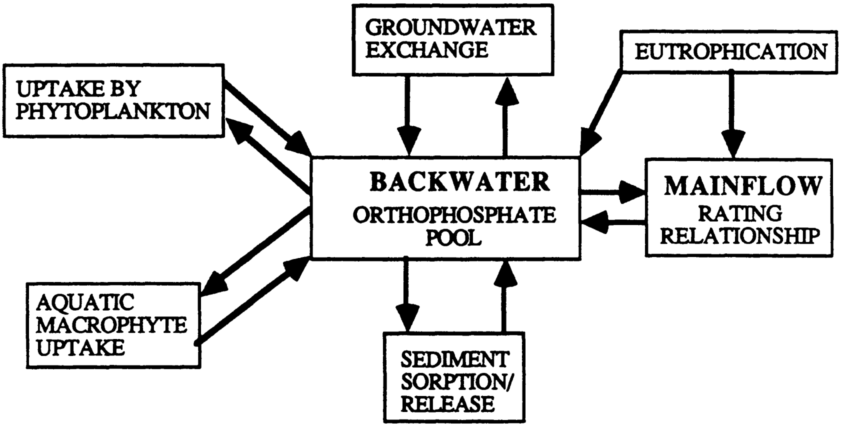
Figure 3.7 shows downstream changes in selected water quality parameters for the River Derwent, UK below the Ladybower Reservoir. In general, all determinands show a progressive increase in concentration with distance downstream which is reflected by the electrical conductivity. The upper reaches of the Derwent and its principal tributaries originate mainly from Millstone Grit catchments which have a characteristically low mineral content. At the confluence with the River Wye (km 24) – a predominantly limestone catchment – there is a corresponding increase in the hardness which remains relatively constant until the Trent at Sawley. Between Matlock (km 29) and Derby (km 52) there is an overall decline in river water quality, mainly due to the River Amber which receives mine-water discharges, treated sewage and industrial effluents. The chloride and heavy metal content of the Amber are considerably higher than in the Derwent resulting in a marked discontinuity in quality downstream of the confluence (km 40). This change is also manifested by the reduced National Water Council (NWC) score which is a measure of the biological quality of the river at this point. Between

Duffield (km 46) and St Mary's Bridge (km 52) there is evidence of a slight biological impact corresponding to the point of intake for the Little Eaton water works abstractions (km 48). Further downstream, the Derwent receives treated effluent from Derby Water Reclamation Works (km 58) and a major industrial complex. The combined effect on the concentrations of ammonia, suspended solids, total organic nitrogen and phosphate is substantial but of a localized nature according to the NWC quality criteria. Finally, the contrast in water quality between the Derwent and the Trent is evidenced by the marked rise in the concentration of all parameters downstream of the confluence at Sawley.

In addition to longitudinal variations in water quantity and quality, large river systems will often demonstrate significant transverse variations as a consequence of floodplain interactions. Although floodplain storages can be supplied by either local runoff or the main river, both these sources of inundating water tend to exhibit the sediment and chemical characteristics of high flows. This bias can lead to the selective capture of fine sediments, which may possess above average concentrations of particulate metal or other surface-adsorbed contaminants (Higgins, 1990). Shifts in chemical equilibria can also arise due to the mixing of river and floodplain stored water allowing the precipitation of heavy metals from solution or mobilization from sediments.

An important concept in river–floodplain systems is that of the 'flood pulse' which describes the periodic, two-way exchange of nutrients between the main channel and riparian ecosystems (Junk *et al.*, 1989). The degree of modification to water quality is a function of the residence time of the floodplain water, thermal and chemical stratification, rates of evaporation or dilution with lateral inflows, and the growth cycles of primary producers. Depending on the frequency and duration of individual flood pulses the floodplain may act as a source of carbon dioxide, hydrogen sulphide, methane, nitrogen, and organic carbon, and a sink for oxygen, phosphorus, nitrogen and particulate inorganic matter. In temperate regions flooding during winter and spring tends to provide more detritus to the main channel than during summer; in the tropics, consistently high temperatures favour high production and processing rates for organic material throughout the year.

Chemical transfers between the river and floodplain therefore involve abiotic and biotic exchanges which transcend conventional ecosystem boundaries. The spiralling concept (Elwood *et al.*, 1983) recognizes the spatial dependence of chemical cycles and pertains to the processing of nutrients within open ecosystems. The spiralling length refers to the distance required for one complete cycle of nutrient uptake from and return to a catchment relative to the rate of downstream transport. The concept is useful in four main respects. First, it is a valuable approach for measuring, reporting and conceptualizing nutrient dynamics. Second,



Figures 3.8 Influences on backwater orthophosphate dynamics (after José, 1988).

it focuses on the interactions between hydrological transport mechanisms (for inorganic sediments and detritus) and nutrient turnover via sorption, retention or microbiological activity. Third, it emphasizes that responses to local perturbations or environmental variations may be propagated downstream. Four, it underlines the fact that nutrient cycling is a three-dimensional process. These perspectives are particularly valid for non-conservative nutrients such as nitrate where there is a need to accommodate in-stream processes such as denitrification, volatilization and fixation. Richey *et al.* (1991) used nutrient spiralling to account for downstream organic carbon concentrations as it is exchanged between the main channel and floodplain of the River Amazon.

Although floodplains receive nutrients directly from the main channel, they seldom correspond directly to the river since the former tend to establish their own distinct biochemical cycles and environmental conditions (Figure 3.8). In a detailed study of the water quality of meander cutoffs and backwaters of the River Trent, UK, José (1988) showed that the degree of similarity with the main channel was a function of the level of hydrological connectivity, backwater morphometry, and distance from the river. For example, variations in the orthophosphate concentration for a backwater site at Shardlow was found to depart markedly from that of the mainflow due to the high residence time of the water and subsequent nutrient uptake by phytoplankton. For a site at Willington the lack of correspondence between the cut off channel and main river (except under flood conditions) was attributed to the high levels of organic matter, plus substrate siltation, which tend to impede groundwater interactions, effectively leaving the backwater as an isolated floodplain pond.

3.3.3 TEMPORAL VARIATIONS

Within large basins the fundamental control of annual runoff is the balance between the prevailing precipitation and evapotranspiration regimes. Of secondary importance are the drainage basin's geology, morphometry, soils and vegetation which largely determine levels of groundwater recharge, storage and leakage. With Britain there is a broad divide between the lowland 'soft-rock' aquifiers of the south and east, and the highland 'hard-rock' of the north and west. The lowland catchments tend to exhibit damped seasonal variations in runoff with less than 35% of the annual precipitation translated into flow. This contrasts with a figure of 65% effective rainfall for the flashy regimes of the upland areas.

Superimposed on the broad river regime will be individual storm events, long-term climatic changes, and anthropogenic impacts which may exert an influence over a range of temporal scales. A major control of the shape of the flood hydrograph will be the rainfall kinematics in relation to the basin drainage network and morphometry. For example, Neimczynowicz (1989) found a 30% difference in the simulated peakflow of an urban area due to storms moving either upstream or downstream of the drainage network. The implications of the study are that identical areal rainfalls over a static network and land-use structure will not necessarily yield identical hydrological responses. In the same way, precipitation events of similar magnitude but contrasting intensities or types (e.g. rain, hail, sleet or snow) will also produce differing hydrographs.

Although the precipitation intensity and channel routing are largely responsible for the speed of delivery to the basin outlet, the volume of storm runoff is a function of the antecedent catchment soil moisture status in each contributing headwater region. As was indicated previously, the soil moisture deficit (SMD) provides a useful surrogate for a 'batch' of runoff processes. In physical terms the SMD is an index of the physical extent of the dynamic contributing area(s), the potential for groundwater recharge, infiltration rates and macropore flow. However, exceptions may occur, for example, whenever the soil is frozen or infiltration is impeded in some way. Similarly, seasonal vegetation or crop changes will also modify the nature of the interception surface, its associated evapotranspiration rate and hence mechanisms of flow generation.

Both the volume and temporal characteristics of the storm hydrograph may be affected by human intervention. Land-drainage schemes, land-clearance and urbanization may all accentuate water flow through catchments by extending the effective channel network or by modifying infiltration rates. For example, Hollis (1974) demonstrated that the urban development of Harlow New Town, UK resulted in a 220% increase in the mean maximum monthly flood on Canons Brook. Furthermore, the post-urbanization hydrographs also revealed greater peakedness, reduced time to peak, and shorter durations. By contrast catchments with impounded or regulated rivers normally exhibit reduced flood peaks due to the temporary storage of flood water within the reservoir and its subsequent, gradual release under low flow conditions. However, the degree of flood mitigation is dependent on the recurrence interval of the event. Following the closure of the Stocks reservoir on the River Hodder, floods with a return period of less than 1.5 years were reduced in size by 17%, whereas rarer events such as the one in 10 year flood were reduced by only 5% (Higgs and Petts, 1988).

As was shown previously, short-term fluctuations in river water chemistry in headwater catchments are closely dependent upon the ion-specific discharge rating relationship, which in turn reflects the variable contributions of contrasting source areas. The same principles apply to the chemicals which predominate in the intensive agricultural systems of many lowland regions. For example, peak concentrations of commonly occurring pesticides (isoproturon, atrazine, simazine, mecoprop and chlortoluron) have been shown to correlate closely with peak river flow and suspended solids concentrations betraying the near-surface, terrestrial origins (Gomme *et al.*, 1991). Variations in the number and concentration of detectable pesticides throughout the year correspond to episodes of application as well as to changing proportions of near surface runoff and groundwater baseflow. The rate of pesticide degradation, solubility and affinity for soil absorption will further determine the amounts mobilized. The net effect is that sequential storms result in the gradual depletion of the available pesticides from the soil store (Figure 3.9) even though individual events typically account for less than 1% of the total application (Williams *et al.*, 1991). Similarly, bacterial concentrations in rivers also demonstrate a strong relationship with flow dynamics and depletion between successive events due to the role of preferential pathways, near-surface land and in-channel stores (Jenkins *et al.*, 1984). Thus, episodic fluctuations in water chemistry may be attributed to a range of diffuse as well as point pollution discharges (Table 3.2).

The seasonal pattern of emergence of terrestrial pollutants such as nitrate in groundwaters and surface runoff is less clearly defined. For example, a detailed investigation of groundwater contamination in the Inner Bluegrass Karst Region of Central Kentucky (Scanlon, 1990) revealed marked temporal and spatial variations in nitrate concentrations in closely spaced wells and springs, indicating that land-use was not the primary control. A general lack of correlation between the times of fertilizer application and peak nitrate concentrations in groundwater

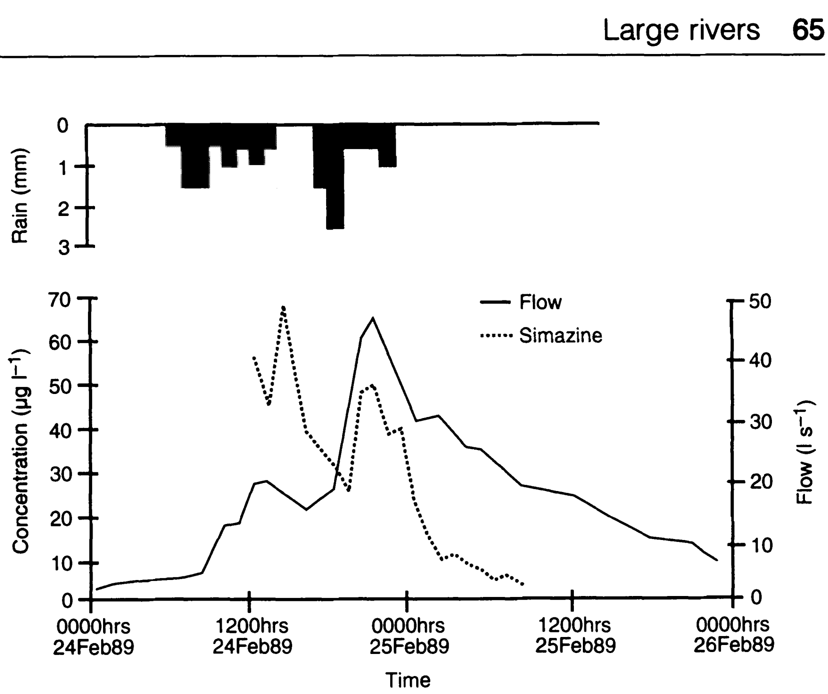


Figure 3.9 Flow and simazine concentrations in a stream draining the Rosemaund catchment following a rainfall event (after Williams *et al.*, 1991).

was also evident. Rather, temporal fluctuations in groundwater nitrate concentrations were governed by the lag between the periods of fertilizer application and the seasonal patterns of recharge and plant growth. Variations in rock permeability, the distance of groundwater flow to major springs and residence time were also found to determine the rate of bacterial die-off and denitrification.

There is considerable potential for hydrochemical change arising from interbasin transfers, followed by water usage, treatment and return to the host channel. Substantial volumes may be involved: for example, the Derwent reservoirs of the Peak District currently supply 186 Ml day^{-1} to the East Midlands including urban centres within the River Soar basin (Higgs and Petts, 1988). The effect of transfers and subsequent discharges of effluent are most noticeable under low-flow conditions. For example, the dry weather flow of the River Tame, UK has increased threefold as a direct consequence of effluent returns which in 1980 comprised over 70% imported water (Higgs and Petts, 1988). Clearly the water quality of such treated effluent will bear little resemblance to that of the original source. In catchments where sewage effluent constitutes a significant proportion of the total flow, winter minima occur for biological oxygen demand (BOD), nitrate and ammonia due to the enhanced dilution of discharges by higher flows. Similarly, long-term reductions in the mean

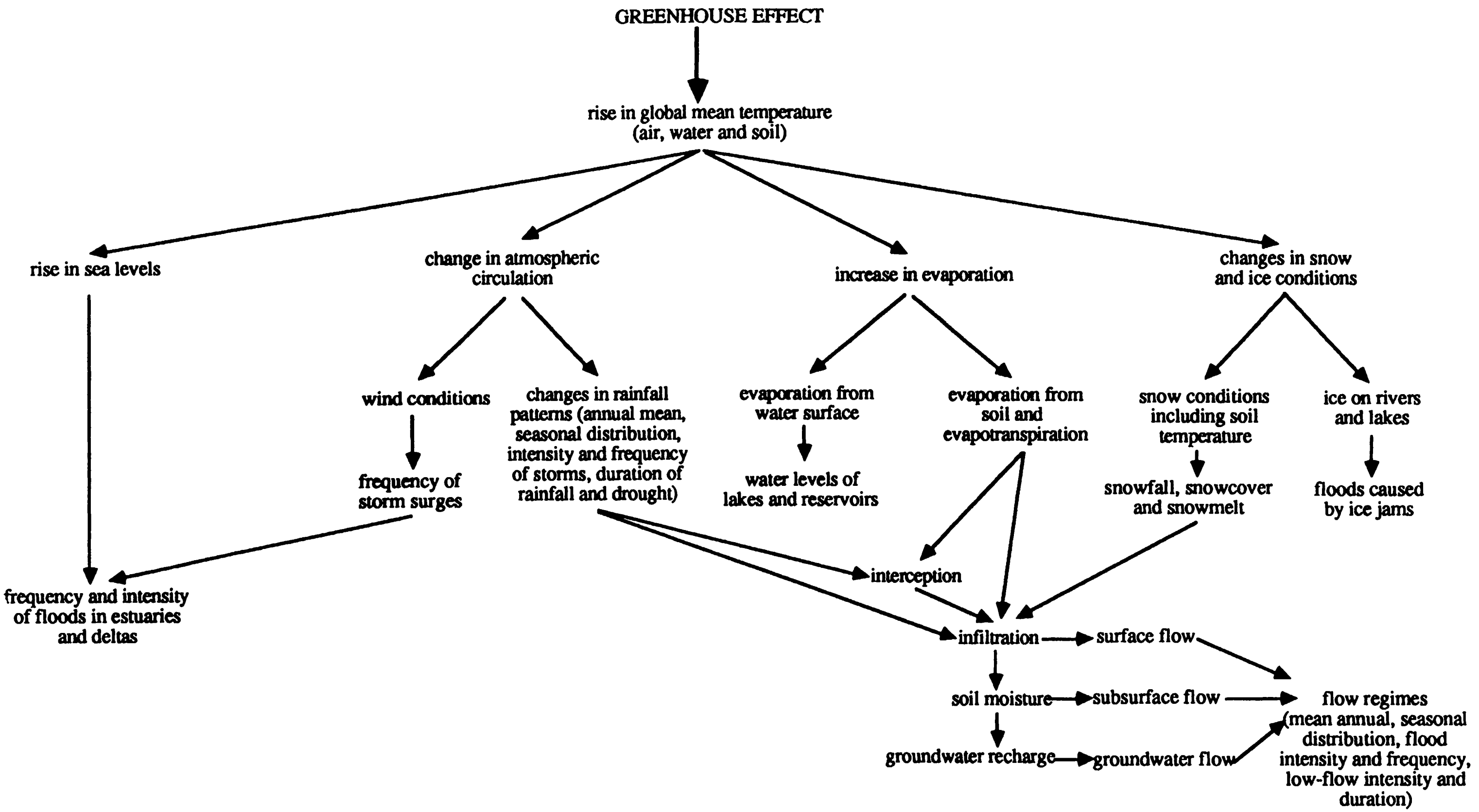


Figure 3.10 Potential impacts of climate change on fluvial hydrosystems (after Lemmela *et al.*, 1989).

annual BOD of the River Clyde, UK have recently been attributed (at least in part) to favourable changes to the runoff regime (Curran and Robertson, 1991).

Temporal variations in the solute concentrations of large basins are therefore a reflection of the prevailing hydrological regime, biological cycling, the mixing of waters from contrasting headwater catchments, land management and water treatment practices. However, the composite effect of these processes are also augmented by underlying, long-term, regional-scale dynamics. Changes may occur to catchment hydrochemistry in response to either variations in the gross input–outputs of the system or, through modifications of the system structure itself.

A growing scientific consensus (Jones and Henderson-Sellers, 1990) would argue that recently observed climate change is an indirect and undesired consequence of our mismanagement of the global carbon cycle. As Figure 3.10 indicates the potential impacts of CO_2-induced climate changes on fluvial hydrosystems are manifold although the precise outcome remains uncertain due to the range of plausible scenarios. Furthermore, valid predictions should also incorporate atmosphere–hydrosphere–biosphere feedback mechanisms as well as the human response to change which in itself may be sufficient to compensate for, adjust or exaggerate the resultant behaviour of fluvial hydrosystems.

3.4 CONCLUDING REMARKS

Although it is convenient to segregate the hierarchical processes governing hydrological and hydrochemical dynamics, spatial and temporal changes should be regarded from an integrated, basin-wide perspective. This embraces parameters such as climate and geology at the macroscale, river networks, runoff routing, soil, land-use, floodplain and topographic processes at the mesoscale and dynamic chemical reactions and hydrological pathways at the microscale. Above all, the increasing scale and diversity of anthropogenic impacts has ensured that the 'human factor' now pervades all dimensions of the fluvial hydrosystem.

Geomorphology of temperate rivers

4

D. Gilvear and J.-P Bravard

4.1 INTRODUCTION

Small headwater tributaries usually flow within steep-sided V-shape valleys. Further down the river network the valley sides tend to be less steep and the valley bottom is often infilled with sediments. Here the river is separated from the valley sides by more or less extensive floodplain. Sometimes bordered by terraces, remnants of former active floodplains form stair-like features up valley sides. However, this generalized change in the downstream character of rivers and river valleys masks considerable variability.

The fascination of rivers, for many, lies in their morphological diversity. In France, for example, the River Loire, meandering within a broad floodplain, differs markedly from multiple channel sections of the River Rhône. At a local scale, salmon fishermen identify reaches and pools of unique character in their quest to catch a fish.

Another fascinating aspect of rivers is that their character can be transformed overnight by a single large flood event, by depositing sediment in some areas and reactivating other reaches by erosion. Rivers are dynamic landscape features that adjust their morphology, both in time and space, in relation to catchment inputs.

4.1.1 VARIABLES AND TIME-SCALES OF CHANNEL ADJUSTMENT

For a given river channel reach, Hey (1978) stated that river channels possess five basic variables, or 'degrees of freedom': channel width, depth, slope, pattern and stream-bed roughness. A number of indices

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Table 4.1 Some key variables used to describe channel morphology

Variable	Definition
RIVER CHANNEL CROSS-SECTIONAL FORM	
Size	
Channel capacity (Cc)	Cross-sectional area at bankfull stage equates to mean depth times width
Channel width (W)	Width of channel between the riverbanks
Channel mean depth (d)	
Wetted perimeter (Wp)	Total length of channel bed and banks
Shape	
Width depth ratio (w/d)	
Channel asymmetry (A*)	A* = (Ar – Al) ÷ Cc where Ar and Al are the areas to the right and left of the channel centre line and Cc = Ar + Al
Efficiency	
Hydraulic radius (R)	CC ÷ Wp. A measure of channel efficiency in conveying water
RIVER CHANNEL PLANFORM	
Sinuosity	
Channel sinuosity	Channel length ÷ straight-line valley length
Meander form (see Figure 4.10a)	
Meander wavelength (L)	Distance between two consecutive meander bend inflexion points
Meander height (H)	
Radius of curvature (r^6)	
Channel multiplicity	
Braid intensity	Two times total bar length ÷ by reach length
LONG PROFILE	
Bed slope (S_b)	
Profile gradient (S_{1085})	NERC (1975); gradient from 10% to 85% of length upstream from river mouth
BED ROUGHNESS	
Bedform wavelength (l)	Use for pool-riffle spacing or ripple-dune forms
Bedform amplitude (h)	
Bed roughness (D84)	Representative percentile of the bed particle size distribution curve
Bed roughness (K)	$K = (5C_1 + 3C_2 + C_3) \div 9$ where 1 = dominant substrate type, 2 = second most dominant substrate type and so on where particle size categories are <0.3 cm, 0.3–3 cm, 3–30 cm and >30 cm

have been used in an attempt to define the three-dimensional nature of river morphology. In respect of cross-sectional form most indices incorporate the fundamental variables width, mean depth and wetted perimeter (Table 4.1). The choice of time-scale within which to study fluvial geomorphology and process–response mechanisms is problematic. Time is a continuous variable but representative time periods can nevertheless be defined:

1. Instantaneous time ($<10^{-10}$ years)
2. Short time-scale (10^1–10^2 years);
3. Medium time-scales (10^3–10^4 years);
4. Long time-scales ($>10^5$ years).

Thus, discharge and sediment loads will vary in instantaneous time as a result of individual flood events whereas human-induced or climatically induced changes in runoff processes and/or river flows can superimpose short- or medium-term trends in flows and sediment load on the system. Examples of processes causing channel change over long time-scales include major climate shifts, massive catchment denudation or geological uplift.

The various degrees of freedom identified by Hey (1978) above adjust their form over different temporal and spatial scales. In general, cross-sectional form parameters adjust over instantaneous and short time-scales, planform and local-scale profile changes over short and medium time-scales and the overall longitudinal profile only over the medium and long time-scales (Figure 4.1a).

4.2 FUNDAMENTAL PRINCIPLES

A knowledge of river flow hydraulics is an essential prerequisite to an understanding of river geomorphology. An appreciation of flow hydraulics is also important because hydraulic processes determine the nature of aquatic biotopes.

4.2.1 PRINCIPLES OF FLUID FLOW

Water within a channel is subject to two principal forces: the force of gravity, which promotes water flow downhill, and frictional forces. Hence, a steep gradient, smooth channel in which gravitational forces are high and channel boundary roughness is low will have a high water velocity. Conversely a low gradient channel with large boulders or infested with vegetation growth, both of which would induce high channel boundary roughness, will have a low water velocity.

Mean water velocity in an open channel can be estimated using the Manning equation

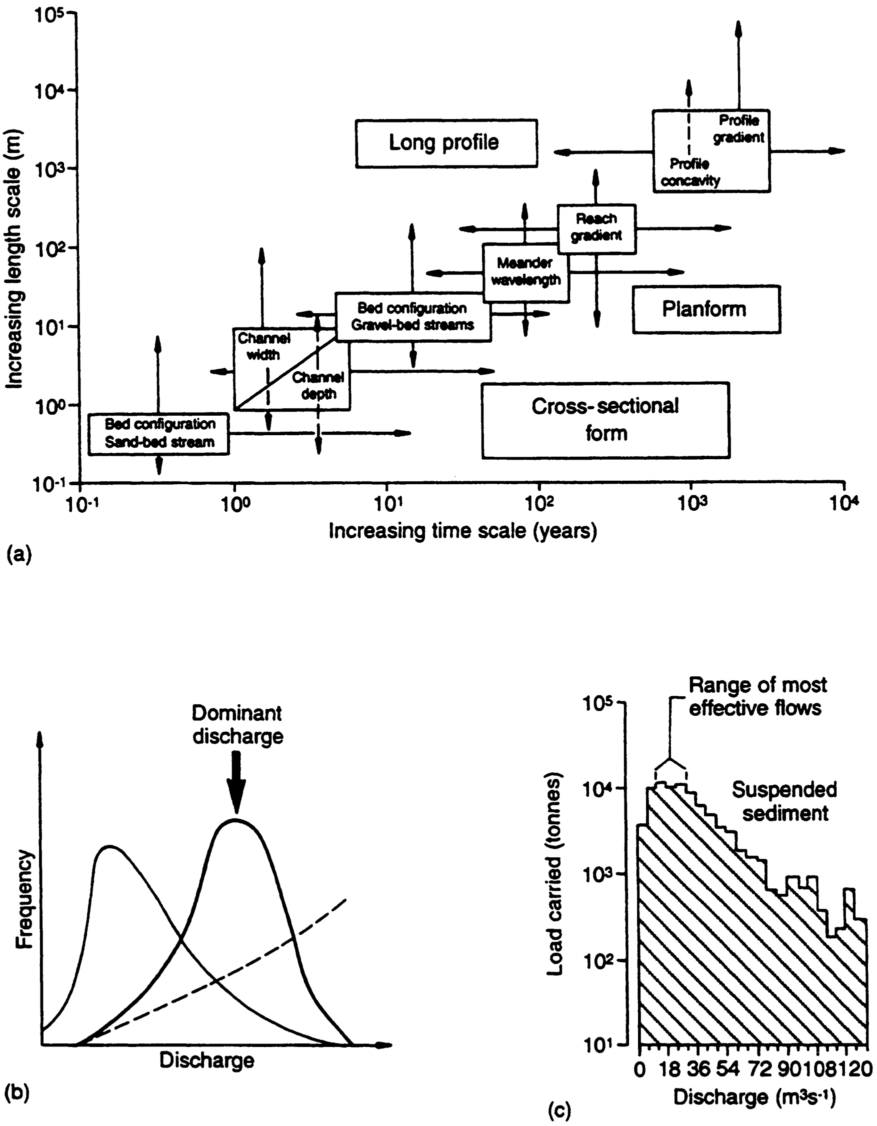

Figure 4.1 Temporal dimensions in river geomorphology. (a) Schematic diagram of the time-scale of adjustment of various channel form components with given length dimensions for a hypothetical temperate river (based on Knighton, 1984). (b) Illustration of the derivation of dominant discharge. The thick line is total sediment load transported by a given discharge. The thin solid line is percentage time of a given discharge. The dashed line is sediment transport capability of that magnitude discharge (where the line meets the x axis is the threshold for sediment transport). Dominant discharge is defined as the flow with the highest total sediment load. (c) The dominant discharge as derived for the River Creedy, Devon (after Walling and Webb, 1982).

$$V\,(\mathrm{m\,s^{-1}}) = \frac{R^{0.66}\,S^{0.5}}{n}$$

where *V* is mean water velocity, *R* is hydraulic radius, *S* channel bed slope and Manning's '*n*' is a measure of channel roughness. The hydraulic radius is the wetted cross-sectional area (*A*) divided by wetted perimeter (*WP*) and approximates to mean depth (*d*) (Table 4.1). Indices of bed grain size are usually used to quantify channel roughness (Table 4.1), but defining a representative value for heterogeneous bed material is problematic since larger particles have a greater effect on roughness than small particles. Representative values of Manning's '*n*' have been defined for channels of different character and using descriptive tables these can be applied to similar channels but at best they will only be an approximation of roughness (Petts and Foster, 1985 and Gregory and Walling, 1973 give representative Manning's '*n*' values). Ignoring the roughness factor the open channel flow equation is effectively a depth–slope product and the Chezy coefficient relates mean velocity to the square root of the 'depth–slope' product.

$$V = c(RS)^{0.5}$$

where *c* is the Chezy coefficient.

The depth–slope product also appears in the equation for the tractive force or shear force exerted on the river-bed (*T*) a major factor determining sediment entrainment;

$$\mu\ (\text{Newtons m}^{-2}) = gyds$$

where *g* is the gravitional constant, *y* is the specific weight of water, *d* is depth and *s* is slope.

4.2.2 TYPES OF FLOW

Several types of flow are theoretically possible in open channels: uniform, non-uniform, steady, laminar, turbulent, tranquil and rapid flow. In reality only a number occur. For example, uniform flow describes flow where there is no change with distance in either magnitude or velocity along a flowline but in reality variations in velocity in space and time occur and non-uniform flow exists. Similarly steady flow relates to no velocity change with time, but in reality, changes in discharge result in velocity fluctuations. Flow in rivers is therefore generally non-uniform and unsteady.

The existence of laminar flow or turbulent flow depends on the Reynolds number (Re), an index of flow turbulence, where:

$$\mathrm{Re} = \frac{pvd}{u}$$

where p is water density and u is dynamic viscosity. This is a dimensionless ratio of the inertial to the viscous forces. Laminar flow occurs when viscous forces predominate but generally speaking laminar flow rarely occurs in rivers. Turbulent flow occurs when inertial forces are large in comparison to viscous forces. Diffusion takes place by groups of molecules and gives rise to additional viscous resistance termed the eddy viscosity.

The criterion for tranquil flow and rapid turbulent flow is the Froude (Fr) number which is a dimensionless ratio of inertial to gravity forces:

$$\mathrm{Fr} = \frac{v}{(gd)^{0.5}}$$

When the Froude number is less than 1, flow is tranquil; when it is equal to 1 flow is critical and when it exceeds 1 it is rapid. Flow is normally tranquil.

4.2.3 STREAM POWER

One of the most important expressions of the hydraulics of channel flow is 'stream power' which is the work expended or energy loss. Stream power is therefore a key parameter in controlling erosion and sediment transport and possibly as a control on aquatic biotopes.

$$\text{Stream power } (\mathrm{W\ m^{-1}}) = yQs$$

where Q = stream discharge in $\mathrm{m^3s^{-1}}$ or $\mathrm{ls^{-1}}$.

Ferguson (1981) showed that stream power at bankfull discharge in British rivers has a 1000-fold range. Unit stream power (P) is an important dimensionless index for comparative studies.

$$P\ (\mathrm{dyn\ s^{-1}}) = \frac{yQs}{w}$$

where w is channel width. Stream power varies as the cube of velocity, and thus slight changes in velocity can significantly affect potential stream power.

4.2.4 THE CONTINUITY EQUATION

In any given reach, in the absence of water inputs, the volume of water moving through a cross-section, even if it is radically different in size, slope or shape from the cross-section immediately above, must equal the amount of water being conveyed from upstream. Thus, the product of the mean velocity of flow and cross-sectional area at the downstream cross-section must equal the product of cross-sectional area and mean velocity of flow upstream (i.e. $A^1V^1 = A^2V^2$). This simple algorithm is known as the continuity equation. In essence it means that if cross-sectional area increases, mean water velocity decreases or vice versa and this implies that channel cross-sectional area and slope are important controls on local variability in water velocity.

4.2.5 HYDRAULIC GEOMETRY

Studies of the spatial and temporal variation of channel morphology and process have been dominated by the 'hydraulic geometry concept (Leopold and Maddock, 1953) which relates channel form and process variables as power functions of discharge (see also Figure 2.8).

$$W = AQ^b \quad d = cQ^f \quad v = KQ^m$$

and since $Wdv = Q$, $B + f + m = 1$ and $ack = 1$.

At a particular river channel cross-section, changes in width, depth, and water velocity can be related to discharge changes with time. In the longitudinal dimension changes in channel width, depth and velocity can be related to the downstream increase in discharge. Thus it has been shown that mean streamwater velocity, both at high and low flow generally increases downstream, despite a reduction in gradient. This occurs since channels tend to increase in hydraulic efficiency downstream because of increased size and reduced bed roughness. Nixon (1959) showed that for 27 channels in England and Wales with bankfull discharges ranging between 10 and 500 $m^3 s^{-1}$, mean water velocity varied with bankfull discharge according to the equation:

$$V = 0.61Q^{0.24}$$

In the absence of detailed data on flow changes, downstream drainage basin area or total channel network length has sometimes been used as a surrogate variable for discharge.

4.2.6 SEDIMENT TRANSPORT

Sediment in rivers may be classified in terms of origin. The bed material refers to material of mixed size found in the stream bed, but may be carried as bedload or suspended load. Transport of fine sediments supplied primarily by soil and channel bank erosion is termed wash load and is dominantly transported in suspension.

Sediment entrainment and transport in rivers is inextricably linked with flow hydraulics. For a particle to be 'lifted' from the stream bed or 'sheared' from the riverbank a threshold has to be passed whereby the critical velocity or shear stress exceeds that of the forces acting on the particle resisting erosion.

Sediment size (described in mm but often transformed into a phi (ø) scale, where $\phi = -\log d$, which provides a better relative measure of size in relation to transport processes) the arrangement and packing of particles and, for fine sediments, cohesion, all influence the resistance to erosion.

Bedload transport is almost entirely a function of the transporting capacity of the flow. As regards the mode of bedload transport, particles roll, slide or saltate (hop) along the bed in a shallow zone only a few grain diameters thick. With further increases in the strength of flow, the smaller particles may be carried upwards into the main body of flow and transported as suspended load. In general terms, critical conditions of particle motion are dependent on gravity, grain size and shape, and immersed weight in relation to the drag force or bed shear stress and fluid kinematic viscosity. Since the material lying on river channel beds is normally coarse, bedload movement is usually restricted to high flow periods and is controlled by the flow competence of the river.

Unlike bedload, suspended load transport is determined not only by the sediment transport capacity of the river, but also its rate of supply from the drainage basin. Indeed, except at very low flows and/or in areas of the channel with very slow flowing water the river will always have the capacity to transport wash load sources which make up the bulk of the suspended load in most temperate rivers. However, bank and hillslope sources are often only activated during precipitation events and high flows and thus the wash load usually increases during higher discharges. Nevertheless, a plot of wash load concentration against discharge often shows a wide scatter of points and no well-defined relationship because suspended solids transport is 'supply limited'.

4.3 CHANNEL ADJUSTMENT

Rivers transport sediment and erode their bed and banks, locally in space and time, in response to flood events. Large floods have greater potential to erode and transport sediment but occur infrequently. Small floods occur frequently but sediment transport is limited and they are generally geomorphologically ineffective. In the long term, the total geomorphic work achieved by a given flood magnitude is the product of the sediment transported during those size floods and their frequency (Figure 4.1b). The flood discharge that achieves the greatest total geomorphic work is referred to as the dominant discharge. Thus, on the River Creedy, South West England, the most effective range of flows for sediment transport are those flows close to channel bankfull capacity (12–30 $m^3 s^{-1}$) rather than extreme events (Figure 4.1c).

Recently, the term 'geomorphic effectiveness' has been introduced to describe the relationship between the amount of work accomplished by a flood and its potential for geomorphic work (Wolman and Gerson, 1978; Newson, 1989). Floods of similar magnitude do not always accomplish the same degree of geomorphological work. This may be explained by the antecedent conditions, the time since the last large flood event, recent channel changes and time of year. The exact relationship between antecedent conditions and geomorphic effectiveness, however is unclear. For example, a large flood event soon after one of similar magnitude may more readily accommodate that flood due to previous channel adjustment but, alternatively, the lack of bankside vegetation and riparian vegetation, removed by the previous flood, may make the channel more susceptible to erosion.

In many large temperate rivers the majority of work is accomplished by flood events which occur on average between twice each year and once in every five years. The hydrological significance of the dominant discharge concept is that rivers will adjust their form to accommodate moderately sized floods between their banks (Harvey, 1975). Bankfull discharge, which should roughly equate to the dominant discharge, when determined from hydrological analysis, has been expressed in terms of specific return periods (Petit and Daxhelet, 1989). A bankfull discharge return period of between one and three years, with a modal value of about 1.5 years has been established for a range of rivers. In a study of 36 North American rivers, Williams (1978) found bankfull conditions to vary between 1.01 and 32 years, although the average value was 1.5 years, and concluded that the frequency of overbank discharges must relate to flood regime. Thus, Harvey (1969) demonstrated that the channel capacity of the Wallop Brook, southeast England with a subdued groundwater-fed flow regime, was adjusted to the 7 year return period flood whereas the channel capacities of the Ter and Nar rivers with more flashy flow regimes were adjusted to 1.8 and 2.0 return period floods, respectively.

4.3.1 SEDIMENT TRANSPORT AND CHANNEL STABILITY

Temporal variations in river channel and valley morphology results from the processes of erosion, sediment transport and deposition. Erosion and sediment transport occurs in areas of high water velocities. At low flows such areas will be very restricted and the movement of sediment minimal. During floods, however, many areas will have high water velocities and large amounts of material, primarily within the river channel but also occasionally on the floodplain, can be eroded and transported downstream. Ferguson (1981) has likened this episodic transfer of sediment along a river to a jerky conveyer belt. Deposition of sediment occurs during decreasing flow velocities, or in areas of the river channel or floodplain that maintain slow-flowing or slack water.

Within a given river channel reach, if erosion exceeds deposition a lowering of the river bed will occur (degradation). If net erosion and deposition are equal, vertical stability will be maintained. Channel and floodplain landforms and their stability, in this context, can also be viewed in terms of the balance or otherwise between sediment supply and transportability. A tripartite classification of rivers can thus be visualized:

1. Eroding – progressive degradation of the stream bed and/or channel widening, due to a deficiency of total sediment load;
2. Stable – no progressive change in channel form, although short-term variations may occur during floods;
3. Depositing – progressive channel and floodplain aggradation and/or lateral deposition along channel margins due to an excessive sediment load.

Rivers are rarely in equilibrium with current flows and sediment discharges but adjustments in channel planform, cross-section and long profile lag behind process change. Central to the concept of an equilibrium between form and process is negative feedback. For example, if a channel is too narrow for a given flow and sediment condition, bank erosion may enlarge the channel and reduce flow velocity.

Thus, river channels can sometimes rapidly readjust towards pre-flood dimensions. The time taken for a channel to return to its original form, after a flood-induced change (relaxation time or recovery period) in temperate rivers is usually fast in relation to the return periods of floods with rapid revegetation being an important component of the recovery process. For example, channel erosion caused by storm Agnes in eastern USA increased channel widths by 160% but subsequently, low and medium flows soon reduced the channel width by deposition along the river margins (Gupta and Fox, 1974). Some adjustments of channel form occur over a longer time than climatically or human-induced changes in river or sediment regime. Consequently, processes at some time in the past can also be important in determining current morphological form (Ferguson, 1981; Starkel *et al.*, 1991).

Furthermore, most large rivers have features that relate to their history over long time-scales. Many rivers within temperate climatic zones were at some time during the Quaternary subject to periglacial and/or glacial processes (Starkel, 1991) and the effects of such processes are often still observable in the present-day river morphology (Ferguson, 1981) or within the floodplain sediments (Starkel *et al.*, 1991).

4.4 THE LONGITUDINAL DIMENSION

Rivers and their floodplains typically show a systematic change downstream in geomorphic and hydraulic variables in response to incremental discharge increases, inputs of sediment, changes in slope and the changing nature of sediment load in transit. Indeed a river, in the longitudinal sense, can be viewed as being a geomorphic continuum. The gradient from headwater reaches to the mouth has been described as a 'spectrum of differentially variable habitats' (Minshall *et al.*, 1985). Local variability, induced for example by bedrock differences, prevents any smooth geomorphological adjustment to changing discharge and sediment load downstream. Tributary junctions, the location of incremental increases in discharge and sediment, are often zones of complex hydraulic and geomorphological adjustment and interrupt any gradual downstream transition through geomorphological river types (Petts and Thoms, 1987; Roy and Roy, 1988; Reid *et al.*, 1989).

4.4.1 LONGITUDINAL CHANGES IN CHANNEL SLOPE

The longitudinal profile of a river is typically concave with progressively lower gradients downstream. Miller (1958) found that when comparable-sized rivers join, the stream gradient below the junction averages one-third of the sum of the two tributary gradients and stream channel width is two-thirds of the sum of the tributary widths. The degree of concavity, however, varies between rivers according to a host of factors including inherited landscape form, underlying rock type and variability in runoff (Figure 4.2a). Abnormal profiles also often occur and profiles can be interrupted by lakes. The essentially concave profile of a river is of paramount importance in affecting stream power and the nature of morphological adjustment downstream of channel form and floodplain development.

At the reach scale the long profile may locally steepen or be reduced in gradient due to localized aggradation and degradation processes and bedrock control. Such local variability in slope will cause stream power to vary over short reaches. Superimposed on the overall longitudinal profile and reach-scale gradient variability are local slope changes; the most common of which are induced by pool–riffle sequences (Keller and Melhorn, 1978). Pools are characterized during low flow by relatively deep slow flowing water with fine bed material, whereas riffles, formed by lobate accumulation of relatively coarse material, are characterized by shallow more rapidly flowing water and gravel-size sediments (Figure 4.2b). The structure and composition of riffle sediment is examined within this chapter under the section on the vertical dimension. The spacing of these rhythmical pool–riffle morphological units are often approximately 5–7 times channel width.

Within channels with well-sorted sand or silty material channel slope, at the local scale, may also show systematic changes in elevation due to the formation of sandwaves forming traverse sand bars and during

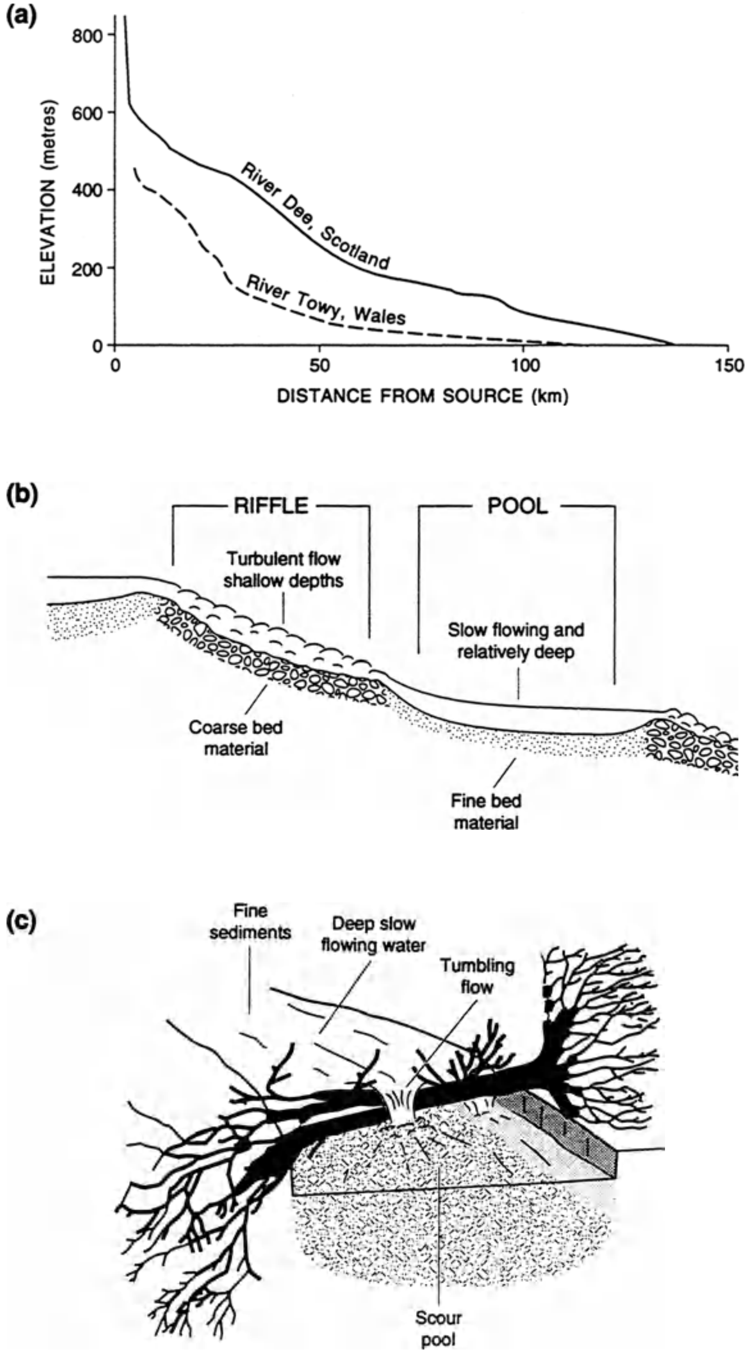

Figure 4.2 Longitudinal variations in channel gradient. (a) The long profile, (b) pool–riffles, (c) log jams.

periods of high discharges sand dunes can be formed. The size and shape of these bedforms change with time since their form is directly related to flow velocity. The bedforms, in turn affect flow properties via their influence on hydraulic roughness (Simons and Richardson, 1966).

Step-pool systems (Chin, 1989) sometimes replace pools and riffles in mountain streams where the size of bed materials is large relative to the size of the channel and/or channel slope is steep. A variation of the step-pool system also occurs in heavily vegetated basins where channels incorporate large organic debris and provide the material to form log jams and steps (Beschta and Platts, 1986; Robinson and Beschta, 1990; Gregory and Davis, 1992). In some Californian creeks, at least 50% of the pools are associated with large organic debris (Keller and Tally, 1979). The hydraulic effects of such steps in the long profile is to provide relatively deep and still water environments upstream and tumbling flow downstream (Figure 4.2c). The internal contrast between pools and riffles and differences in comparison to step-pools and log jam-induced geomorphological forms provides varied ecological niches for aquatic life with unique substrate and hydraulic characteristics.

4.5 THE VERTICAL DIMENSION

4.5.1 LONGITUDINAL CHANGE IN BED SEDIMENTS

The nature of the channel substrate surface is critical in terms of channel bed stability during flood events and as a substratum for biotic colonization. The characteristics of the channel bed sediment is also important in determining the depth and nature of the hyporhoeic zone. The frequency of substrate disturbances is also an important reset mechanism within the stream environment. For example, within substrates disturbed frequently, invertebrate populations remain young, whereas in protected substrate environments, invertebrate populations are skewed towards older populations (Minshall *et al.*, 1985). The nature of the substrate will depend on the sediment transport characteristics within any given section of channel. For example, in areas of high stream power, in the absence of large sediment inputs, the substrate may be bedrock; more commonly, channel substrates consist of a surface layer of stones with finer material beneath (Figure 4.3a). Thus the average grain size of a riffle armour layer on the Rivert Trywery, Wales was 62 mm, and yet the mean particle size of the underlying substrate material was 23 mm. (Figure 4.3b)

The particle-size distribution of the finer material beneath the armour layer will normally show a bimodal distribution (Figure 4.3b). The percentage of fine material relates to the relative importance of intrusion of fine sediments during low flows (Beschta and Jackson, 1979) and removal

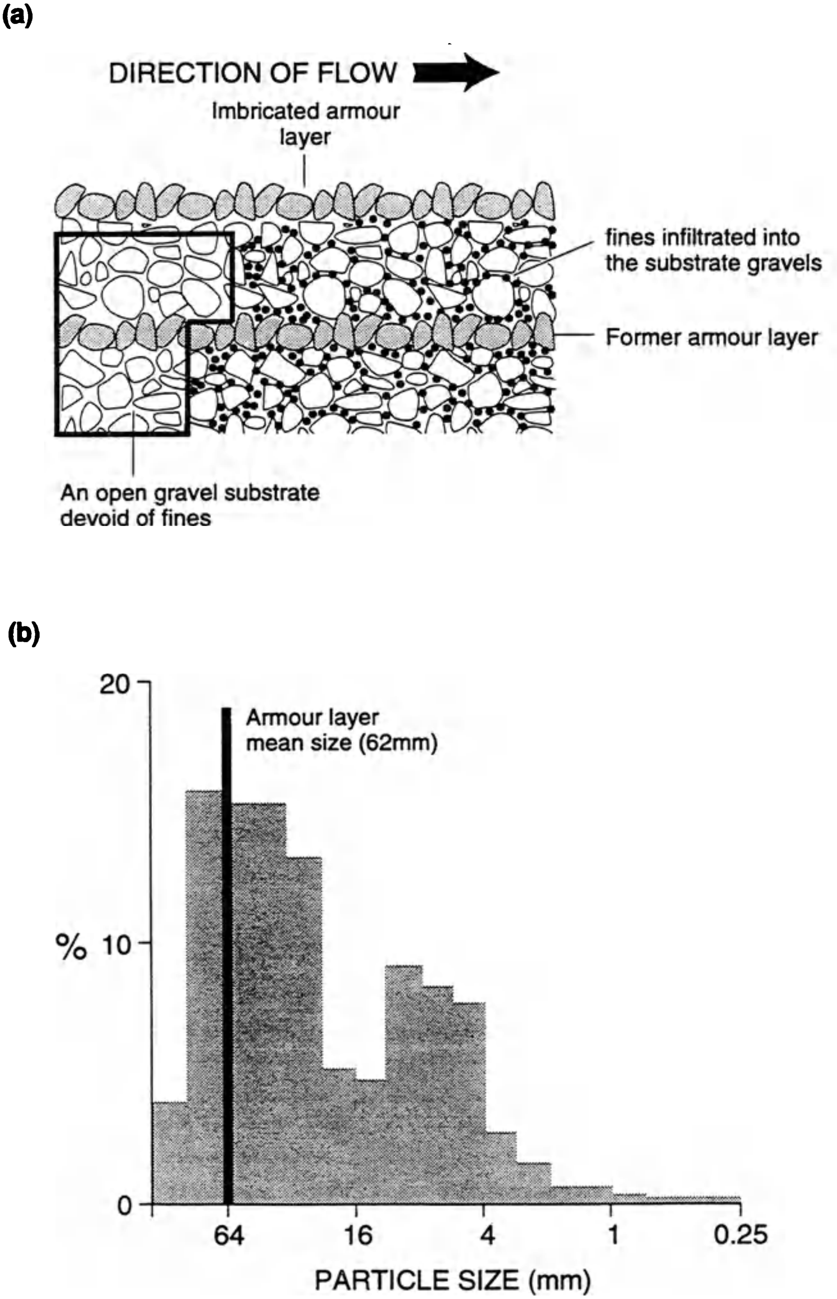

Figure 4.3 (a) Typical changes in structure and grain size of a substrate within a gravel-bed river. (b) Histogram of the grain size distribution of substrate gravels on the River Tryweryn, Wales.

of the fine material during high flows (Carling and Reader, 1982), disruption of the armour layer being needed if fine sediments are to be flushed from substrate framework gravels (Bathurst *et al.*, 1979). Absence of these flows or excessive deposition of fine material can cause clogging of gravels at depth; in extreme cases water flow through the gravel is prevented and this can be detrimental to biota (Gustafson-Greenwood and Moring, 1991).

Bed material size and the amount and mode of transported sediment changes markedly downstream usually reflecting large-scale and local variations of slope. Bed material grain size tends to show an exponential decline downstream due to particle sorting and abrasion. Particle sorting occurs because smaller particles are preferentially entrained and transported further downstream and because in headwater streams small particles are absent because they cannot resist high bed shear stresses. Abrasion is a summary term covering such mechanical processes as grinding and chipping. For the River Noe, Derbyshire, UK mean grain size decreases from 65 mm close to the source to only 30 mm at 20 km downstream (Knighton, 1980). Generally the reduction in bed material particle size follows an exponential decline curve but introduction of coarse sediment, via tributaries, lithological differences in bed material and reach variability due to stream power changes can all introduce scatter in the relationship (Troutman, 1980). Lakes can also interrupt sediment transport via sedimentation and cause the nature of the bed material to be markedly different from that upstream. Abrasion and sorting, not only affect particle size, but also tend to cause the bed material to become more rounded and better sorted downstream (Knighton, 1982).

4.5.2 LONGITUDINAL CHANGES IN CHANNEL CROSS-SECTION

Channel capacity adjusts to accommodate the discharge and sediment load from the drainage basin, within the constraints of boundary composition and valley slope. Since discharge and sediment load increase downstream channel capacity should similarly vary. Generally, changes in channel form can be summarized by stating that as one moves downstream there is an increase in channel capacity. The rate of increase in channel capacity downstream can be highly variable (Figure 4.4) Park (1976), using hydraulic geometry, found that channel capacity increases more quickly on steep catchments and the rate of increase varies with rock type because both these variables control the rate of discharge increase downstream.

The downstream hydraulic geometry relations of Leopold and Maddock (1953) given as averages for selected rivers in the midwestern

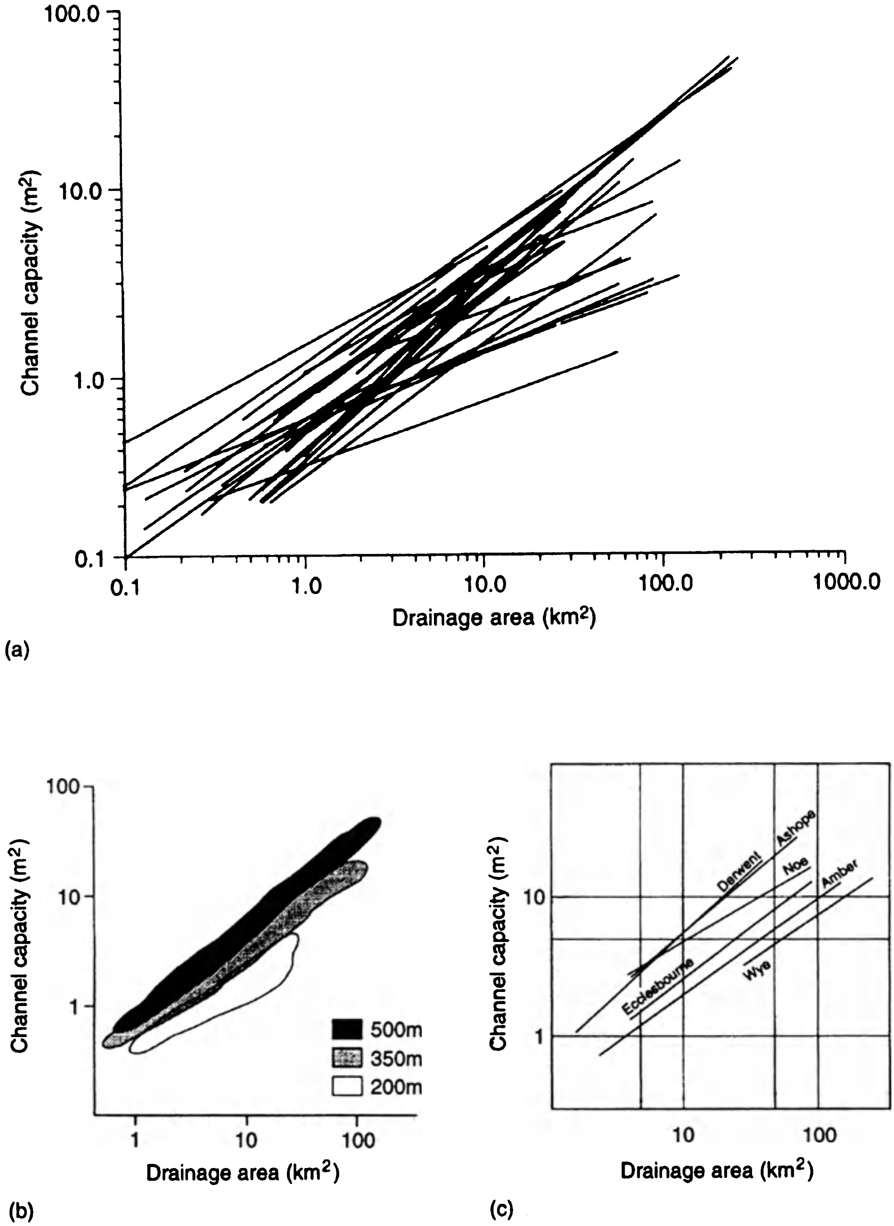

Figure 4.4 Channel capacity and drainage area relationships: (a) for temperate zone drainage basins (after Gregory and Maizels, 1991); (b) showing the influence of relief for rivers in Devon, UK (after Park, 1976), and (c) of bedrock rock types in the Derwent basin, UK (after Petts, 1977): the Derwent and Ashope drain impermeable basins and the Wye drains a permeable (limestone) catchment, the other rivers drain basins of mixed rock types.

United States are

$$w = aQ^{0.5}$$
$$d = cQ^{0.4}$$
$$v = kQ^{0.1}$$

Such relations imply an adjustment of channel shape whereby the depth becomes proportionally smaller in relation to width while velocity only increases slowly downstream.

Factors other than hydraulic ones may also control channel morphology inducing scatter in the hydraulic geometry relationships. Perhaps the most important non-hydraulic factors are the channel boundary sediments and the sediment load. Schumm (1971) after examining the relationship between channel shape and percentage silt-clay in channel boundary materials concluded that channels with dominantly a suspended sediment load tend to be narrow and deep, whereas channels dominantly transporting material as bedload tend to be wider and shallower. Parker (1979) has predicted that for a given discharge, a 30% increase in gravel load leads to a 25% reduction in depth but a 40% increase in width. In such channels shear stresses are directed more against the bed than banks inducing width increases. Obviously the composition and strength of bank material will also be important in determining the importance of bank erosion and cross-channel width. Vegetation can also be important in controlling channel cross-sectional form via its influence on bank stability. Riparian vegetation increases bank stability, leading to channel narrowing. Charlton *et al.* (1978) found that channels with grassy banks were on average 30% wider but tree-lined channels 30% narrower than the overall width–discharge hydraulic geometry relationship would suggest.

4.5.3 LONGITUDINAL CHANGES IN RIVER PLANFORM

A classic paper by Leopold and Wolman (1957) distinguished between braided, meandering and straight river channel planforms based on the criteria of sinuosity and channel multiplicity (Figure 4.5, Table 4.1). Meandering channels are single thread channels that wind their way down valley via a series or arcs of more tortuous bends. Straight and meandering channels are defined by an arbitrary sinuosity value of 1.5 but values below this can also be braided. Braided rivers consist of a number of channels separated by gravel islands that tend to be highly mobile, due to high rates of bedload transport.

In reality a spectrum of channel types between extensively braided and meandering exists (Rust, 1978; Kellerhals and Church, 1989). Indeed, Ferguson and Werrity (1983) identified a transitional class of 'wandering gravel rivers' having low to medium sinuosity and combining features

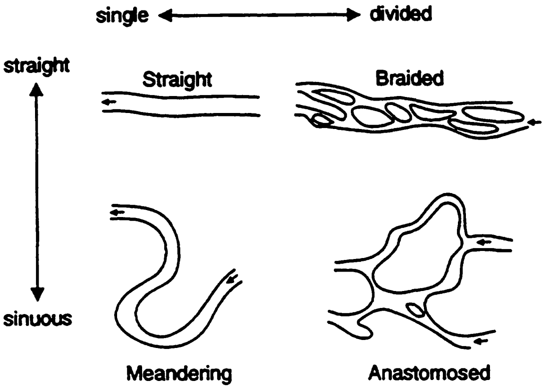

Figure 4.5 Channel pattern types as defined by the classification of Rust (1978) based on channel sinuosity and channel mulitiplicity.

of both meandering and braiding with wide shallow channels, flanked and locally divided by gravel bars. Another planform type consists of low energy stable channels that occasionally divide and then rejoin further downstream. They are associated with subsiding sedimentary basins or rising local baselevel and high sediment yields and are termed anastomosed rivers (Smith, 1983).

Leopold and Wolman (1957) identified two primary controlling variables on channel planform; discharge and slope. Given that both these controlling variables systematically change downstream, concomitant changes in river channel planform should be evident. Leopold and Wolman's work together with a number of other studies substantiate two rules with respect to the influence of slope and discharge in controlling channel planform. First, for any given discharge and bed material there is one threshold slope above which channels will meander and another higher one above which they will braid and second, that the critical slope decreases with increasing discharge. Ferguson (1981) interpreted the slope control as thresholds of specific stream power. In a study of 95 British rivers, Ferguson identified three river channel planform types each with a specific range of stream powers. Inactive straight or sinuous channels tended to have low specific power, actively shifting low sinuosity channels had high power and actively meandering channels were intermediate.

Since stream power generally decreases downstream, and abrupt thresholds in planform transition from braided to meandering are evident, one might expect a rapid transition from braided to meandering planforms somewhere along the long profile. Although in some cases this occurs and upland rivers are more prone to braiding than lowland streams, which tend to meander, because of the complexity and number of variables affecting river planform, there is not always a systematic change in planform type downstream.

A common factor in causing anomalies or blurring the division between types is downstream changes in boundary material composition, bank erodibility and sediment load. Where the bed material is coarse, bank material highly erodible, or the dominant form of sediment transport is bedload there will be a tendency towards braiding. In areas where bank erosion cannot occur, such as bedrock channels, channels tend to be straight. Elsewhere river channels are likely to meander. Mackin (1956) described a channel in Idaho that braids on emerging from forest to grassland and reverts to meandering on re-entering the forest and explained this in terms of vegetation control on bank erodibility.

Although there is often no simple transition in planform type downstream, within meandering rivers, systematic changes in meander morphology do occur. Meander forms (Figure 4.6a) tend to become larger downstream, since meander form is correlated with discharge or a surrogate variable such as drainage area (Figure 4.6b) and are frequently 10–14 times channel width. Boundary materials and sediment load, however, can distort this general rule. For a given channel width, sand and gravel rivers tend to have greater meander wavelengths than silt–clay transporting rivers.

4.6 THE TRANSVERSE DIMENSION

Rivers and floodplains exhibit large morphological diversity in the transverse dimension. From the centre of a river channel to the valley-side, morphological changes are caused by variability in the competence of flows to transport sediment, past river channel changes and modification of fluvial landforms by subaerial processes. The transverse changes can most easily be examined with reference to flow characteristics, within channel morphology, and floodplain form. Morphological variability across floodplains relates, to a large extent, to river channel changes and as such, material relevant to this section is also covered in the section on river planform changes.

4.6.1 FLOW CHARACTERISTICS

Within a river channel cross-section, considerable variation in water velocity and flow characteristics occur. The velocity distribution can be shown by isovels, lines of constant velocity. Generally water velocities are greatest in mid-channel and much lower at channel margins and close to the stream-bed. This spatial variability across the channel is well exemplified by the case of the River Swale, England, both at low and

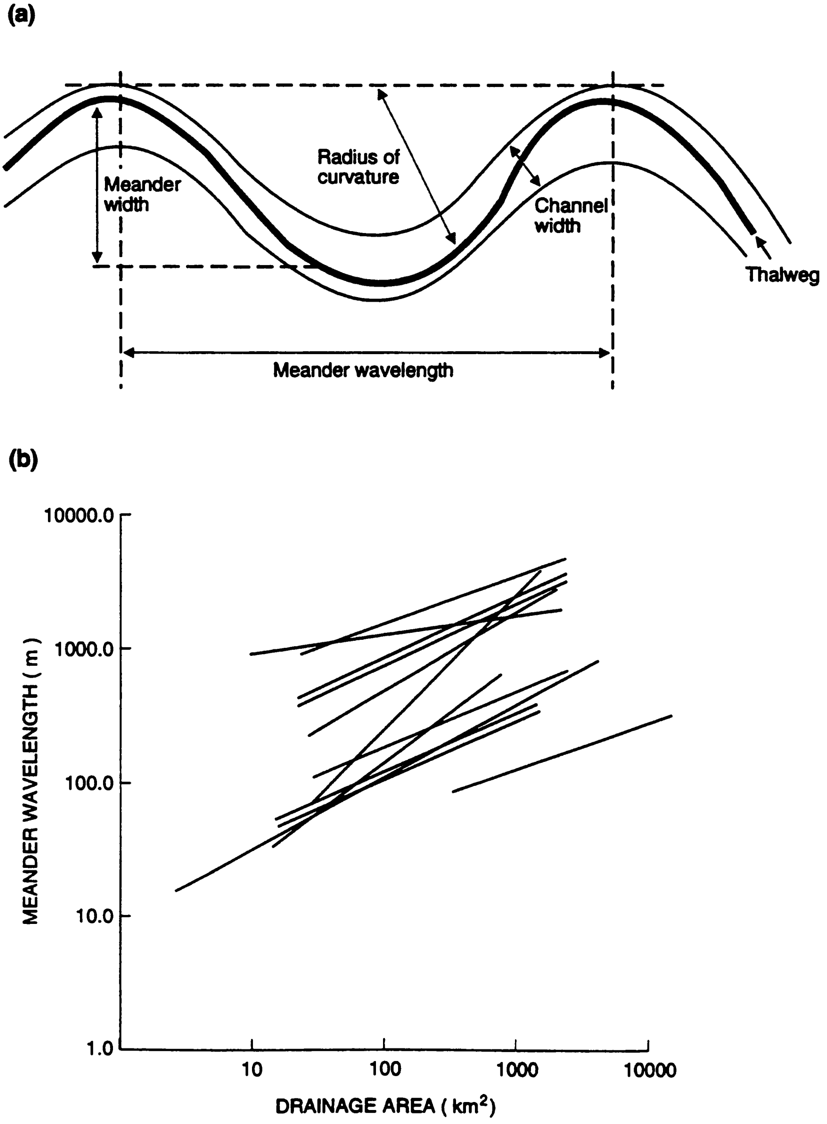

Figure 4.6 (a) Definition of meander form variables. (b) Relationship between meander wavelength and drainage area for temperate rivers (based on Gregory and Maizels, 1991).

high flows (Bathurst, 1979). With an increase in discharge, at a given channel cross-section, not only does mean water velocity increase as predicted by hydraulic geometry relationships, but high velocities are also found in proximity to the channel boundary sediments (Figure 4.7a);

these two factors also promote an increase in boundary shear stress which also generally exhibits highest values towards the centre of river channels (Figure 4.7b). At river bends, however, centrifugal forces give rise to an excess fluid pressure on the outer bank and a deficit on the inner bank. This induces a surface water gradient between the inner and outer bank and a circulatory pattern of flow, termed helicoidal flow, is superimposed on the downstream movement of the water (Hooke and Harvey, 1983; Geldof and de Vriend, 1983); flow is outward close to the water surface, downward at the outer river bank and inward towards the inner bank on the apex of the meander bend. The area of maximum water velocity or 'thalweg' in response moves towards the outer bank (Figure 4.7c).

Water velocities and boundary shear stress across the floodplain during inundation are generally much lower than within the channel itself. Along linear depressions within the floodplain, which often represent 'old' river courses, streaming of floodplain waters can occur with associated high water velocities (Figure 4.7d).

In planform, the transverse variability in flow pattern may be shown by streamlines (Figure 4.8) which are lines parallel to instantaneous water velocity vectors. In a uniform and straight channel flowlines would be parallel but due to changes of cross-sectional form such as between pools and riffles or due to obstructions such as large boulders flowlines often converge and diverge. Meander bends also cause streamlines not to be parallel with convergent flow towards the apex of the bend being characteristic with divergent flow between successive bends. On the floodplain streamlines will be controlled by the surface topography.

4.6.2 CHANNEL BEDFORM

River channel bed morphology is often complex in form and relates to the movement and subsequent deposition of bed load material. Accumulations of bed material are referred to as bars; for example riffles are lobate gravel bars, but are usually studied independently of other bar forms due to their regular spacing. Bars may consist of coarse or fine material, be relatively stable or mobile, be attached or detached from the river banks and take on a variety of symmetrical and asymmetrical forms (Church and Jones, 1982). In general, mid-channel bars are found on braided rivers (Figure 4.8a), lateral bars and diagonal bars on straight or wandering gravel-bed rivers (Figure 4.8b, c) whereas point bars form on the inside of bends within meandering rivers (Figure 4.8d). The diversity of bar forms and changes in bar morphology through time makes it difficult to formulate simple models of bar form and growth. Bar morphology may either consist of one simple form, represent the coalescence of individual elements or lobes, or result from the modification of a

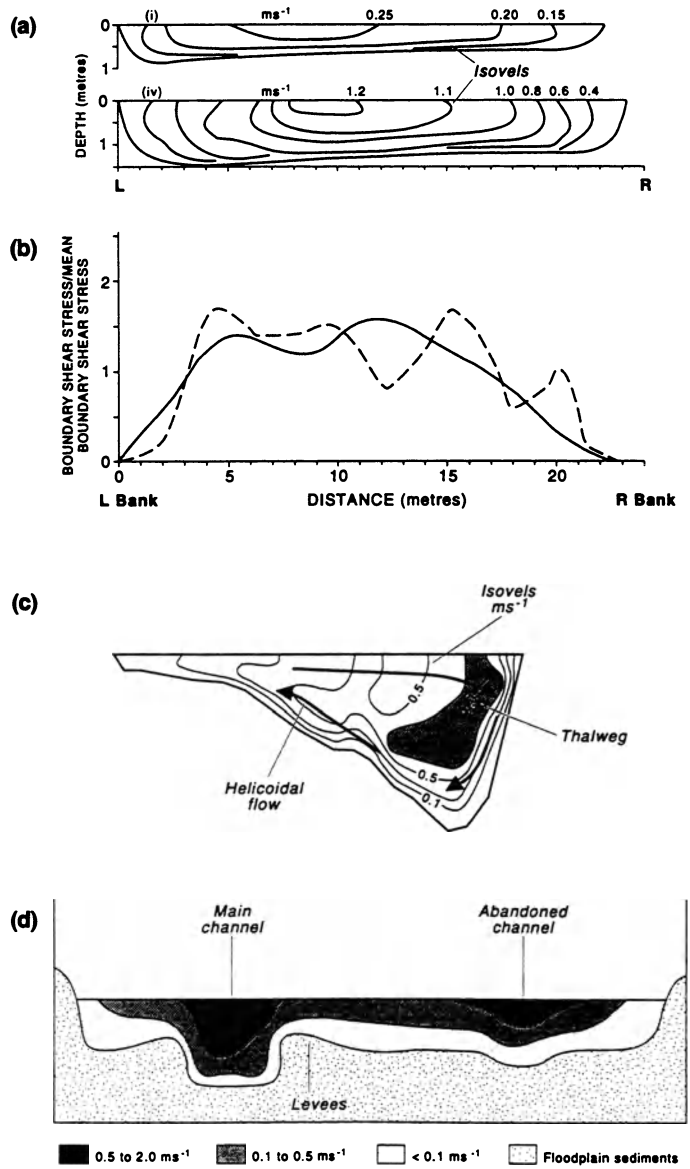

Figure 4.7 Variability in flow characteristics within channel cross-sections. (a) A typical cross-section on the River Swale, England, showing the pattern of water velocity across the channel both at high and low flow (after Bathurst, 1979). (b) The pattern of boundary shear stress on the River Swale for the same cross-section as above (after Bathurst, 1979). (c) The nature of cross-sectional water velocity on the apex of a meander bend. (d) A schematic diagram of the effect of floodplain topography on the depth and velocity of floodwaters.

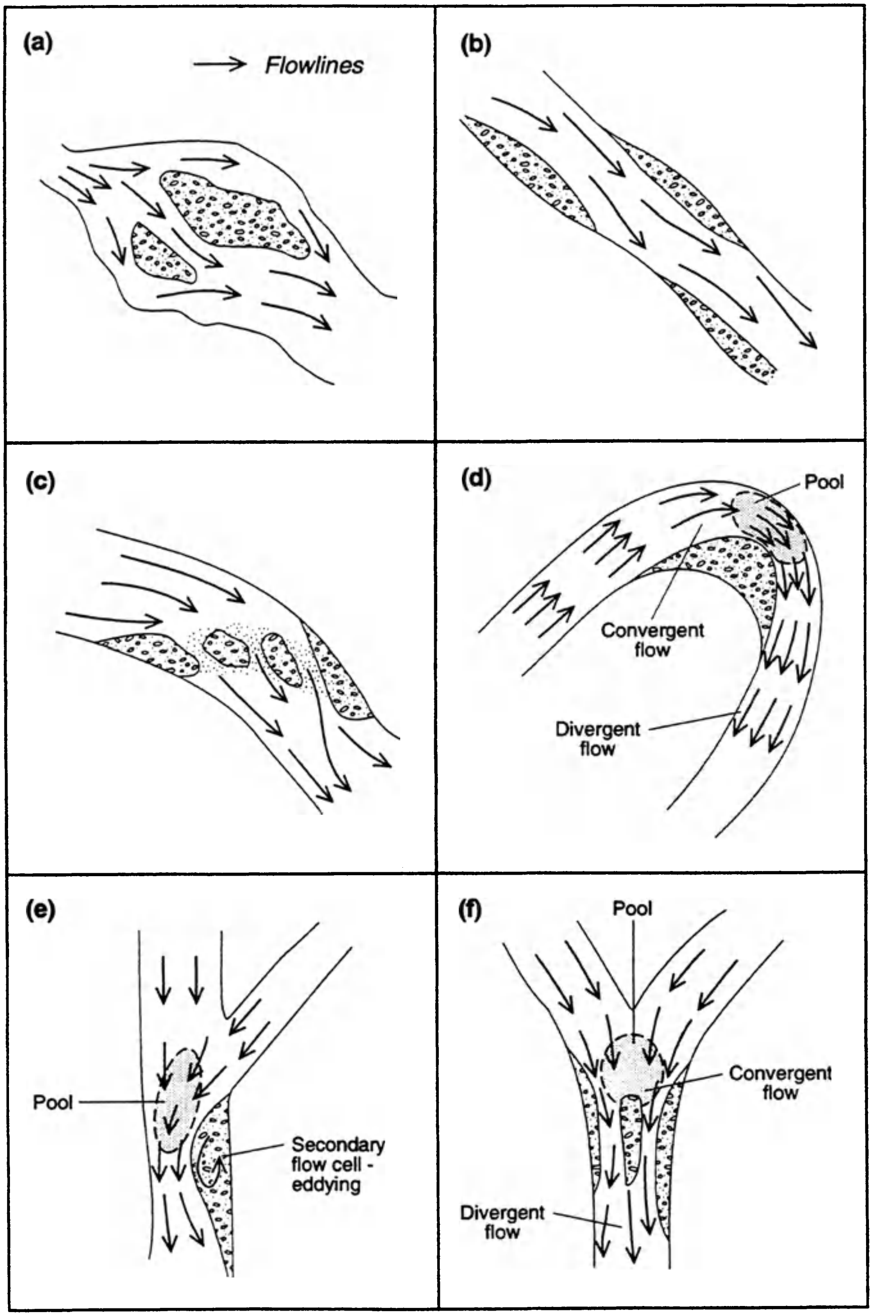

Figure 4.8 Simple bar forms and flow patterns found within temperate gravel-bed rivers. (a) and (c) Mid-channel bars, (b) and (d) lateral bars, (e) diagonal and (f) tributary confluence bars.

of individual elements or lobes, or result from the modification of a simple form by marginal erosion and chute dissection. Most bar forms consist of an upstream portion of coarse sediment, otherwise known as the the bar head, with a 'tail' of finer material downstream. Inner depressions on lateral or point bars, sometimes with slack water, may represent unsedimented portions of the former river channel blocked off from the main flow. In some cases, bar morphology may not be simple because subfeatures within the bar complex relate to various stages of development and/or the effects of extreme floods. Figure 4.9a shows a complex bar feature on the River Tummel, Scotland with two distinct 'tails'. The tail closest to the main flow (bar tail 1) formed during a large flood event in 1990 in the lee of further vertical and lateral bar head growth during the same flood. Subsequently a third bar tail formed during a large flood in 1993 (not shown in Figure 4.9a).

Associated with bar forms and channel bed topography is variability in bed material grain size. Grain size tends to be greatest in the centre of the channel where water velocities are greatest with finer material accumulating at channel margins. Within meander bends because the water velocity is greatest close to the outer bank, grain size tends to be at a maximum here and slowly decreases towards the inner bank. However, because bar morphology is often complex, variability in grain size across the channel does not always conform to a simple pattern. Moreover, changes in bar particle size occur through time in response to bar development. Thus, despite no change in mean grain size of a gravel bar on the River Tulla, Scotland, over a two-year period, Bluck (1982) demonstrated a change in the pattern of particle size variability (Figure 4.9b).

4.6.3 FLOODPLAIN MORPHOLOGY

Floodplains represent sediment sinks in which eroded sediments are sorted, reworked and undergo pedogenic or biogenic processing. Transverse changes manifest themselves in the variability in surface elevation, soil type and lateral and vertical variability in underlying stratigraphy. Lewin (1978) identified three general floodplain types reflecting the nature of sedimentation and channel migration (Figure 4.10): some are simply dominated by overbank sedimentation with relatively stable channels, others are dominated by relict point bar forms and actively meandering channels, whereas floodplains with multiple channels that switch from one side of the valley floor to another produce a highly varied and complex morphology. Rates of bank erosion can vary considerably even within a single climatic zone (Table 4.2). Rates of floodplain aggradation are also highly variable both between and along rivers (Walling *et al.*, 1992). Thus, Shotton (1978) reports an average rate of deposition of 0.5 cm yr^{-1} over the past 3000 years on the floodplain

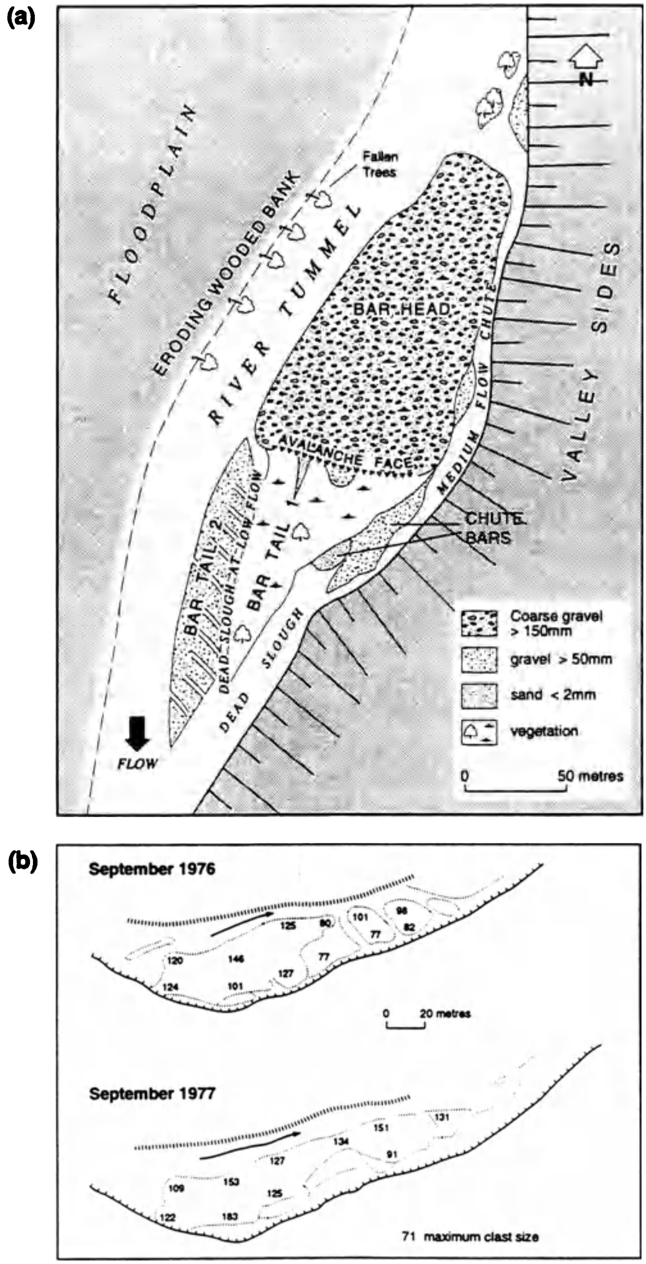

Figure 4.9 (a) A complex bar form modified by bar head growth during a flood in 1990; River Tummel, Scotland. (b) Changes in the form and grain size of a bar on the River Tulla, Scotland, between September 1976 and September 1977 (after Bluck, 1982).

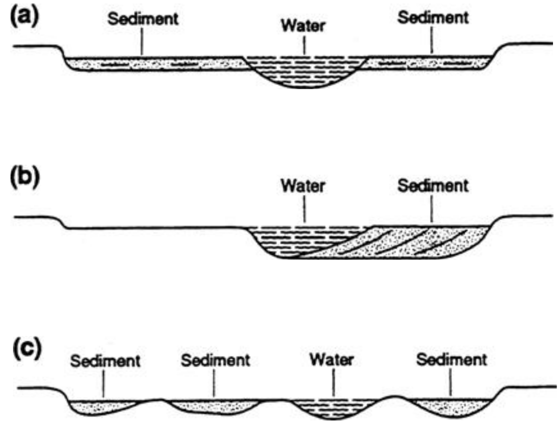

Figure 4.10 The three basic types of floodplain formation. (a) vertical accretion, (b) lateral accretion and channel migration, (c) island formation and channel abandonment.

Table 4.2 Measured rates of temperate river bank erosion

River and location	Average rate of bank retreat (m yr^{-1})	Source
Axe, Devon, UK	0.15–0.46	Hooke (1980)
Bollin Dean, Cheshire, UK	0.0–0.9	Knighton (1973)
Wisloka, Poland	8.0–11.0	Klimek (1974)
Mississippi, USA	4.5	Stanley *et al.* (1966)
Exe, Devon, UK	0.62–1.18	Hooke (1980)
Severn, UK	0.5–0.7	Thorne and Lewin (1979)

of the River Avon, Warwickshire, UK whereas on the North Tyne, UK, Macklin *et al.* (1992) quote a figure of 2.4 cm yr^{-1}.

4.6.4 CHANNEL DYNAMICS AND MECHANISMS INDUCING CHANGE

Variability in rates of channel adjustment to flows and sediment inputs also varies downstream and quite dramatic local changes in channel stability are often apparent (Desloges and Church, 1989; Gilvear and Winterbottom, 1992; Harvey *et al.*, 1984).

Changes in channel pattern vary according to the nature of the planform geometry. Meandering channels shift their position primarily by extension, translation, rotation or enlargement although differences in bank strength ultimately cause complex changes in form to occur (Figure 4.11a) (Hooke, 1977). Briaded river channels change chaotically in response to bar development and shift their position laterally across the floodplain

(Ferguson and Werrity, 1983). Wandering gravel bed rivers exhibit a number of types of movement including meander development and avulsion. Avulsion is the process whereby a channel shifts from an old course to a new course leaving an intervening area of floodplain intact. Generally, rates of channel shifting are greater for braided rivers, then wandering gravel bed rivers and slowest in the case of meandering rivers, although locally bank erosion on the outside of meander bends can be quite rapid.

In actively migrating river channels changes in river planform can occur over short time-scales and the full floodplain width can be 'swept' by channel migrations within a few centuries. Channel migration since 1840 on the River Dane, Cheshire, UK has affected virtually all of the current floodplain (Figure 4.11b) (Hooke and Redmond, 1989) implying limited soil pedogenesis and relatively little time for vegetation succession. Lewin and Weir (1977) concluded that the lower Spey, Scotland has reworked about half of its valley floor since the 1880s. Harvey *et al.* (1984) working in the Middle Cargill Valley, Northern England, also demonstrated that below the most recent terrace level (approx. 1000 BP) approximately 50% of the valley floor sediments were post-mid-19th century and of these young deposits 50% were less than 50 years old.

4.7 VALLEY FILLS AND FLOODPLAIN SEDIMENTOLOGY

Typically in headwater areas a V-shape valley form is characteristic with little or no floodplain development and often a reasonable correlation is found between maximum valley-side slope angle and basal stream gradient. In these areas, valley-side fluvial processes and valley floor are inextricably linked; for example, channel erosion at the base of a valley side may induce a landslip which inputs a large amount of sediment into the river and alters its morphological form. In streams greater than fourth order the relationship between hillslope and channel gradient is weakened as a floodplain develops and valley-fill reduces the linkage between slope and stream.

Floodplain size is generally related to the discharge of the river. For example, floodplain widths for three major Welsh rivers varied between 250 and 1100 m (Lewin and Manton, 1975), whereas the active floodplain width of the lower Mississippi is 16 km. A study of the River Ouse, Sussex, UK, over a source to mouth distance of 66 km demonstrated a progressive increase in floodplain width from 50 m to 1250 m, an increase in mean depths of alluvial sediments from 1.5 m to 32 m and an increase in cross-sectional area of alluvial fill from 63 m^2 to 40 000 m^2 (Burrin and Jones, 1991) (Figure 4.12). The study also demonstrated that the valley-fill lithology became increasingly complex downstream and included perimarine facies close to its mouth. Inclusion of marine sediments into current river floodplains indicates either the build up of

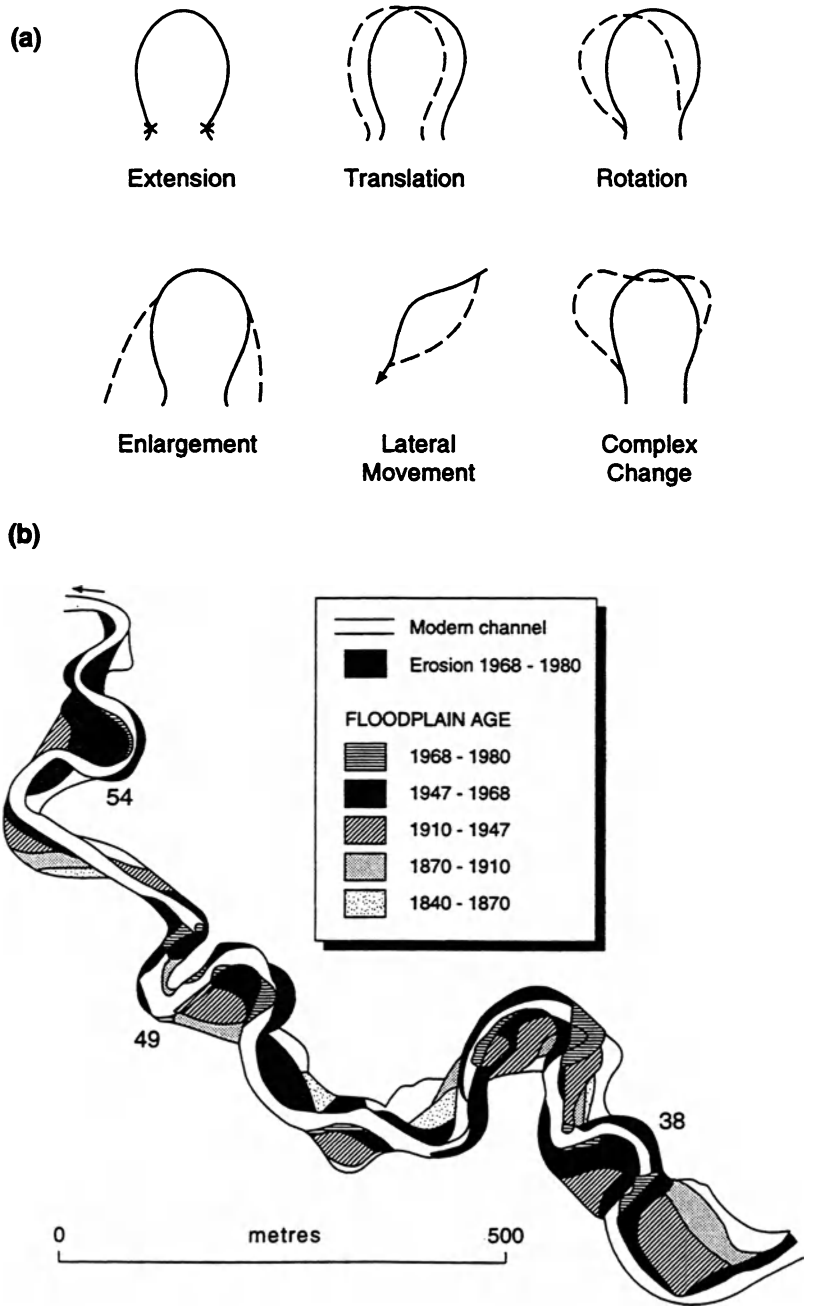

Figure 4.11 (a) Modes of meander bend development (after Hooke, 1977), (b) The effect of channel changes on the sedimentology and floodplain surface age; River Dane, Cheshire, UK (Hooke *et al.*, 1990).

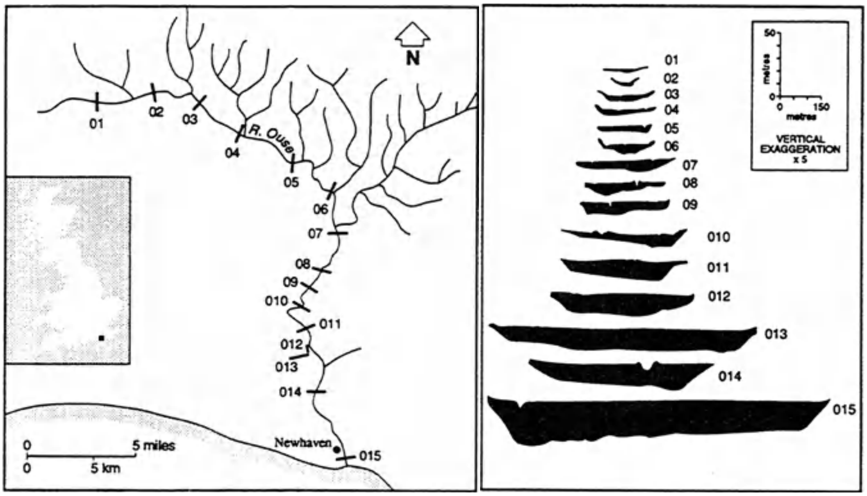

Figure 4.12 Longitudinal change in the size, lithostratography and morphology of the River Ouse floodplain, Sussex, UK (after Burrin and Jones, 1991).

riverine sediments above sea-level or that sea-level was once higher and flooded the lowest portion of the river long profile.

River terraces are another important feature of river valleys, and represent former floodplains abandoned when river incision leaves them at a height above the river where the frequency of inundation is significantly reduced. Terrace remnants may be only a few metres above river level and may be periodically flooded by large flood events. Older terraces can be found at considerable elevations above the current valley floor although more often than not only discontinuous remnants of the former surface exist. Terrace forms may be preserved for several million years and former channels with 1–3 m of relief can be preserved on terraces of the order of 10^5 years under humid temperate climates (Coleman, 1983). They therefore provide important indicators of former fluvial processes, but depositional variation, terrace modification and complex response make interpretation difficult.

Floodplain sediments and valley fills are generally composed of fluvial sediments transported by the river at sometime in the past. The thickness of many valley fills emphasizes the length of historical record that they represent. Vertical variability in the sediment also demonstrates that a range of environmental processes may have occurred over these long timespans. For example, valley fills can contain fluvioglacial or aeolian sediments deposited at the end of the last glaciation. Similarly, the depth of valley fills in lowland temperate rivers often relates to sedimentation induced by a rising sea level throughout much of the Holocene (Kiden, 1991). A vertical sequence of floodplain sediments thus represent a library of information with regard to former fluvial processes and sedimentary conditions.

Hydrological and geomorphological structure of hydrosystems

5

J.-P. Bravard and D. J. Gilvear

5.1 INTRODUCTION

Chapter 4 described the basic mechanisms of river dynamics, emphasizing longitudinal and transverse variability in morphology and flows of water and material. This chapter applies information on river morphology and dynamics to examine the physical structure of hydrosystems. The interplay between river channels and the set of environmental variables determines geomorphological 'styles'; the basis of 'functional sectors' with their distinct patchworks of special habitats.

5.1.1 LONGITUDINAL PATTERNS

Previous chapters have demonstrated the relatively progressive nature of the downstream changes which take place in the character of watercourses: increased flow, width and depth of the channel; progressive reduction in sediment size and gradient. This general model describes an upstream–downstream continuum which has been incorporated into ecological models. Without challenging such general principles, subsequent contributions to our understanding of the fluvial continuum have substantially enriched this concept. First, it has been shown that the functions linking the elements of the system together are rarely continuous and are often 'stepped', reflecting the organization of the

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drainage network. Thus, a major tributary can substantially affect the characteristics of a watercourse. Bruns *et al.* (1984) have shown on the Middle Fork of the Salmon River (United States) that an input of coarse material from a heavily sediment laden tributary resets the ecosystem to the condition typical of a stream of lower order. This occurs because the recipient watercourse becomes steeper downstream from the confluence and the current speed increases. Also, frequently along a large watercourse there will be a discontinuous downstream gradient in physical parameters although the conventional development from a braided style to a meandering style, which is characteristic of a mountain/piedmont section followed by a plain section is not always the case. This type of complex upstream to downstream gradient is particularly frequent in western Europe, where the effects of the Alpine orogeny, fragmentation of the Hercynian basement or local subsidence, and finally the effects of the Quaternary glaciations, all act together. Thus the Rhine has three base levels: Lake Constance (a glacially overdeepened lake), the Bingen Gorge passing through the Rhenish Schiefengebirge and finally the North Sea. It approaches an equilibrium profile in these three successive sections and develops a meandering style three times in the downstream portion of each section. In France the upper Rhône shows a complex profile with a similar origin, but without the influence of recent tectonics as in the case of the Alsatian Rhine or the Danube. On leaving the Jura, the braided style of the Rhône, which is of an Alpine nature, is interrupted for a few kilometres by large meanders which wander over the surface of a glacial depression filled with lake sediments. It becomes braided again further downstream when the Ain brings into the Rhône bed load derived from fluvioglacial accumulations (Bravard, 1987). Thus the concept of a 'patchwork' can be expressed as the complex juxtaposition of river sections which are characteristic of upstream and downstream stretches along one watercourse.

Discontinuities also influence the ecological functioning of rivers and their adjacent alluvial plains. Thus the advantage of introducing relatively complex hydraulic parameters, such as the Reynolds and Froude numbers, into aquatic ecology has been demonstrated (Statzner and Higler, 1985). A natural watercourse is thus marked by longitudinal discontinuities in the strength of the shear force, which often passes through two maxima, one in the upstream braided zone, the other downstream from the meandering zone.

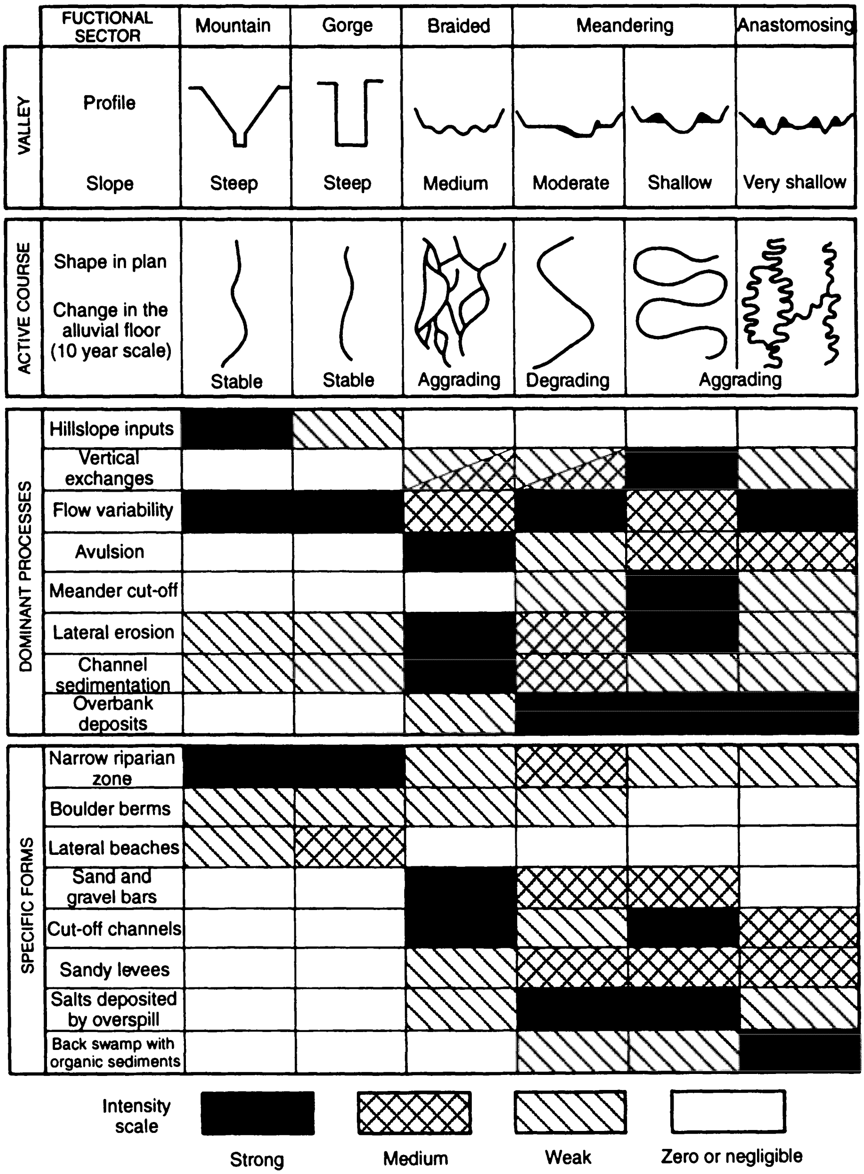
5.1.2 THE TRANSVERSE DIMENSION

One characteristic of recent research has been consideration of interactions between the main channel and the floodplain. Welcomme (1985) has emphasized the importance of the magnitude and duration of floods in the plains of tropical rivers. In large valleys where lateral constraints are weak (i.e. the ratio of the width of the floodplain to the width of the bankfull channel is high), the strength of the interactions between the river and the floodplain is such that in terms of both the dominant processes and biological productivity the longitudinal model is no longer applicable (Chapter 9). For example, Sedell *et al.* (1989) have demonstrated that the speed of flood water over a plain determines the nutrient dynamics. Rapid passage of a flood through a valley with a moderately steep gradient gives rise to rapid recycling and the productivity of the system is higher than that of areas which are permanently flooded or which are covered with stagnant water. In general the hydrological and geomorphological functioning of a river is affected by the climatic and geological characteristics of its catchment. This upstream–downstream determinism is modulated by interactions between the main channel and the adjacent riparian system, (Swanson *et al.*, 1982; Hickin, 1984). Regardless of the nature of the biome, in desert or tropical environments, the riparian zone forms a 'ribbon of continuity' (Cummins *et al.*, 1983) or 'fluvial corridor' (Minshall *et al.*, 1985). The landscape 'patchwork' concept has enriched our understanding of the fluvial continuum not only by revealing longitudinal discontinuities but also by focusing attention on transverse exchanges between the main channel and the floodplain.

5.1.3 THE VERTICAL DIMENSION

The fluvial hydrosystem is also characterized by a vertical dimension which further expands the river patchwork concept. Hydrobiologists have revealed the ecological importance of the hyporhoeic zone, which is more than 1 m thick, located at the contact between the surface water and groundwater (Chapter 9). In an alluvial plain, the functioning of this zone is highly influenced by the sedimentary deposits which govern the surface structure of the alluvial aquifer. As a general rule, in-channel deposits are dominated by relatively permeable gravels and sands. Of particular ecological importance is the volume of voids, which governs the habitability of the substrate for benthic fauna or the suitability of the gravel beds to act as spawning grounds for salmonids.

Overbank deposits of fine sediments raise the level of the floodplain surface and fill cut-off channels, governing exchanges between the water table and the surface, as well as the thickness of the unsaturated zone. The particle size of these deposits, and their permeability, depend closely on the overflow processes: bars and levees close to the main channel are generally sandy, well sorted and permeable; those at the floodplain margins, in bankswamps and in cut-off channels, are fine deposits which can block vertical exchanges.



	FUCTIONAL SECTOR	Mountain	Gorge	Braided	Meandering		Anastomosing
VALLEY	Profile						
	Slope	Steep	Steep	Medium	Moderate	Shallow	Very shallow
ACTIVE COURSE	Shape in plan Change in the alluvial floor (10 year scale)	Stable	Stable	Aggrading	Degrading	Aggrading	
DOMINANT PROCESSES	Hillslope inputs	■	▧	□	□	□	□
	Vertical exchanges	□	□	▧ ▩	▧ ▩	■	▧
	Flow variability	■	■	▩	■	▩	■
	Avulsion	□	□	■	▧	▩	▩
	Meander cut-off	□	□	□	▧	■	▧
	Lateral erosion	▧	▧	■	▩	■	▧
	Channel sedimentation	▧	▧	■	▩	▧	▧
	Overbank deposits	□	□	▧	■	■	■
SPECIFIC FORMS	Narrow riparian zone	■	■	▧	▩	▧	▧
	Boulder berms	▧	▧	▧	▧	□	□
	Lateral beaches	▧	▩	□	□	□	□
	Sand and gravel bars	□	□	■	▩	▩	□
	Cut-off channels	□	□	■	▧	■	▩
	Sandy levees	□	□	▧	▩	▩	▩
	Salts deposited by overspill	□	□	▧	■	■	▧
	Back swamp with organic sediments	□	□	□	▧	▧	■

Intensity scale: ■ Strong ▩ Medium ▧ Weak □ Zero or negligible

Figure 5.1 Types of functional sectors characterized by valley morphology, the style of the active course, the dominant processes and the specific forms that make up the geomorphological patches within the hydrosystem (after Petts, 1990).

5.2 THE MAIN TYPES OF FUNCTIONAL SECTOR

Each functional sector may be defined by hydrological and geomorphological criteria. Different types of sector (Figure 5.1) are marked by typical

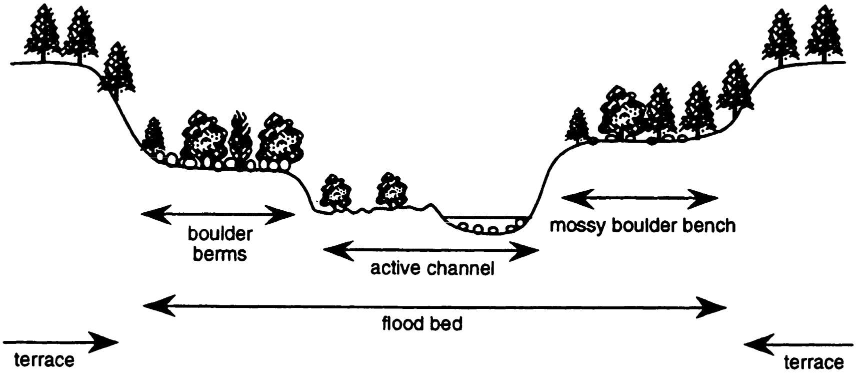


Figure 5.2 The patchwork in mountain sectors transverse profile across a low order valley in the Cascades Chain, Oregon (after Grant, 1986).

assemblages of specific forms and processes which to a large extent govern the nature and operation of the associated ecosystem.

5.2.1 MOUNTAIN SECTIONS

Patchworks of river forms, organized along the axis of a steeply sloping channel consist of a succession of pools, waterfalls, rocky rapids, pebble bars and steps created by accumulations of coarse woody debris. The associations of fundamental forms vary greatly from one river to another, depending on the nature and relative importance of the underlying rock in controlling the long profile, and the existence of inherited forms related to palaeoprocesses.

These accumulations of wood nevertheless form unstable environments because they can be displaced by debris flows and floods. Decomposition of the organic matter also contributes to the eventual destruction of even the most stable structures.

Thus in the valleys of the western side of the Cascades Chain (Oregon), the elements may be distinguished (Figure 5.2). First, the surfaces of the active channel sculpted by normal hydromorphological processes, i.e. floods with a recurrence frequency of 1–2 years. The vegetation is

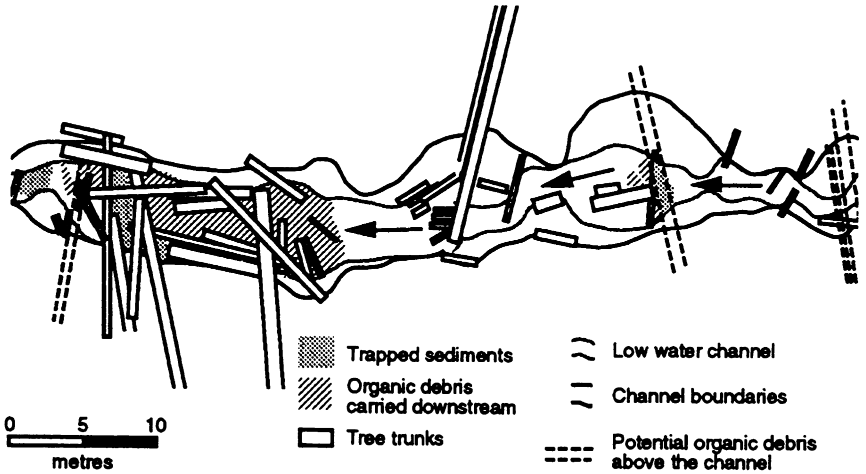


Figure 5.3 Organic debris in a small second order watercourse in the Cascades Chain, Oregon (modified after Keller and Swanson, 1979).

restricted to narrow strips of alder less than 2 years old. Secondly, boulder berms with boulders 1–2 m in diameter deposited by debris flows in those parts where the valley widens and becomes less steep (<4%). These berms, which have an elevation of 1–3 m, are populated by alder, poplars and Douglas fir. Thirdly, surfaces covered with young alder and moss-covered boulders, created by less frequent floods (3–50 years) which deposit 50 cm boulders, these destroy the conifer forest, and allow recolonization by alder. Alder benefits from the stability of the boulders, the abundance of organic material and the deposition of interstitial sand by small floods (Grant, 1986).

Heede (1981) has shown that mountain streams do not adjust laterally (by widening or varying sinuosity) but dissipate energy by establishing breaks in the longitudinal profile. These breaks may be zones of rock, pebble bars or log jams. One study has shown that 30–80% of offsets in level are due to tree trunks, which occupy 20–35% of the surface area of rivers in the Western Cascades (Oregon). The amount of debris stored in the active channel falls as the order of a watercourse increases. Beyond order 5 accumulation takes place on the banks, and no longer in the bed (Keller and Swanson, 1979).

It will be seen, therefore, that the landscape and the functioning of headwaters can be greatly influenced by the presence of log jams (Figure 5.3). These cause storage of the bed load (which only constitutes some 10% of the volume of material solely stored in the bed) and give rise to a great variety of habitats for aquatic fauna (refuges, spawning grounds, etc.).

In these mountain systems it is the coexistence and alternation of 'normal' fluvial processes and torrential processes which explain the features of the river patchwork. Following major floods, the river reforms its basic geomorphological units (rapids and pools) in only a few years but the alluvial floor retains a memory of major changes. Benda (1990) has shown that these types of mountain or submontane channels may be subject to a cyclical fluctuation of aggradation which generates a pebbly bed morphology, and degradation, which gives rise to a mixed morphology dominated by bedrock outcrops and boulder steps.

The patchworks of mountain rivers are highly unstable because of the frequency and random nature of the disturbances affecting the ecosystems. Wissmar and Swanson (1990) emphasize that valley bottoms have little resistance and little capacity for the storage of materials, so that reaction and recovery times following a disturbance are particularly fast. There are three essential characteristics: (1) short violent flood pulses, because of the steepness of the gradient and the narrowness of the flood channel; (2) the magnitude of the load, which essentially has its origin in mass movements on slopes (Swanson *et al.*, 1987); and (3) longitudinal variations in gradient and transverse constraints exerted by the slopes (narrowing and widening) which affect the dynamics of deposition and erosion.

5.2.2 BRAIDED SECTORS

Downstream of mountain sectors, braiding develops in valleys where the alluvial floor has a steep gradient (>0.07% for the Rhône and up to 0.3% for the Durance) where bed load is abundant and typically where the hydrological regime is marked by major flood peaks. Braiding develops in several biomes in arctic and alpine regions where there are spring or summer floods, in arid and Mediterranean regions subject to torrential rain, and in some tropical regions subject to monsoon rains.

Braided channels have multiple, low sinuously, unstable channels enclosing bars carrying little or no vegetation because the reworking of materials is intense (Figure 5.4). The transverse profiles are broad and shallow; their detailed morphology is determined by the number and position of channels and bars. Pools develop immediately downstream of the confluences between channels (Ashmore *et al.*, 1992). Bars retain an approximately rhomboid shape despite their high mobility although the exact shape of the bars depends on the relative size of the two upstream channels, in the same way as downstream from conventional confluences (Best, 1986). Bars are generally stony, but braiding also develops in rivers with a sandy load like the Loire (Babonaux, 1970).

Braided sectors are characterized by highly 'patchy' landscapes. The active strip, a few tens to hundreds of metres wide, is a very unstable

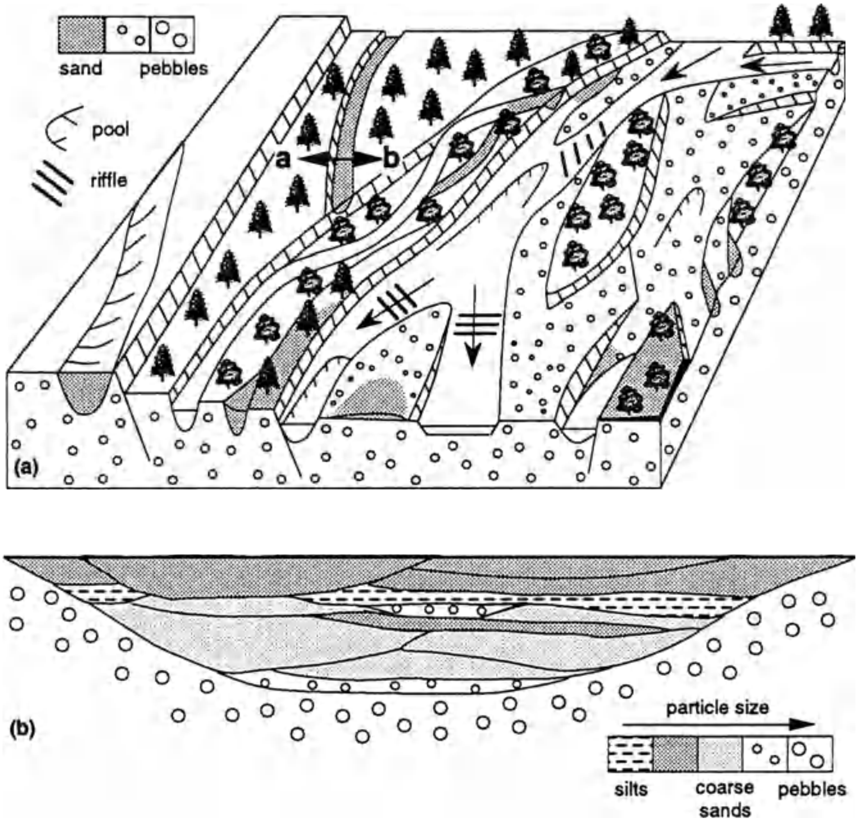


Figure 5.4 Block diagram of a braided plain (a) and a transverse section through an old braided arm (b) (modified after Baumgart-Kotarba, 1989).

environment reworked by frequent floods, which occur on average every year. The bars are of various types and the main features of their morphology are due to the dissection, during the low water stage, of the major bars created during the last flood season. On the microform scale, Miall (1977) distinguishes a dozen possible sedimentary facies defined by the particle size and structure of the deposit. The sedimentary characteristics of each functional unit and its relative elevation with respect to the water table are likely to affect the colonization of pioneering plants and epigeal aquatic fauna. Channels in the active strip have a flow which varies greatly over time. Secondary channels collect flood waters which sweep over the bars. When fed by water table draw-off they provide excellent habitats for aquatic fauna (Chapter 7).

At the edge of the active strip lies a patchwork of vegetated old bars, which have been aggraded to a greater or lesser extent, separated by channels clogged with sediments. These environments remain relatively ephemeral, because lateral displacement of the active strip causes periodic rejuvenation. Nevertheless, relict patches (in the sense of Forman and Godron, 1986) usually remain and these can be forested but retain a patchwork structure maintained by 'chronic disturbance'.

5.2.3 MEANDERING SECTORS

Meandering is a feature of the downstream zone, but may well develop on alluvial floors with a relatively steep gradient containing pebbly material, i.e. in the transit zone where the braided style is in continuous progression (Tricart and Vogt, 1967). In fact if the materials are too coarse a river does not reduce its gradient by cutting back but moves over a surface of pebbly fill which forms a pavement. In most cases there is a dual response, i.e. the river cuts down into its bed and meanders (Schumm, 1977). The transition between the two styles occurs through decrease in the extent of gravel bars and the number of channels.

The driving force for geomorphological diversity, lateral migration of a single channel, builds up lateral bars on the convex side and erodes concave banks (Figure 5.5). A distinction is normally made between geomorphological units on the basis of the height of lateral bars (upper and lower platforms) and particle size, which decreases along bars in a downstream direction. Meandering rivers may be characterized by progressive migration of the channel, and by the formation of very flat alluvial plains coated with flood silts. Other alluvial plains have an undulating surface of ridges and swales which Hickin (1974) relates to a hydrological regime with a marked seasonal cycle and by the existence of sandy (i.e. non-cohesive) bank materials. On the Beatton, a tributary of the Peace river (northeast British Columbia) the average migration rate is 0.3–0.7 m per year (Nanson and Beach, 1977) and dating of the ridges by dendrochronology has shown that on average they form every 27 years, during high floods. Fine sedimentation nevertheless occurs every year on the surface of the plain (Figure 5.6), but without obliterating the original topography. This continues for about 50 years, reaching a thickness of 2.50 m, and then decreases sharply.

An important component of the ecological patchwork in meandering sectors consists of aquatic environments which have been abandoned by the river. 'Oxbow lakes' are created by meander cut-off. As a general rule rivers with a steep slope and vigorous flood regime give rise to chute cut-offs across the necks of the meanders. The cycles of meander formation are generally rapid, particularly where bank sediments are non-cohesive (e.g. 10–30 years in the lower valley of the Ain, a tributary of the Rhône). Migration of the convex banks frequently occurs suddenly,

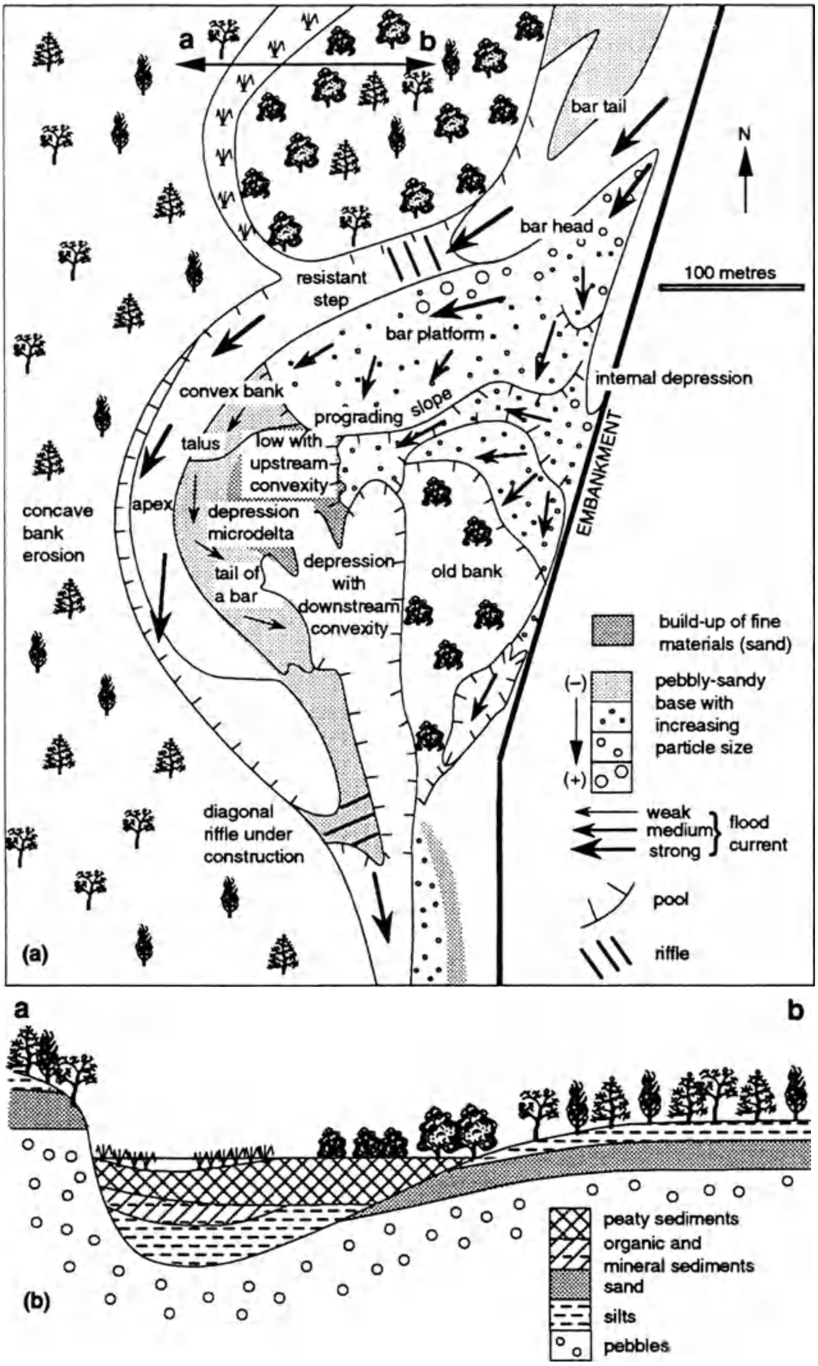


Figure 5.5 Geomorphological units of a meander in the French Upper Rhône.

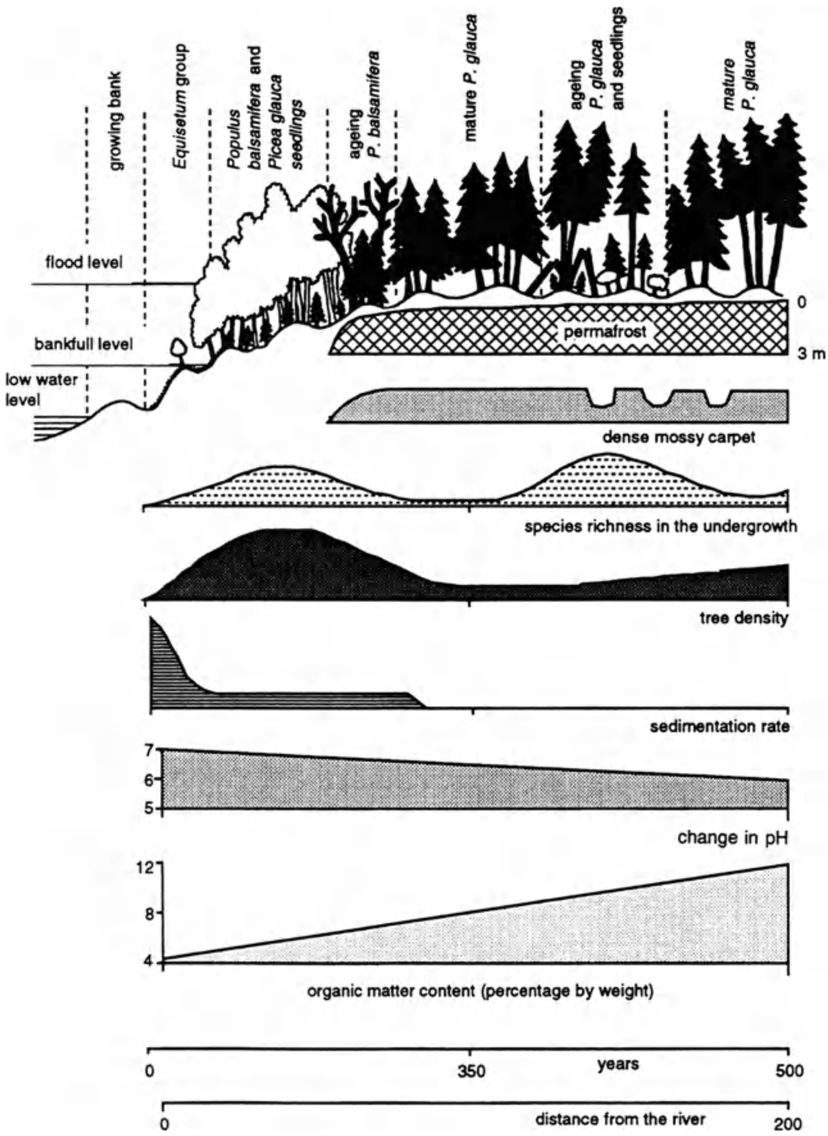


Figure 5.6 An undulating scroll bar plain: diagrammatic cross-section of a convex bank of a meander on the Beatton in British Columbia (modified after Nanson and Beach, 1977).

isolating narrow, shallow water bodies downstream, in which fine sedimentation occurs, known as 'convexity depressions' (Figure 5.7a).

In the downstream zone of river systems, the accumulation zone

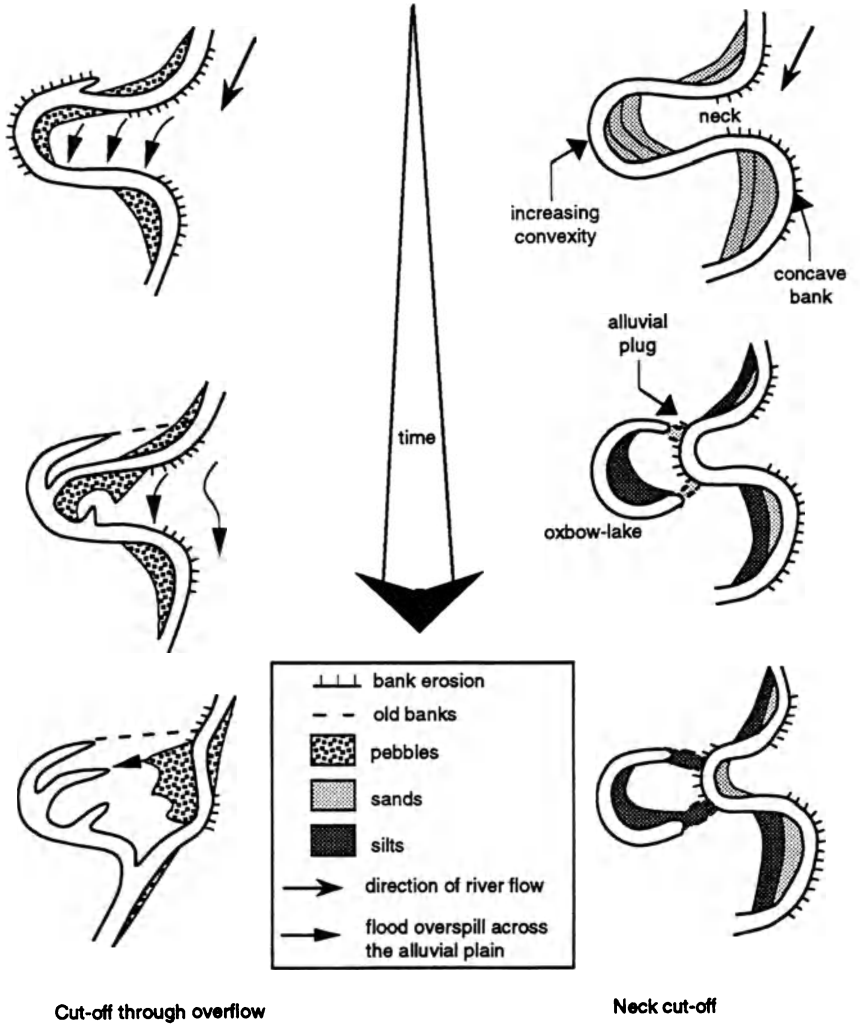


Figure 5.7 Two types of meander cut-off.

(Schumm, 1977), plains are constructed by vertical growth (Fenneman, 1906), in particular, where there is rapid deposition of suspended materials. The development of sinuosity is accompanied by levee construction along concave banks, which become most marked where the rate of lateral migration is low. Meanders can be abandoned by neck cut-off (Figure 5.7b). Sedimentation in the old meander is slow once it becomes isolated at the upstream and downstream ends by alluvial plugs. Floods frequently break through levees and the overspilling water flows through breaches which allow silt sedimentation in frequently swampy flood basin 'backswamps'. The raising of a meandering belt, which is frequent in subsiding areas, may give rise to 'avulsion', vast changes in the line of meander trains, as described by Fisk (1947) for the Mississippi. In these environments the ecological patchwork is essentially based on the degree of hydromorphism and on the relative fineness of the sediments in a low energy environment (Allen, 1965).

5.2.4 ANASTOMOSING SECTOR

Anastomosing channels (frequently confused with braided channels in literature) are a geomorphological type marked by relatively stable multiple channels enclosing vegetation-covered islands. Their highly sinuous course and slow rates of flow favour fine sedimentation which contributes to spatial stability by increasing bank cohesion. Braiding and anastomosis are styles which are apparently similar because of the multiplicity of channels, but they are produced by very different processes.

Several types of anastomosis can be distinguished. First, 'intramontane anastomosis' develops on the boundaries of aggrading braided strips, as found on the Alexandra and North Saskatchewan rivers, in Alberta, where the rate of vertical accretion is 3–5 cm per century (Smith, 1973). Secondly, 'sedimentary basin anastomosis' occurs in basins subjected to active tectonic subsidence (Smith and Putman, 1980). The Magdelena (Colombia) has formed a sandy fluvial belt bordered by vast extents of fine organic sediments. Anastomosis replaces braiding when the sudsidence exceeds a rate of 10 cm per century. Thirdly, 'arid region anastomosis' is formed by small floods capable of transporting sand in sinuous incised channels, whereas braiding develops during major floods, which deposit silts at high flood levels (Rust and Nanson, 1986). Fourthly, 'forest plain anastomosis' often occurs in tropical and boreal biomes. Savat (1975) has shown for the Zaire, and Baker (1978) for the Solimoes, that these major rivers are not conventional hydraulic units but a juxtapostion or coalescence of active channels for which regime equations do not apply. The forest encourages bank stabilization and an enormous output of wood, which plays a part in obstructing channels during flood conditions. There is an extreme diversity of aquatic environments, as demonstrated by Drago (1976), who distinguishes 14 types of lentic environment abandoned by channel migration in the Argentine Pantanos.

5.3 PATCHWORK DYNAMICS

River patchworks consist of geomorphological units which are nested at different spatial scales. These units are provided with some mobility depending on the set of reversible or irreversible processes causing landform renewal, or which contribute to integrating parts of the heritage into the river system.

5.3.1 PATCHWORKS IN A STABLE FUNCTIONING HYDROSYSTEM

Regardless of the position of a sector in the upstream–downstream gradient, and the fluvial style expressed, the fluvial patchwork comprises two major groups of units or 'mesoforms'.

First there is a group of units created and reworked by active mobile channels. On the geomorphological or biological time scale, units such as bars, pools, and berms are synchronous in the sense that infrequent events such as floods cause general rejuvenation of the units. Aquatic and terrestrial ecosystems show juvenile features, associated with the youth of the substratum (Chapter 10). This 'topographic instability', in the sense given by Tricart (1984), is perfectly compatible with stability of the river system. In fact the system persists in its manner of operation, even though the geomorphological units have an ephemeral spatial expression.

It should be noted that the elements in a patchwork of mesoforms may remain stable, but the constituent elements may be mobile when viewed at the microscale. For example, Church and Jones (1982) have demonstrated that if the supply of sediment is small the morphology of diagonal riffles and lateral bars in a pebbly bed is stable. Sediment moves across a sequence of sites of stable deposition. When the load is abundant, however, the bars themselves migrate downstream.

Secondly, there is a group of units belonging to the alluvial plain. Migration of a channel leaves bars on its edges which are subject to accretion by flood silts, and old channels which have reached various stages of siltation. The diversity of a valley bottom patchwork depends on the rate of production and frequency of destruction of these mesoforms (Lewin, 1978). Thus, the formation and cut-off of meanders follows a cycle lasting from one to several centuries in low energy rivers. In the River Ain (mean flow: 130 $m^3 s^{-1}$; gradient of the alluvial floor: 1–2%) this cycle had a period of less than 20 years during the years 1930–1970.

The complexity of the patch mosaic depends not only on such regeneration processes, but also on the conservation of mesoforms in marginal positions. The spatial distribution of the energy of overbank flows is of primary importance because it controls the extent and nature of sedimentation on the surface of the alluvial plain. Low energy environments with persistent floods which are charged with suspended material have a uniform topography whereas valley bottoms subjected to short floods carrying little load preserve a complex patchwork for several centuries, or even several millennia, particularly if an alluvial forest acts as a filter for suspended material (Chapter 9). This ability to preserve palaeoforms is largely dependent on the supply of suspended material from the catchment basin. Caselius (1971) has explained the very long life time of palaeomeanders in some Finnish valleys by the lack of load, which consists of 25–40% humus during floods. In general this is the situation in wooded basins and forest biomes (boreal conifer forests, tropical forests). Deforested mountain areas, on the other hand, or biomes with a cover of open vegetation, produce large quantities of sediments which are responsible for raising the level of the alluvial plain. This has been recorded in the United States following land clearance by the wave of early pioneers, and is currently affecting major valleys in the Himalayan piedmont.

5.3.2 ROLE OF EXTREME EVENTS

Infrequent events, which are regarded as being catastrophic because of their immediate effects on ecosystems or on human activity, are capable of leaving long-lasting traces in valley bottom morphology. In this respect they can affect the organization and composition of the patchwork.

It is in lower order mountain rivers that the landforms generated by these exceptional episodes are most durable. Such processes have been described by Tricart (1974) in the valley of the Guil (Hautes-Alpes), where some 20 years after the 100 year flood of 1957 the valley bottom consisted of a patchwork associating low-energy forms and flood deposits colonized by populations of larches. A similar situation was described in the Cascades Chain (Oregon), which in 1964 was devastated by a 100 year flood following an episode of 200–400 mm of rainfall and snow-melt. A muddy debris flow abandoned blocky levees which can still be seen on the banks (Grant, 1986), but the material, which has a great variety of particle sizes, was remobilized in the main channel by flows having a 10–50 year frequency so that the rivers were restored to a typical morphology of riffles and pools after the trunks forming log jams had decomposed.

The intensity of the processes associated with exceptional episodes is explained by the fact that energy is dissipated over a narrow corridor.

This is not the situation in the alluvial sectors of major rivers, where the extent of the area subject to flooding attenuates the variations in flow. Above bankfull flow some of the energy is dissipated at the surface of the main channel creating specific forms – pebble layers across levees, crevasse-splays, etc. Coarse material issuing from the main channel may be carried onto the alluvial plain and incorporated into the fine overbank deposits. However strong the disturbances are, flood 'scars' generally heal over quickly; major floods do not disturb the structure and functioning of the patchworks.

5.3.3 PERSISTENT CHANGES IN THE CONDITION OF A SYSTEM

It has been well established that rivers, regardless of the biome, have been subjected to great changes in hydrological regime and sediment transport over the Holocene. There are many reasons for this – fluctuations in rainfall, evaporation and run-off, and variations in vegetation cover – without taking into account the effect of human activities (Chapter 11). The change in the variables represented by bed load and flow are reflected in multiple adjustments in the geometry of a channel (Table 5.1).

Table 5.1 Changes in channel geometry caused by changes in flow and load (adapted from Knighton, 1984 and Schumm, 1977)

Variables		Channel geometry					
Discharge	Bedload	Width	Depth	WiD ratio	Meander wavelength	Sinuosity	Gradient
+	+	+	±	+	+	+	±
–	–	–	±	–	–	+	±
+	–	±	+	±	±	+	–
–	–	±	–	±	±	–	+

+ = increase; – = decrease

Table 5.2 Channel response to change in sediment load (*Qs*) with respect to the flow (*Q*) (after Starkel, 1983)

	Alluvial floor	Channel pattern	Channel width	Channel depth	Meander wavelength	Sinuosity	Gradient
$Q^- < Qs^-$	incision	meandering	–	+	–	–	+
$Q^- > Qs^-$	aggradation	meandering	–	–	–	–	+
$Q^+ > Qs^+$	incision	braiding	+	+	+	+	–
$Q^+ < Qs^+$	aggradation	braiding	+	–	+	+	–

This response by a river is reflected by a change in the fluvial style, and by downcutting or channel aggradation and floodplain accretion as a result of the change in bed load with respect to flow (Table 5.2).

Although providing only general guidelines, in as much as flow and sediment load are not the only variables in question, these principles are essential to an understanding of many of the relict river forms to be found in large alluvial plains. The most obvious structures are sinuous palaeochannels, whose wavelength and width have nothing in common with those of the present meandering watercourses. The plains of Northern Europe, like that of the Vistula, frequently retain several generations of relict functional stretches produced by a river which braided and meandered alternately during the Holocene. These changes in river style have been experienced by mountain basins in Europe since the end

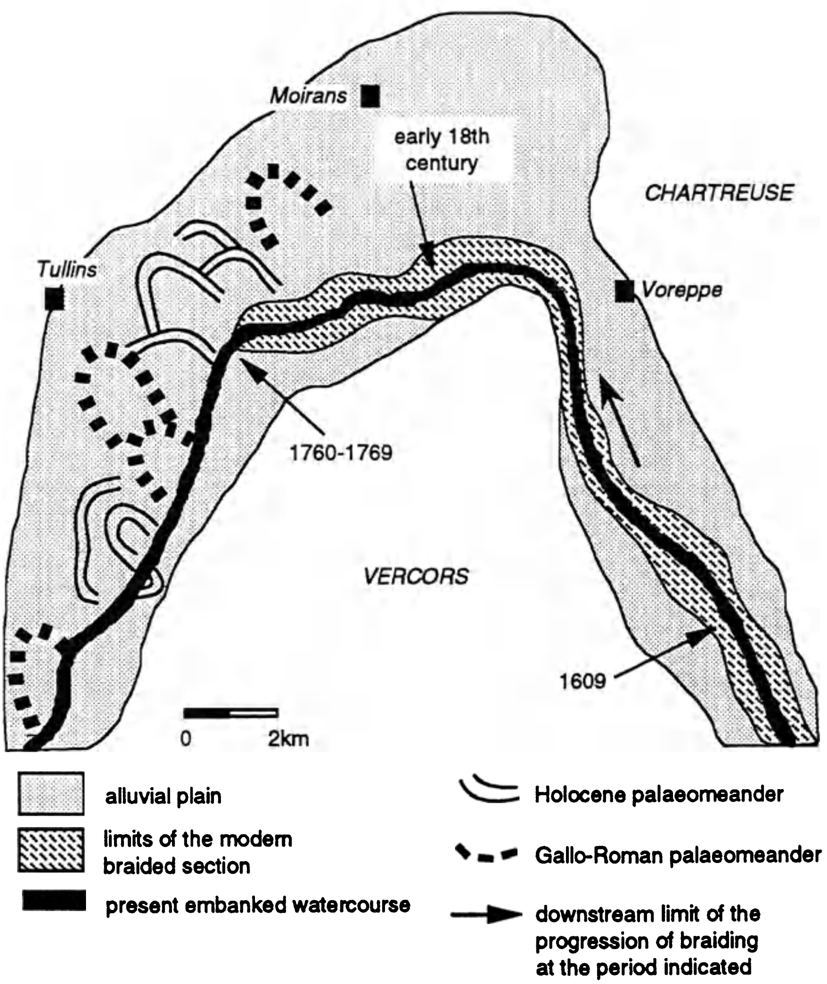


Figure 5.8 Metamorphosis of the Isère where it leaves the Alps.

of the Middle Ages, as a prelude to the cooling during the modern era known as the Little Ice Age. From the end of the 14th century the high alpine valleys witnessed high bed-material loads and a progressive change towards channels of a higher order (6–7) which were then subjected to metamorphosis (Bravard, 1989).

The alluvial plain of the Isère (Figure 5.8) thus preserves the relics of Gallo-Roman meanders and a braided section which was actively moving downstream in the 18th and early 19th centuries (Salvador, 1991). The aggradation of the river bed associated with this progradation was accompanied by increased flooding and increased fine sedimentation on the margins of the plain, so that peat in the abandoned channels has been buried by several tens of centimetres of silt. This example shows that in addition to the change in river style, metamorphosis also affects the nature of sedimentary fills, and therefore the ecological functioning of biotopes and the dynamics of flow across the plain. Valleys which have experienced one or more alternations between braiding and meandering are generally located in a piedmont situation – an alluvial floor with a steep gradient, naturally contrasting hydrological regimes and the proximity of sources of sediment which have produced a heavy load during some periods of the Holocene, making it possible to cross the geomorphological threshold separating the two types of river style. In these valleys there has not been a 'normal' progress towards floodplain accretion, reduced flooding, evolution towards hardwood forests and the inevitable disappearance of abandoned channels; partial regeneration through metamorphosis of the active channel has caused a more complex evolution.

Palaeoepisodes of functioning are recorded in the three dimensions of the hydrosystem. Recent work has shown that most large European alluvial valleys have a floodplain (or flood channel) consisting of geomorphological sectors formed during the Holocene under different hydrological and sedimentary regimes. In this respect the distinction made by Graf (1988) in arid environments applies perfectly well to the temperate biome. He describes a surface adjacent to the channel and built up with materials deposited by the current regime as a floodable plain. The infrequently flooded low terrace was formed during a hydroclimatic palaeoregime. Thus, Striedter (1988) dated seven terraces, six of Holocene age, in the main channel of the Rhine downstream from Strasbourg by dendrochronology and mapping. Waterlogging and inundation by floods tends to govern the ecological structure of the plain, particularly as each terrace has a characteristic soil profile which depends on the degree of decalcification and browning (Schirmer, 1988).

This diversification of the ecological patchwork is found at the scale of the active channel, which frequently preserves relics of functioning which it experienced several thousand years ago. This applies for example to the sandy deposits high on the rocky slopes of canyons. These slack water deposits are typically found at the confluence of tributaries, on the convex side of meanders, downstream from narrows or rocky promontories, and even in caves (Patton *et al.*, 1979). It is also the case that large erratics present in the beds of Alpine torrents, create stable forms colonized by the benthic fauna. Graf (1979) demonstrated that the major features of the Grand Canyon rapids on the Colorado are fixed under present hydrological conditions.

Rivers cutting down into alluvial or fluvioglacial sheets can mobilize coarse sediments which help to pave the channel bed and ensure its stability during high and medium frequency flows. Schumm (1977) has shown that many rivers dissipate their energy by meandering over steeply sloping alluvial floors inherited from episodes when sediment transport was vigorous. In this case the coarse particle size distribution, which governs the gradient, inhibits the tendency for downcutting and plays a more than negligible part in the spatial instability of the patchwork. However, in other cases channel incision may also exhume fine sediments (silts, clay) of glacial-lacustrine origin deposited in areas of glacial overdeepening, such as in the Alps and their adjacent piedmont. Two problems may arise for biota. First, removal of coarse materials with a sandy matrix gives way to cohesive substrates in which interstices are lacking, and which are therefore unfavourable to fauna. Secondly, incision releases very fine suspended materials which have the effect of reducing water transparency and primary productivity, and of clogging the substratum of calm-water functional units.

Primary production and primary producers

6

A. R. G. Large, G. Pautou and C. Amoros

6.1 INTRODUCTION

The distribution of plant species and their productivity in a fluvial hydrosystem is dependent on the complex interactions between hydrodynamic processes (e.g. flow velocity, shear stress, the nature and stability of the substrate etc.), hydrochemical processes (e.g. nutrient cycling, pH etc.) and the use of solar energy by their photosynthetic processes (influenced in turn by water transparency, shade etc.). Diverse adaptive strategies permit plant communities to colonize a range of patches in the fluvial unit, but they are sensitive environmental indicators (Naiman and Décamps, 1990). However, environmental changes affecting plant distributions in fluvial hydrosystems are now recognized as complex phenomena, giving rise to transient states in plant communities which may persist for decades.

Primary production is carried out by the vegetation's chlorophyll through the process of photosynthesis which allows the plants in the fluvial hydrosystem, in addition to producing oxygen, to produce organic material from mineral nutrients, solar energy and carbon dioxide. This primary production is equivalent to the intensity of the production of biomass per unit surface area and per unit time. It is expressed either as the mass of dry organic material (kg ha^{-1} yr^{-1}) or as the amount of energy contained in that organic material (joules m^2 day^{-1}). The total amount of solar energy assimilated or fixed by photosynthesis is expressed as the *gross productivity* (P_B). The part of P_B consumed by the vegetation itself to ensure proper metabolism is expressed as its respiration (R). The actual quantity of vegetative biomass available in the ecosystem for herbivores,

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detritivores and decomposers (bacteria, fungi etc.) corresponds therefore to the *net primary productivity* (P_N) where $P_N = P_B - R$. Early estimates of in-channel primary productivity in comparison with other sources, particularly with regard to the import of allochthonous organic matter from the drainage basin itself (Hynes, 1975) suggest autochthonous productivity to be essentially irrelevant. Whereas, on one hand, the primary productivity of the running waters at the head of the drainage basin appears relatively negligible in comparison to the overall quantity of organic material being produced in the total reaches of the drainage basin, on the other, the aquatic vegetation and the vegetation of the riparian and floodplain zone in large rivers plays an important role – not only in providing a trophic resource for herbivore and detritivores, but also in modifying habitat conditions (e.g. obstacles to flow, shelter for animals, protection against erosion, etc.).

6.2 ADAPTIVE STRATEGIES

Water, the essential feature of fluvial hydrosystems, exercises the major constraint on the distribution of vegetation; examples include variation in the speed of flow and shear stress for aquatic species, variations between high and low flow for littoral species, and variation in the length of inundation for the more terrestrial species found in the riparian zone. Faced by these constraints, the adaptive strategies of plant species including their morphology, their modes of reproduction and spread as well as their physiological adaptations. In terms of these strategies, only those plants sufficiently large to be seen by the naked eye (here defined as macrophytes) are considered in this chapter.

6.2.1 MORPHOLOGY

The species which have shown maximum adaptation to the riverine environment are those which grow in the channel itself and especially those growing in the faster flowing sections. The plants which live in flowing waters display for the most part a flexible structure with leaves being generally long and thin, offering minimum resistance to the current (Figure 6.1). Their system of establishment, colonizing the interstitial spaces in gravels and shingles, constitutes an efficient anchoring system, whereas their leaf arrangements reduce their frictional resistance by presenting less surface area to the water flow. Once past a critical threshold however, the stems will break with loss of leaf material leaving the rooted tissue still in place. The damage caused by abrasion and ripping out of the vegetation is often compensated by a high rate of growth and enhanced production of this adventitious root tissue (Figure 6.2). In the calm and often turbid waters, numerous species produce floating leaves which

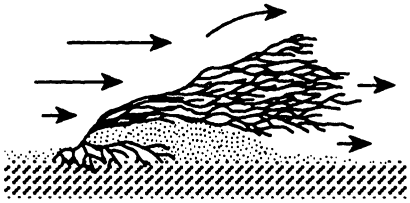

Figure 6.1 *Ranunculus fluitans*: an example of an aquatic plant in running water, very flexible, with long and laciniate leaves (after Haslam, 1978).

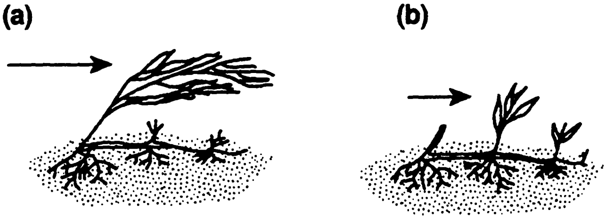

Figure 6.2 Compensation for damage caused by floods by vegetative multiplication giving rise to rhizomes, roots and young shoots (a) before, and (b) after a flood (after Haslam, 1978).

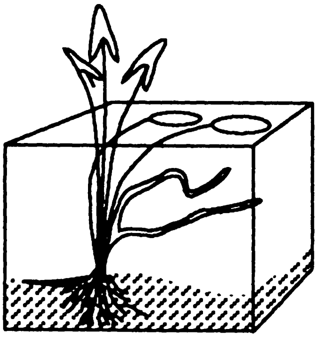

Figure 6.3 Example of polymorphous leaves: *Sagittaria sagittifolia*.

permit them to utilize solar energy directly at the surface (e.g. *Nuphar lutea, Potamogeton natans*). In cut-off meanders completely isolated and protected from all but flood waters, free-floating plants abound (e.g. *Lemna minor, Hydrocharis morsus-ranae*). The littoral zones are generally submitted to the greatest variations in water level and are colonized by emergent plants (helophytes) which are capable of producing different types of leaves depending on the water level (Figure 6.3). The shrubby and arboreal species of the riparian zone, which are able to emit adventitious roots, are themselves nourished by the deposition of alluvial material by floods (*Salix alba, S. purpurea*), often being submitted to, and adapted to, long periods of inundation (e.g. *Salix cinerea, Alnus glutinosa*).

6.2.2. REPRODUCTION AND DISPERSAL

The flowers of aquatic plants appear to be very badly adapted. Including the species with floating leaves which are often submerged at the time of flowering, the efficiency of their sexual reproduction is extremely weak or negligible in certain cases (Sculthorpe, 1967). On the other hand, the aquatic environment is particularly favourable for a diverse variety of modes of vegetative multiplication. With numerous species of submerged plants (e.g. *Ceratophyllum, Myriophyllum, Callitriche* spp.), the fragments of stem, broken by the current or by animals, have the ability to grow adventitious roots, and after being dispersed by the flow, establish themselves in new sites (natural cuttings). Division of the rhizome can also produce new individuals (e.g. *Nuphar lutea, Potamogeton pectinatus*). This is also the case for those species which produce stolons that are easily broken (e.g. *Sagittaria sagittifolia, Luronium natans, Berula erecta*). Aquatic plants are themselves also capable of producing specialized organs such as tubers (dormant buds) which detach from the parent plant when they themselves degenerate during the winter season.

The littoral plants which are emergent in growth form, combine both sexual and vegetative modes of reproduction. Seeds are more important modes of dispersal among rooted floating-leaved, emergent and riparian plants, and their flowers, despite being poorly adapted, are usually wind or insect pollinated (e.g. *Glyceria maxima, Nuphar* spp.). Whereas sexual reproduction generally assures wide dispersal in the aerial environment, the production of rhizomes allows certain species to spread rapidly by vegetative methods, and these species form the spacious monospecific plantations (e.g. *Phragmites australis, Phalaris arundinacea, Typha latifolia*) often seen in these environments. With shrubby and riparian woody species, sexual reproduction predominates, but the capacity for vegetative reproduction remains high, in particular for the species of willow which colonize the sides of the water (via breakage of small branches, removal by the current, and emission of lateral shoots torn out and later embedded by deposition of material eroded from banks further upstream).

6.2.3. PHYSIOLOGY

The plants of fluvial hydrosystems have adapted their physiology to cope with alterations and imposed stresses in the physical environment (Larcher, 1980). In general, individual plants increase photosynthetic carbon fixation with increasing light, temperature, nutrient concentration, inorganic carbon concentration and water movement (Farmer and Adams 1989). As a result of long-term alteration in any of these parameters, species may undergo biochemical and morphological changes in an effort to increase carbon gain (e.g. Sand-Jensen, 1987).

In the aquatic environment, the role of sediment as a direct source of nutrients (nitrogen, phosphorus and trace elements) is significant as their concentrations in the water itself can be extremely low (Rattray *et al.*, 1991). The amount of nutrients dissolved in the water appears, however, to be the major factor which regulates the distribution of aquatic plant species and controls their productivity. Amongst the *hydrophytes* (aquatic plants which are submerged or have floating leaves), one can distinguish between *rhizophytes* where basal parts penetrate the substrate, and *haptophytes* without root or rhizome adaptations (e.g. *Lemna, Hydrocharis* etc.). Haptophytes rely on nutrients suspended in the water column, whereas rhizophytes have the capability in times of scarcity to obtain nutrients from both the water column and sediments.

Aquatic ecosystems are habitually classified as a function of their nutrient status (e.g. Holmes and Newbold, 1984; Moss, 1984). Among the *oligotrophic* ecosystems which consist of water which is poor in mineral nutrients (especially nitrates and phosphates) one can distinguish oligotrophic waters *sensu stricto* which are very poor in minerals and low in calcium, and calcareous oligotrophic waters which are a little more productive than the former (Dussart, 1966; Hutchinson, 1975). At the opposite end of the spectrum are the *eutrophic* waters, which are rich in nutrient elements ($N\text{-}NO_3$ approx. $= 1$ mg l^{-1}; $P\text{-}PO_4 > 0.5$ mg l^{-1}). The *mesotrophic* waters are intermediate between the former two types. In *dystrophic* ecosystems, the decomposition of the organic matter is strongly related to situations where the water is charged with colloid or dissolved organic matter (humic acids) but poor in mineral nutrient salts.

Apart from nutrients, the distribution and productivity of aquatic plants is governed by their capacity to utilize different sources of carbon. Whereas the helophytes are able to utilize atmospheric carbon (CO_2), submerged hydrophytes and the floating-leafed plants have developed mechanisms which allow them to utilize dissolved CO_2 in the water column as well as bicarbonate ions (HCO_3^-), albeit with reduced efficiency (Hutchinson, 1975; Lucas and Berry, 1985). Examples of these plants include *Ceratophyllum demersum, Elodea canadensis, Myriophyllum spicatum, Potamogeton crispus* and *P. lucens*. However, some species characteristic of mineral-poor water (e.g. *Myriophyllum verticillatum, Lobelia dortmanna, Isoetes lacustris*) appear to be incapable of utilizing HCO_3^- (Maberly and Spence, 1983), and *Potamogeton polygonifolius* can only use dissolved CO_2 (Westlake *et al.*, 1980). pH probably plays a secondary role here. For example, species of *Potamogeton* appear not to occur in waters that are more acidic than pH 6.0, whatever the calcium content (Hutchinson, 1975).

In the terrestrial environment, the growth of plants in wetland soils is strongly affected by reduced substances such as ammoniacal nitrogen, manganese, ferrous ions or sulphides (Blom *et al.*, 1990; Ernst, 1990; Laanbroek, 1990). The length of the waterlogging period will influence the necessary physiological adaptations to these chemically reduced states. The principal effect of flooding is to reduce primary production by terrestrial species in the riparian and floodplain zone as these can only use CO_2 as a carbon source, whereas the aquatic plants can often utilize HCO_3^-. Two strategies for successful survival in waterlogged and frequently flooded soils can be identified: (a) superficial rooting and (b) enhanced development of the internal gas spaces in the primary and secondary cortex of the root (which act as efficient conduits for the transport of CO_2 from the root system).

6.3 DISTRIBUTION AND PRODUCTION

The spatial and temporal heterogeneity which differentiates the units of the fluvial mosaic governs the timing of dispersal of the plant species and their productivity. In aquatic ecosystems, the factors that most frequently affect the rate of photosynthesis (and hence primary production) are the availability of nutrients, CO_2 and O_2, light and the intensity of grazing. In natural systems these can be coupled both seasonally (light, temperature) and diurnally (e.g. dissolved O_2 and CO_2) and therefore have combined effects in governing the productivity of the system.

6.3.1 THE LONGITUDINAL ZONE

The physical variables within a river system present a continuous gradient of physical conditions (Vannote *et al.*, 1980) from source to mouth, as discussed in previous chapters and elicits a characteristic series of responses within the plant communities. Small mountain streams at the head of the drainage basin are characterized by two major constraints – the very strong flows and high amounts of shading – which limit the diversity and productivity of the vegetation communities. Vegetation in this zone is restricted to fixed mosses on the rocks (e.g. *Fontinalis*) and populations of microscopic algae (diatoms) which comprise a very thin film on rocks and sufficiently stable stones. The position of these communities as a thin covering of the rocks gives rise to their name of *perilithon*. The productivity of these communities is limited by the shading of these reaches by trees and also by the temperature of the water which remains relatively low in summer. In this situation, the ecosystem functions essentially as a supplier of allochthonous organic matter to

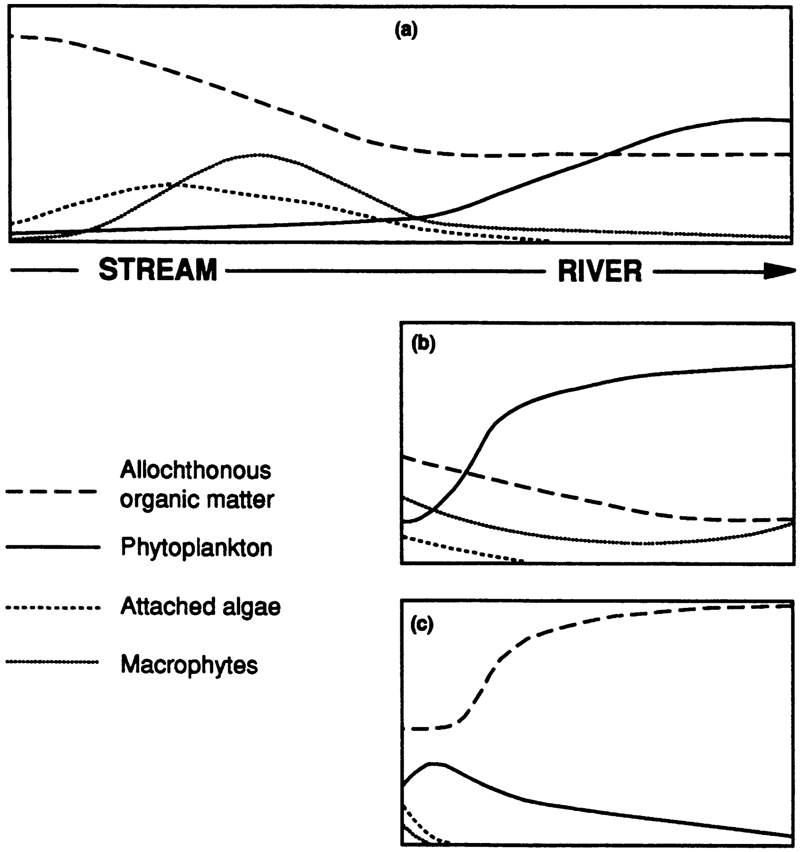

Figure 6.4 Modification of trophic structure along the long gradient in an upstream–downstream direction (a); the situation where the flow is regulated by impoundment (b); the case where the flow is polluted by organic material (c) (after Wetzel, 1975).

downstream areas (Figure 6.4). The vegetation on the banks is influenced at the same time by altitudinal conditions (principally temperature and slope), which characterize in turn the water flow and the fluvial dynamics (Chapter 5). Usually the riparian woodland has little or no diversity in this zone (Figure 6.5).

With an increase in floodplain width and a decrease in slope, the diversity of the riparian fringe attains its maximum in the larger plains along the lower reaches of the river, manifesting itself as a heterogeneity which expresses itself in the transverse dimension of the hydrosystem (section 6.3.2). In the natural situation, significant gradients (associated with changes in water content of the soil, sediment deposition and

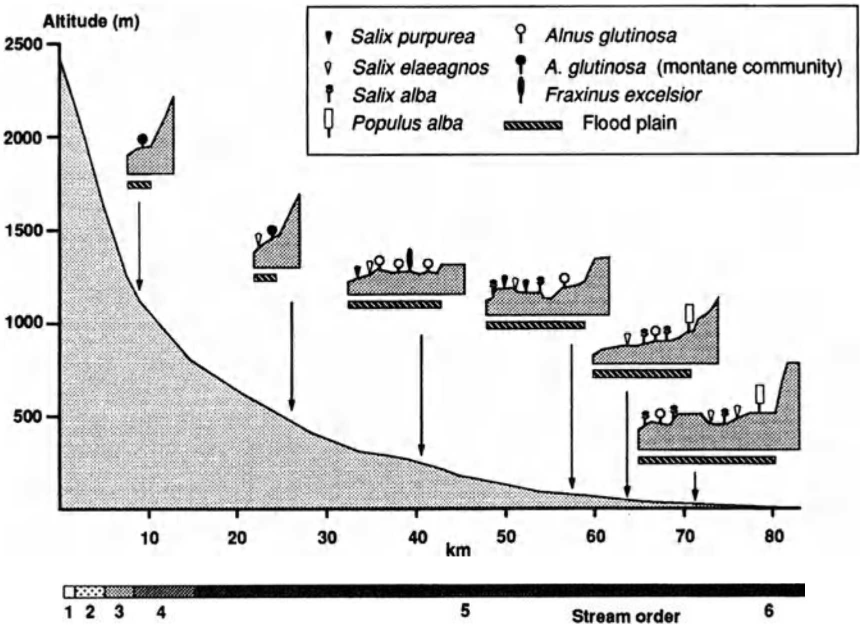

Figure 6.5 Longitudinal modification of the riparian zone as a function of increase in width of the water course. The River Tech, France (after Pinay *et al.*, 1990).

displacement) across the corridor are seen to be related to the influence of the river itself.

In the downstream sections of the watercourse (Figure 6.6), the deposition of sand, silt and mud in the calmer waters and the increase in insolation due to the increasing shallowness of the bed, permits the development of submerged plants (e.g. *Elodea, Ranunculus*) and emergent species in the littoral zone (e.g. *Sparganium erectum, Phalaris arundinacea*). These plants themselves serve to support communities of fixed algae (notably the filamentous algae) which constitute a kind of furry layer round the stems and the petioles – these are termed the *periphyton* (*aufwuchs*). In the calmer and deeper parts of the watercourse there develop open water communities of microscopic algae (phytoplankton) and of floating-leafed plants (e.g. *Nuphar lutea, Potamogeton natans*). Gently sloping banks are colonized by communities of helophytes which become more and more abundant and diverse downstream. Generally the number of ruderal species increases significantly in a downstream direction (Nilsson *et al.*, 1989). In reality, therefore, the upstream–downstream zonation of vegetation is the result of interaction between physical

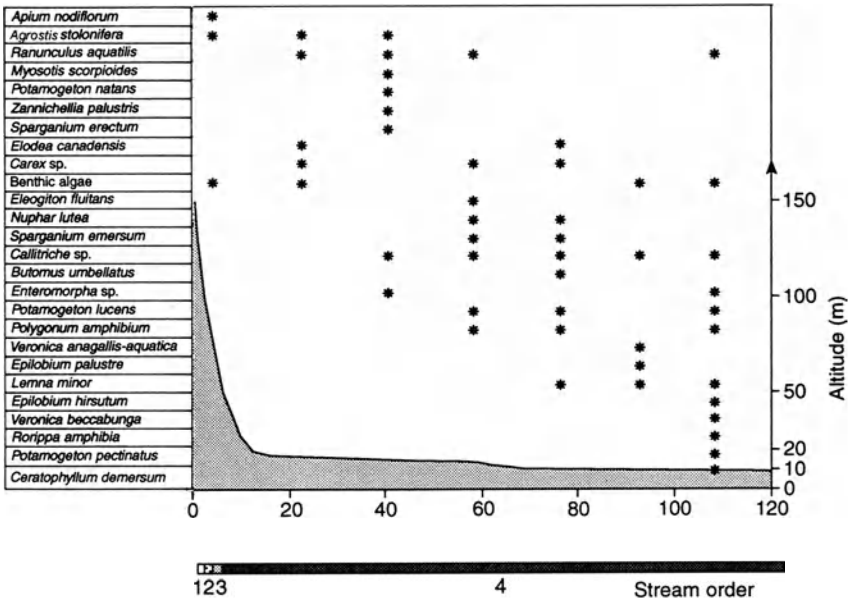

Figure 6.6 Modification in the longitudinal direction, of non-woody vegetation as a function of increase in width of the water course. The long profile of the River Derwent, UK (adapted from information from Haslam, 1978).

parameters (decrease in slope and increase in width) and chemical parameters (increase in concentration of dissolved nutrient salts).

The result is that, in the absence of human impacts, the upstream communities are generally composed of species characteristic of oligotrophic ecosystems, those downstream by species characteristic of more eutrophic conditions and intermediate zones by those species of mesotrophic waters. Associated with this increase in the trophic status of the water is an increase in suspended material (mineral elements, inert organic matter and phytoplankton) which in turn lowers the transparency of the water, and hence the insolation available for the plant's growth. In these conditions, the maximum productivity is shown by the algae and phytoplankton, as they are the first to intercept the sun's rays. This feature is accentuated when the depth is increased by channel management (Figure 6.4b) whereas, when the water is polluted by organic matter, phytoplankton production is equally reduced and the ecosystem functions for the most part in a heterotrophic mode (Figure 6.4c).

With the exception of the latter case, the zonation of the river shows a general order, with a generally weak primary productivity in the upstream reaches essentially provided by the algae of the perilithon. In intermediate zones, increases in productivity are associated with the macrophytes and the periphyton. Further downstream, these two types of production are reduced, but production as a whole is augmented by the free algae and phytoplankton.

6.3.2 THE TRANSVERSE DIMENSION

The plant communities of the fluvial hydrosystem vary not only along the long profile of the river, but also in a transverse gradient from the main channel itself, through the riparian zone to the edge of the floodplain. Thus the definition of the stream corridor encompasses not only the channel margins but also the floodplain and those parts of the valley sides influenced by high flows. The nature of this transverse dimension is, however, dictated to a large extent by longitudinal changes and in particular along the upstream–downstream succession of the diverse functional sectors (Chapter 5). An extreme example of this is shown by the contrast between the headstream sectors, with their narrow and sometimes non-existent corridor, and the meandering floodplain sectors which are much wider and composed of a number of abandoned channels and terrace steps resulting in a diverse range of habitats. Primary productivity rises dramatically where the floodplain communities include those associated with ox-bows and wetlands (e.g. Pautou *et al.*, 1985; Amoros *et al.*, 1987b). This high degree of heterogeneity is expressed across the transverse dimension in the form of a complex patch mosaic, in which a range of successions at different stages between aquatic and terrestrial plant communities can be observed.

(a) Aquatic vegetation

The structure of aquatic plant communities and their productivity depends on the interaction between their position on a hydrodynamic gradient (a function of distance from the active flow, Chapter 4) and on the other hand on a hydrochemical gradient (the amount of nutrients or toxic elements in the river itself, or in the waters which laterally feed the aquatic environments of the floodplain either via surface or groundwater flow). In reality there is a less obvious (but no less important) third gradient, that of the temporal dimension, which interacts with the other two gradients. It acts to modify the vegetation communities over the course of time, inherently via the process of ecological succession (explained in detail in Chapter 10). These successions explain the coexistence in the same sector of floodplain, and in areas similar in terms of their hydrodynamics and hydrochemistry, of plant communities different in their structure and their productivity. In general, the less mature communities are characterized by a low biomass but a high productivity, and as the succession progresses through time, the total biomass of the community accrues at a greater and greater speed. The ratio of photosynthesis to biomass, which is very high in the pioneer stages of succession, diminishes in value throughout the course of development of the ecosystem towards a more mature state. In absolute values, the helophyte communities of marshes and wetlands, intermediate stages of aquatic–terrestrial successional sequences, have productivities among the highest measured in the biosphere (Table 6.1).

Table 6.1 Primary productivity of some communities of fluvial hydrosystems in comparison to other ecosystems (after the works of Woodwell *et al.*, 1970; Westlake *et al.*, 1980; Moss, 1984)

Vegetation type	Annual productivity (organic matter (g m^{-2} yr^{-1})		
	Extreme values	Minimum	Mean
Phytoplankton	Negligible–6000	—	—
Submerged plants			
Temperate	—	1300	650
Tropical	—	1700	—
Plants with floating leaves			
Lemna spp.	—	1500	500
Eichornia crassipes	4000–6000	—	—
Swamps			
Typha spp.	—	3700	2700
Carex spp.	340–1700	1700	—
Phragmites	—	3000	2100
Cyperus papyrus	6000–9000	15 000	—
Humid forest			
Alnus/Fraxinus	570–640	—	—
Picea	—	—	500
Taxodium	692–4000	—	—
Hard woods	692–4000	—	1600
Comparisons			
Humid tropical forest	—	—	2250
Boreal forest	—	—	900
Marine phytoplankton	—	—	140

In the zone of lentic (slow-flowing) waters in the active channel or in old side-arms frequently inundated by higher flows, the most adaptable species selected along the hydrodynamic gradient are those with laciniate leaves and an efficient rooting system (e.g. *Ranunculus fluitans, R. circinatus, Berula*). The species of these environments are characterized by a very high potential for vegetative reproduction through the breaking off of plant fragments by the speed of the current. This allows them to rapidly colonize areas laid bare by flooding. The older side-branches of the river, less frequently and less intensely swept by flood waters are colonized by more fragile species (e.g. *Chara* spp., *Callitriche* spp.) and sometimes by floating-leaved species (e.g. *Potamogeton natans*). In these environments, situated a greater distance from the active channel, and often separated from it by alluvial plugs or levees are the zones colonized by shrub communities and tree species which considerably slow overland discharge by floods. At the other extremity of the hydrodynamic gradient from the headwater zone are situated those flat plains established by ancient meanders or old anastomosed side-arms. As a result of the high channel sinuosity, the length of the active channel in these environments is in general very elongated and the slope locally very gentle. The deepest zones of these old channels are colonized by the microscopic algae of the phytoplankton, whereas the most shallow zones are colonized by floating-leaved plants (e.g. *Nuphar, Nymphaea*). In these environments there are also abundant non-rooted species floating at the surface (e.g. *Lemna minor, Hydrocharis morsus-ranae*) or in the middle of the water-body (e.g. *Ceratophyllum demersum*).

Because of its influence on the plant communities, the hydrodynamic gradient exerts a direct influence on the primary production by controlling the amount of solar energy available for the aquatic vegetation. In effect, solar energy is reduced by the turbidity of the water, by the amount of material in suspension, and by shading from the branches of the woody species of the riparian zone. The amount of the material in suspension, which is very high in the upper courses of the river, declines along the gradient in question, and the shading of the riparian zone is inversely proportional to the width of the old channel. As, following their separation from the flowing water, former braids are generally narrower than old meanders (e.g. 8–20 m for the old braids of the French Upper Rhône versus 80–110 m for the old meanders), the reduction of solar energy due to shading of the riparian zone can be seen to diminish down the length of the hydrodynamic gradient. The combination of these features explains why the cut-off side-arms of braided channels, situated near the active channels have a low primary productivity and a heterotrophic type function based on organic matter of terrestrial origin (similar to the small streams at the head of the drainage basin). In contrast, former meanders further distant from the active channel have a high primary productivity and an autotrophic-based function.

The hydrochemical gradient which interacts with the fluvial dynamics depends in part on the water quality in the active channel and also on the type of functional sector under consideration. The type of functional sector influences the type of nutrient enrichment: it will differ according to whether the input is via superficial fluvial flows by overflowing or ebbing of floodwaters, or whether there are underground waters infiltrating from the river or from the phreatic watertable of the adjacent hill slopes. In general, where the soils of the alluvial plain are very permeable, older arms are strongly influenced by infiltration from the river, whereas in meandering sectors composed of finer alluvium, cut off channels are influenced more by over-bank flows from the river or runoff from the adjacent slopes. Local conditions can also influence the mode of nutrition of the waters: on the Upper Rhône, former meanders which form a channel in fluvioglacial terraces are able to drain phreatic waters which have light nutrient loadings (Reygrobellet and Dole, 1982) and like the former side-arms of the drainage network add nutrients to oligotrophic waters (Carbiener, 1983: Bornette and Amoros, 1991). Thus, the species composition and the productivity of the aquatic vegetation communities vary considerably according (a) to the nature of the transverse dimension and (b) as a function of the river and the functional sector under consideration. For example, in the floodplain of the Rhine, the communities of eutrophic waters in local sites near to the present channel are replaced by communities characteristic of mesotrophic waters in proportion to their distance from the channel (Eglin and Robach, 1992; Figure 3.8), whereas in the Upper Rhône, communities of mesotrophic waters situated close to the river channel are replaced by communities of eutrophic waters towards the margin of the floodplain in the sector of the Brégnier-Cordon (Balocco-Castella, 1988) but by oligotrophic communities in the sector of the Miribel-Jonage (Bornette and Amoros, 1991).

(b) Terrestrial vegetation

Elevation differences along the topographic gradient across the river corridor (Figure 6.7) provide a surrogate for the factors outlined above which exert a control on the distribution of terrestrial vegetation. With altitude the surface soil horizons become increasingly separated from the groundwater aquifer, the frequency and intensity of disturbance by flooding diminishes, and the texture of the soil becomes finer (Chapter 5). In reality, the structure and productivity of the terrestrial vegetation are not simply dependent on these three factors as the terrestrial communities modify themselves through the course of succession (Chapter 10).

The structure and productivity of a unit depends on the age and type of succession with which it is associated. A major differentiation appears between the successions which develop in former channels during their infilling (for example groups 3, 5 and 7 in Figure 6.7) and those which are associated with the more elevated areas of the banks, islands and levee areas (for example groups 1, 2, 4, 6 and 8 in Figure 6.7). Among the factors responsible for this differentiation is the amount of organic material in the soils. Extremely low in the sand-based alluvial soils, swept clean again and again by flooding, the concentration of organic matter does not even reach 5% in the highest parts of the floodplain. On

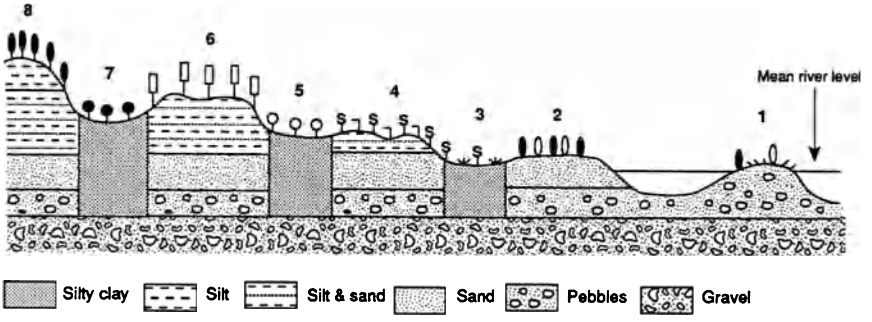

Figure 6.7 Schematic cross-section (not to scale) across the alluvial floodplain of the French Upper Rhône in the braided sector. Group 8 is situated 2–3 m above the level of the permanent watertable, and the width of the plain reaches 1500 m on both sides of the active channel. The elevation gradient appears very regular on the schematic diagram, whereas in reality it is extremely complex; the highest units are found in the centre of the plain, and the lowest in the marginal zones (modified after Pautou, 1984). 1, Heath with *Phalaris arundinacea* and diverse *Salix*; 2, *Salix* thicket; 3, *Salicetum* with *Salix alba* and *Carex acutiformis*; 4, *Salicetum* with *Salix alba* and *Impatiens glandulifera*; 5, *Salicetum* with *Salix cinerea* and *Acrocladium cuspidatum*; 6, *Alnetum* with *Alnus incana* and *Equisetum hiemale*; 7, elm groves with *Ulmus minor*; 8, oak–ash woodland with *Quercus robur*, *Populus alba* and *Arum maculatum*.

the other hand, the soils associated with former meanders and the marginal wetlands (eutrophic peats) contain more than 80% organic matter, and intermediate amounts are seen in the beds of former braided channels (Pautou, 1984).

If the duration of inundation selects plant species as a function of their ecophysiological characteristics (Figure 10.4), the time of the year during which they are submitted to inundation exerts an equal influence. Thus, in the floodplains of the Upper Rhône, while the units are primarily regulated by fluvial inundation, being submerged during the warmer season, distinct differences between the units are related to the rainfall regime which causes submersion during the cold season (Figure 6.8). The influence of flooding is particularly apparent in the more dynamic zones around confluences where the hydrology is influenced by the tributary and main river regimes. On the Upper Rhône, tributary flows cause higher levels at the end of the spring and at the beginning of the autumn (Pautou, 1984). Such complexity results in a plant community distribution which is extremely diverse and in which the individual zones are overlain to form what is often a continuous and stratified covering. For example, in the Hungarian plain of the Danube, Karpati and Karpati (1958) outlined up to 16 distinct groups of shrubby and tree species. For the Rhône–Ain confluence, Girel (1986) outlined over 60 different communities of arboreal and non-arboreal species.

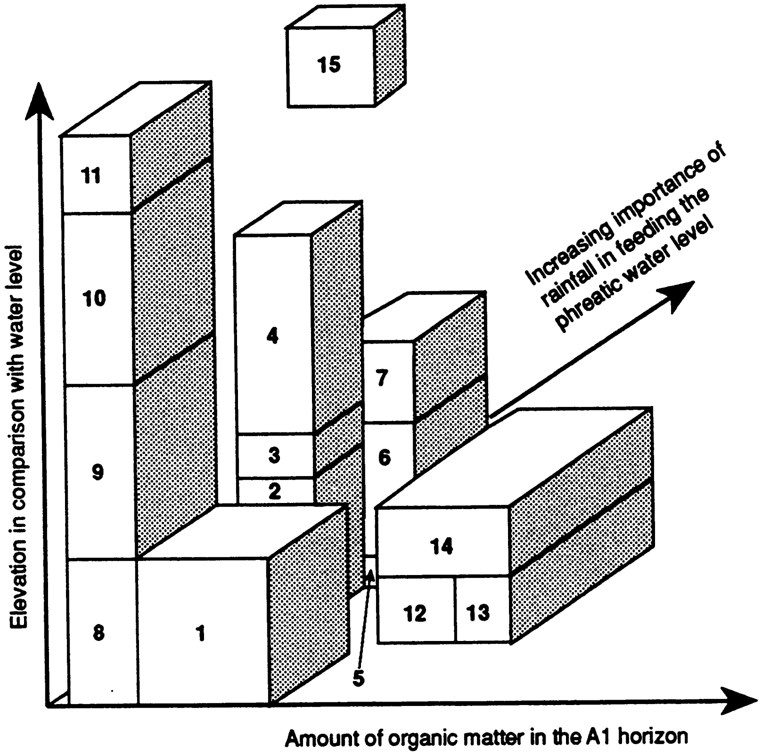

Figure 6.8 Distribution of the principal vegetation communities in the alluvial plain of the Upper Rhône between Geneva and Lyon displayed as a function of three major ecological factors: elevation in comparison with the permanent piezometric level, the amount of organic material in the soil and the amount represented by the input of rainfall in comparison to imports from the phreatic slope (after Pautou, 1984). For simplification, certain groups of species are combined: 1, diverse forests of *Salix*; 2, *Salicetum* with *Salix alba* and *Impatiens glandulifera*; 3, *Alnetum* with *Alnus incana* and *Equisetum hiemale* and *Alnetum* with Alnus incana, Fraxinus excelsior and *Hedera helix*; 4, Oak–ash woodland with *Populus alba* and *Arum maculatum* and oak–ash woodland with *Populus alba* and *Aegopodium podagraria*; 5, *Salicetum* with *Salix triandra, Salicetum* with *Salix alba* and *Carex acutiformis, Salicetum* with *Salix cinerea*; 6, elm groves of *Ulmus minor*, 7, oak–ash woodland with *Populus alba* and *Carex pendula*; 8, *Salicetum* with *Salix elaeagnos*; 9, clearings in poplar stands with *Populus nigra* and thorn bushes; 11, heath with *Robinia pseudacacia*; 12, *Alnetum* with *Alnus glutinosa* and *Carex elata* and *Alnetum* with *Alnus glutinosa* and *Fraxinus excelsior*, 13, forest of *Frangula alnus*; 14, ash stands with *Alnus glutinosa* and *Carex remota* and ash plantation with *Allium arsinum*; 15, oak–hornbeam stands with *Carpinus betulus*. The texture of the sediments are not represented in the schematic diagram and are partially correlated with the amount of organic matter. Groups 1, 2, 3 and 4 develop on the silty sandy soils of levee banks and islands; groups 5, 6 and 7 on the silty and silty–clay soils of the depressions between elevated areas; groups 8, 9, 10 and 11 on sandy and gravely soils, groups 12, 13 and 14 on silty–clay soils, humic soils and peaty soils of cut-off meanders, old anastomosed side-arms and marshy wetlands; group 15 on clay soils of levees and high areas of the floodplain (after Pautou, 1984).

Downstream and across a transverse profile, the number of woody species increases as the frequency and intensity of flooding decreases; from four species on average in the *Salix alba* and *Carex* communities at the side of the active channel and in the groups characterized by *Alnus glutinosa* of former meander beds the number of woody species can exceed 50 in the long-lasting *Querco–Ulmetum* forest and wood communities. In the latter group, the increase in the number of species is accompanied by an increase in the biomass, with this development favouring the growth of species which can attain 40 m in height and 1 m in diameter (Table 6.2). The groups of shrubs or trees that are inundated for the major part of the year appear a lot less productive than their counterparts which are only seasonally inundated (Connor and Day, 1982). In general, the productivity of a species increases as the frequency and duration of the flood diminish; however, beyond an optimum amount, the reduction in flooding entails a decrease in productivity (Gosselink *et al.*, 1981).

Table 6.2 Aerial biomass (dry matter in tonnes ha^{-1}) of some terrestrial units (after Pautou, 1984)

Thickets of diverse *Salix*	53
Forest group of *Salix alba*	130–150
Forest group of *Alnus incana*	200–225
Forest group of *Quercus robur* and *Fraxinus excelsior*	350

6.3.3 EFFECTS OF DISTURBANCE ON PRIMARY PRODUCTIVITY

In the natural condition, disturbance constitutes a key factor in the distribution of plant species and the intensity of their production. A disturbance here is defined as a significant change from the normal pattern in an ecological system (Forman and Godron 1986). Pickett and White (1985) have discussed the relationships between disturbance and patch dynamics in terrestrial systems and Resh *et al.* (1988) apply this concept to include relatively discrete spatial and temporal events which disrupt aquatic ecosystem structure and function, and change resources, the availability of substrate or the physical environment in general. In fluvial hydrosystems, such disturbance can be direct (e.g. inundation, desiccation, erosion, siltation, bar formation) or indirect (e.g. change to the hydrochemical gradient) and can follow on from other changes in the ecosystem (e.g. redirection of succession sequences). However, apart from human influences, the major natural disturbance factor in the fluvial hydrosystem is undoubtedly the flood.

A flood event has two types of effect on the mosaic pattern of the fluvial unit. It can, by inundating the unit, affect the communities without altering the biotope, or transform the biotope through erosion and deposition, provoking a lasting change in the species composition of the aquatic communities. The latter case corresponds with the process of ecological succession (analysed in detail in Chapter 10). Besides importing nutrients, floods carry organic debris which accumulates in the form of litter throughout the fluvial environment and principally around and within the main channel. As well as providing valuable habitat for instream fauna such as fish and invertebrates, this debris is consumed by the detritivores and mineralized by the decomposers (Chapter 9) to fuel secondary production within the system. In this chapter, however, only the effects of disturbance on the primary production of the fluvial hydrosystem is examined.

At the level of the large alluvial plains along large rivers, the water of the main channel is generally rich in dissolved nutrients (Chapter 3). One of the effects of flood will be to import nutrients into the aquatic and terrestrial units of the alluvial plain (Figure 6.9). There, this excess of nutrients encourages rapid growth and multiplication of algae and phytoplankton and an increase in the growth of macrophytes. When such nutrients are in abundant supply, the rapid and massive growth of phytoplankton can produce algal blooms which last for a number of days after which there is an extremely high death rate. The decomposition of dead algae results in severely depleted dissolved oxygen levels, the harmful effects of which are then translated to the invertebrates and fish in the systems, resulting in high mortality rates of these species.

In the riparian zone unit of the fluvial hydrosystem, the import of nutrients by flood events favours primary productivity (Brown and Lugo, 1982), but the difference here is that the major part of the biomass remains stocked in the form of wood and the degradation and recycling of the biotic resource operates over a much longer time-scale. When this nutrient spiralling is expressed in terms of a helical flow the storage of organic matter manifests itself in the form of a tightening of the length of the helix – in other words as a slowing down of the transfer of material in a downstream direction (Figure 6.10). Of course, between the two extremes represented by woods with their long periods of growth, long periods of storage of organic matter and slow decomposition, and the unicellular algae with rapid growth and decomposition, lie the aquatic macrophytes and the herbaceous species where the speed of growth and decomposition are intermediate.

When under natural conditions, a flood destroys a unit of the floodplain mosaic and carries away its organisms eventually eroding the biotope, it contributes at one and the same time to the increase in the total biodiversity and primary productivity of the fluvial hydrosystem. In effect the influence of the flood is to form a mosaic of units at different ages and stages of development (i.e. at different seral stages). Through the course of ecological succession, these units tend to evolve from

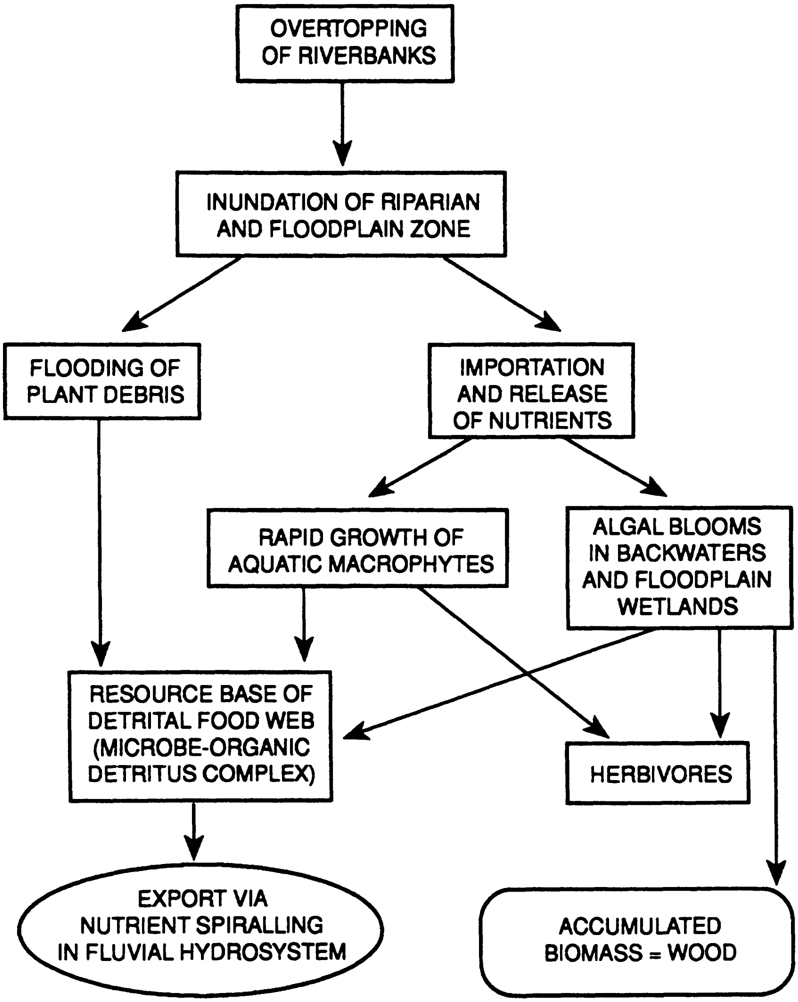

Figure 6.9 Influence of floods on the primary productivity and the trophic structure of fluvial hydrosystems in the temperate zone.

pioneer and young stages towards more mature and relatively more stable conditions (Chapter 10). In destroying the stages which are close to maturity, disturbances permit the re-establishment of species characteristic of pioneer stages. As well as being favoured by geomorphological instability, pioneer communities are more productive (P/R ratio > 1) than the mature communities (P/R approx. = 1) where the major part of the assimilated energy is stored in some form of biomass (notably wood). This ratio can fall below 1 in certain forest units where there is

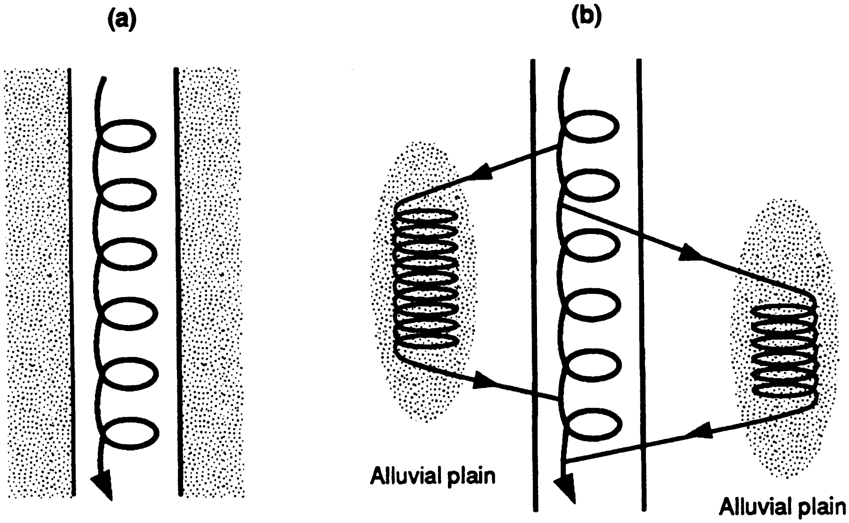

Figure 6.10 Helical flows of nutrient salts in a water course separated from the floodplain (a) and in a fluvial hydrosystem (b) where flooding induces regular exchange between the main channel and the ecosystems of the floodplain. The tightening of the helix is explained by stagnation of flows and stocking of nutrients in the form of biomass which only decompose and recycle very slowly (in the case of woody material, the nutrients are kept in one place in the system often for a period of decades.)

high accumulation of organic matter and where photosynthetic activity is proportionally very low. The situation is in reality therefore extremely complex. Where there is a surplus of primary production ($P/R > 1$) this situation is only achieved for relatively short periods during the course of the year. Nevertheless, that period provides a reserve of organic material sufficient to ensure the efficient functioning of the ecosystem during the rest of the year. In general, the aquatic macrophytes of lotic environments attain their maximum production in spring, or in early summer, whereas the algae and periphyton are most productive at the beginning of spring and/or in autumn. In the riparian zone, creepers such as ivy (*Hedera helix*) can also enrich the litter as their leaves fall chiefly in spring, whereas the majority of the woodland species drop their leaves in autumn (Trémolières *et al.*, 1988). On the other hand, the utilization of the yield of the P/R ratio to characterize the functional energetics of the aquatic system must be done with caution. Fisher and Likens (1973) emphasize the need to include the quantities of organic matter imported and exported in all energy balances for a watercourse (as an example, if the imports are less than the exports, P/R will tend to be less than 1 at the same time that the system is dominantly autotrophic).

6.4 CONCLUSION

It can be seen from the above discussion, that a heterogeneous interaction of physical and chemical variables characterizes fluvial hydrosystems, and the plant species within fluvial hydrosystems respond by a variety of adaptive strategies which are concerned with both their morphology and physiology. The species which most markedly display these adaptations are those which are most capable of colonizing the flowing waters and the aquatic and terrestrial environments close to them which are frequently disturbed by high flows and flooding.

Whereas the small streams at the head of the drainage basin function fundamentally in a heterotrophic mode, and the portion represented by allochthonous energy diminishes in a downstream direction, the large floodplain rivers tend towards autotrophy. The alluvial floodplains and deltas form a complex mosaic, which by nature and function is very diverse. It is in this part of the fluvial hydrosystem that the incessant interaction between fluvial dynamics and biological processes serve jointly to increase both biodiversity and primary productivity.

The living vegetation plays a very important role in the fluvial hydrosystem and influences at one and the same time the aquatic and terrestrial ecosystems, not only in the provision of a trophic resource but also in creating a diverse range of habitats and microclimates for fauna. Whether the vegetation depends directly or indirectly on the geomorphological processes operating in the fluvial hydrosystem, it in turn can exert strong influences on the system (Chapters 5 and 9). Taking these (sometimes very important) consequences into account can allow the vegetation itself to be used in the environmental management of the fluvial hydrosystem (Chapter 12). By production of organic matter (which can be remobilized), by absorption of dissolved substances such as phosphates and nirates (through modification of chemical fluxes), by the formation of physical structures which form an obstacle to certain flows (through reduction of the kinetic energy of flowing waters) and by reduction of available solar energy (through shading and flooding), vegetation plays a major role in the exchanges and interactions between the diverse units of the hydrosystem. This is often most apparent at the ecotones or zones of interaction between ecological units of the system (Chapter 9). All the functions that vegetation plays alter over the course of time through modification of the vegetation communities by ecological succession, by interactions with water flows resulting in the transformation of the biotopes by erosion and deposition and through the biological processes responsible for vegetation dynamics (Chapter 10).

Aquatic invertebrates 7

M. T. Greenwood and M. Richardot-Coulet

7.1 INTRODUCTION

From the source of the river, the longitudinal gradient of ecological conditions corresponds to a spatial sequence of faunal communities. This distribution of species is the result of (a) adaptive strategies to physical parameters such as, water temperature, flow velocity and shear stress, and bed-sediment size, and (b) strategies which optimize the utilization of food resources and available living space. Along a river, the flow of water determines both the connectivity between, and the general characteristics of, the different sectors. Similarly, in the floodplain the aquatic environments (cut-off channels and permanent backswamps) are fed from the main river either directly during floods or indirectly, by exchanges with the alluvial aquifer. However, hydrological connectivity between aquatic environments within the floodplain is discontinuous both in space and time, and the importance of this linkage depends not only on its strength and duration (Figure 7.1) but also on its timing. A variety of aquatic environments are created by the differing degrees of connectivity and give rise to a mosaic of interlinking habitat patches and communities. Three concepts have been proposed to explain the functioning of the river and its floodplain: the River Continuum Concept (Vannote *et al.*, 1980), the Nutrient Spiralling Concept (Webster, 1975; Newbold *et al.*, 1981) and the Flood Pulse Concept (Junk *et al.*, 1989). This chapter uses these concepts to examine, at a variety of spatial scales, the ways in which the heterogeneity of aquatic habitats influences the distribution of invertebrate communities. In particular, how are the distribution patterns related to the degree of connectivity with the river?.

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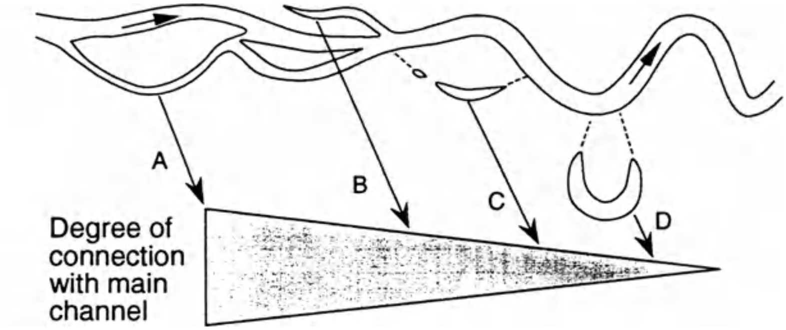

Figure 7.1 The different types of aquatic ecosystem found on a floodplain, arranged according to the degree of connection with the main channel. A, secondary channel; B, cutoff channel isolated at its upstream end; C, cutoff channel; D, cutoff channel isolated from the main channel.

What are the effects of floods and low flows on the distribution of species and, more generally, what are the effects of different flow regimes on the organization of populations in the different aquatic environments of the floodplain?

7.1.1. SCALE, DIMENSIONS, SECTORS AND UNITS

Within the river and its floodplain, patterns of faunal distribution can be observed at different scales and in differing dimension. For example, at the catchment scale (macroscale), the headwater communities in sections of high altitude, high slope, turbulence and low temperatures, give way to different species, associated with the more depositional, warmer, lowland reaches. This longitudinal sequence in distribution can be illustrated by the case-less caddisflies (O. Trichoptera; F. Hydropsychidae), a group of closely related species in which the larvae spin silken nets to capture food particles from the flow. In the river Usk (Wales), the headwaters are characterized by the presence of *Diplectrona felix* and *Hydropsyche instabilis*. Then in the main river, *H. siltalai* and *H. pellucidula* coexist throughout much of its length, with *H. contubernalis* and *Cheumatopsyche lepida* present only in the lower reaches (Edington and Hildrew, 1981). Species that are typical of particular sectors or units are known as 'describers'.

At a mesoscale (of metres–kilometres), riffle-pool sequences create contrasting habitats each with a characteristic fauna. For many taxa the preference for riffle or pool is precise. Examples characteristic of riffles can be found from the Ephemeroptera (*Baetis muticus*), Trichoptera (*Hydropsyche siltali*), Plecoptera (*Protonemura meyeri*) and Simuliidae, whereas the Odonata, Diptera, Coleoptera (Dytiscidae) and some Trichoptera (*Polycentropus flavomaculatus*) are abundant in pools.

At a microscale, within a patch size of >1 m^2, the interface between the flow and the substratum creates a microcosm; a unique set of environmental conditions where subtle patterns of distribution relate to hydraulic conditions. Wetmore *et al.* (1990) characterized the hydraulic habitat of *Brachycentrus occidentalis* (O. Trichoptera), a filter-feeder inhabiting the shallow cobble reaches of Wilson Creek (Manitoba). Larvae were found in zones of converging streamlines and within a narrow range of a Froude number, optimal for filter feeding.

The classification of a river into 'functional sectors' provides the template for descriptive ecology. At this scale, hydrology and geomorphology are seen to determine habitat diversity and ecological functions. Within each functional sector, sets of 'functional units' are defined. Each unit is the biotope or 'organic overlay' of each landform. An evolutionary (successional) sequence of units forms a 'functional set'. Ecologically, this scale of resolution focuses on communities, their functional characteristics and autogenic successional processes.

7.2 LONGITUDINAL PATTERNS: *MACROSCALE*

In the main channel, the distribution of species is, to a large extent, a function of adaptations to *hydraulic stress* (Figure 7.2). Flow, as described by Statzner and Higler (1986) is considered a compound variable, with critical changes taking place along the river creating and distributing, unique animal assemblages. Figure 7.2 indicates that the spring habitats have a typical fauna (A) and give way to an assemblage of species adapted to fast flowing water (B). As the river enters the floodplain a new assemblage can be identified with species adapted to the slow moving, depositional zone (C), which leads to estuarine assemblages tolerant of saline conditions (D). At the transition points between each section of the river there is an overlap of taxa, with some species unique to each transition zone (T).

The thermal characteristics of the river are also important determinants of faunal pattern, especially in the influence they have on the developmental cycle of species. It should be remembered that in this open system, the adults are mostly aerial stages for reproduction and dispersal, whereas the aquatic habitats, with a rich food source, act to support the immature growth stages; the nymphs and larvae. This can be illustrated by comparing the egg-hatching success of Plecoptera, regarded as cold-water species, with the Ephemeroptera, most commonly associated with warmer waters (Figure 7.3). For *Mesocapnia oenone* and *Leuctra digitata* (O. Plecoptera), a hatching success rate of 90% is achieved in temperatures as low as 2 °C is found in the Plecoptera whereas the Ephemeroptera

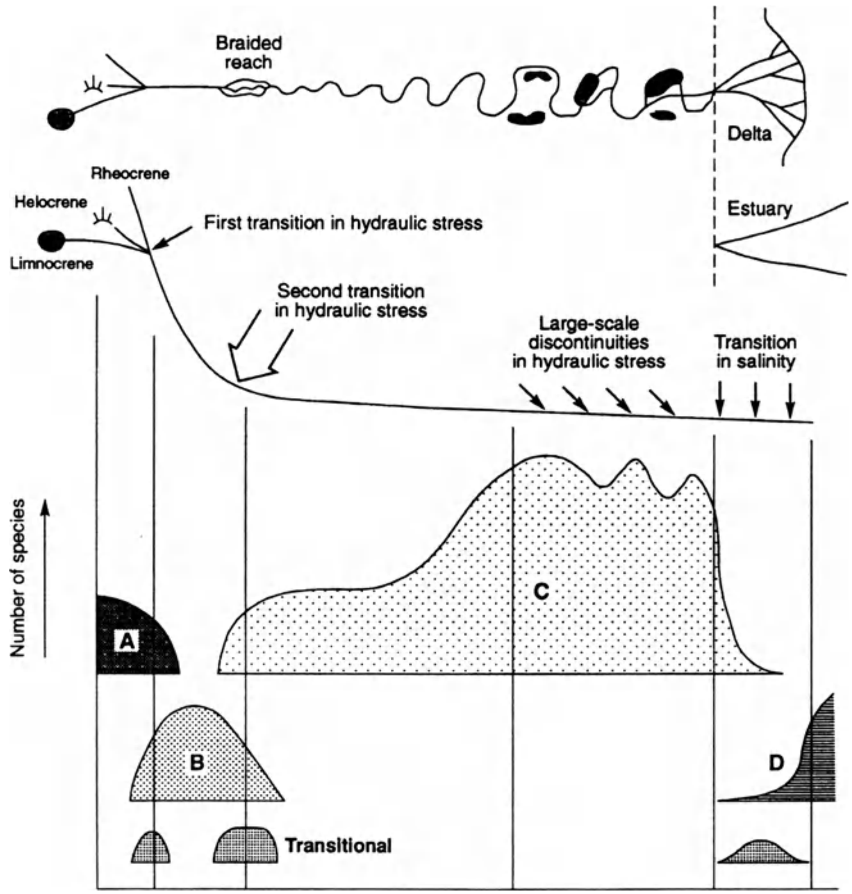

Figure 7.2 A model representing macroinvertebrate zonation patterns along the river profile. Communities of springs (A), fast-flowing, turbulent water (B), slow flows (C), estuaries (D) and transitional communities (T) (after Statzner and Higler, 1986).

maintain a success rate >50% at temperatures > 25 °C. Studies of egg incubation show that, for most Ephemeroptera, the amount of heat required for development (in degree-days), increases rapidly as temperature decreases in contrast to the more thermally independent Plecoptera (Brittain, 1990).

The spatial distribution of communities is a function of complex interactions between two sets of parameters: the ability of species to adapt to ecological factors such as the composition and size of the substrate, discharge etc. and the demand for certain food resources (allochthonous debris, filterfeeding, carnivory etc.). Based on these two groups of par-

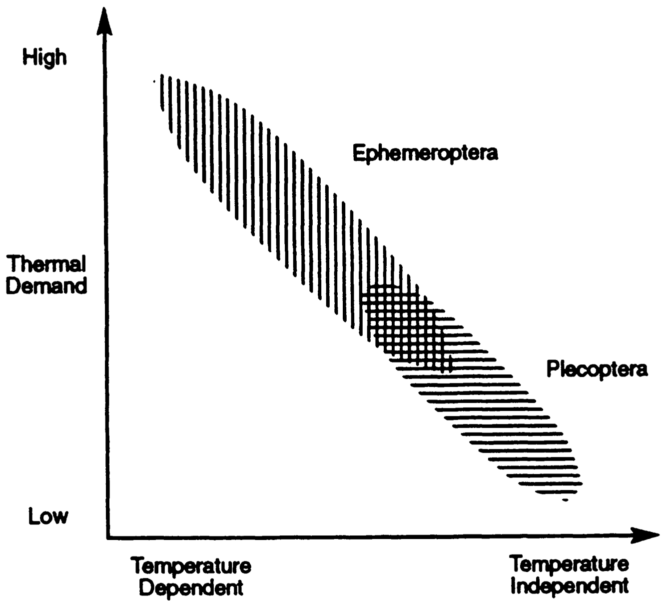

Figure 7.3 Thermal demand of Ephemeroptera and Plecoptera, based on embryonic development (after Brittain, 1990).

ameters, Illies and Botosaneanu (1963) suggest a system of longitudinal zonation in which three main zones are defined (crenon, rhithron and potamon), each characterized by a 'type' of invertebrate community. More recently, Vannote *et al.* (1980) have shown that the progressive modification of physical conditions (geomorphology, hydrology) from upstream to downstream, generate a continuous gradient of available food (trophic) resources. The distribution pattern of invertebrates is governed by the different strategies developed by the species taking advantage of the available food. Thus, along the length of the river a succession of communities exists (Figure 7.4). In the tree-lined headwaters, communities are dominated by shredders (e.g. *Nemurella picteti*), species adapted for processing the allochthonous input into coarse particulate organic matter (CPOM). The wider, middle-reaches of the river, where production outweighs losses due to respiratory or breakdown processes (P/B>1), has an invertebrate community dominated by collectors; those filtering collectors (e.g. *Simulium ornatum*), sieving particles from the water column, or gathering collectors (e.g. *Centroptilum luteolum*), which browse the surface deposits. Species described as scrapers (e.g. *Baetis rhodani*), are in high proportion in this zone. These feed on the periphyton or perilithon (the biological film comprising mainly algae and bacteria), which grows on the surface of plants and stones. Downstream, the system

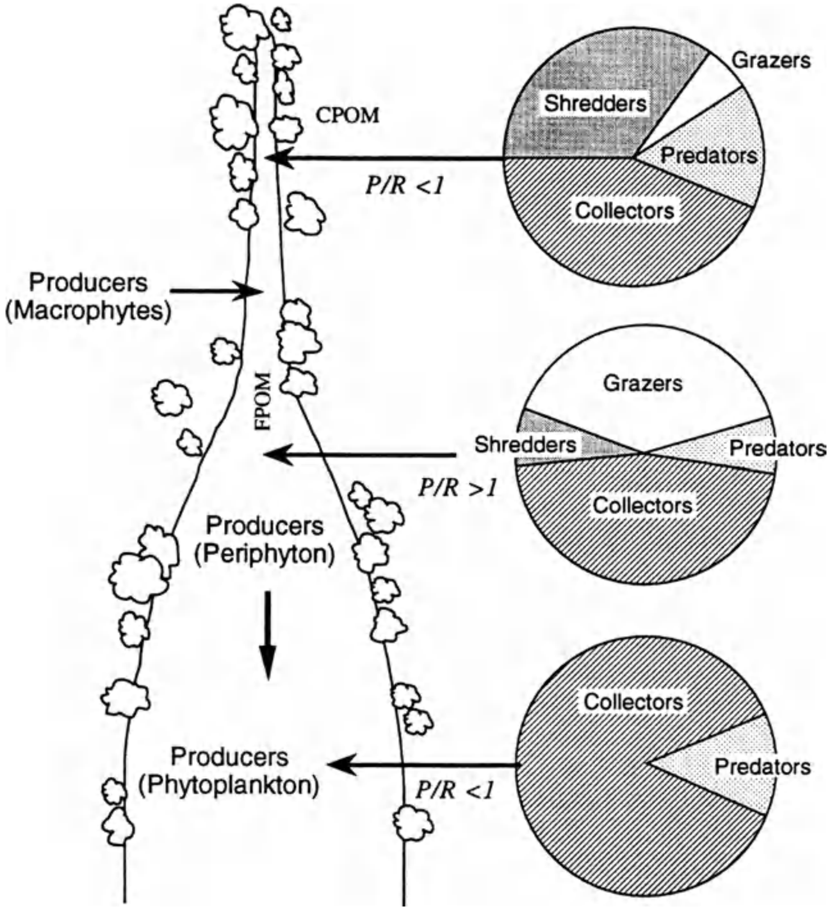

Figure 7.4 Distribution and trophic status of invertebrates along the river profile (from Vannote *et al.*, 1980).

becomes more autotrophic. Species in this zone are predominantly collector–filterers (e.g. *Ephemera danica*). Benthic primary production is limited by increasing depth and turbidity, and the macroinvertebrates feed mainly on FPOM and UFPOM flowing from upstream. Phytoplankton primary production, enhanced by the slowing of the current and increase in water surface, also supports zooplankton communities, which provide a further food source for the collectors. Thus, there appears to be an adaptive response by the macroinvertebrates to the food type, structure and availability, along the river continuum. Along all sections of the river, predatory species (secondary consumers) are part of all invertebrate communities. This longitudinal continuum concept is a general model and may require modification when applied to other regions and climatic zones (Statzner and Higler, 1985).

7.3 SPATIAL VARIATION WITHIN FUNCTIONAL SECTORS: *MESOSCALE*

The mosaic and variety of aquatic habitats on the floodplain develop as a consequence of the degree of connectivity with the main channel. As habitats become more isolated so the flow is reduced and trophic resources affected. The distribution of species is the result of two types of response: to environmental constraints (e.g. current speed) and to the amount and quality of the food resource. Flow characteristics, e.g. velocity, which are greatest in the main channel, limit a number of macroinvertebrate species (Statzner *et al.*, 1988). Those species found on the gravels, pebbles and boulders of the stream bed have to withstand the full forces of the flow. Such adaptations may be morphological and/or behavioural. Many adopt anchoring mechanisms, one of the most common being the use of suckers (e.g. fly larvae of the family Blephariceridae). Among the molluscs (F. Ancylidae), *Ancylus fluviatilis* (Figure 7.5a) uses the aperture of the streamlined shell and the muscular foot to produce suction. The edge of the shell is non-calcified, and flexible which allows for adhesion on irregular substrate surfaces. The freshwater 'zebra' mussel (*Dreissena polymorpha*) clings to rocky surfaces by tufts of filaments (byssus threads) secreted by the organism. At the end of each thread is an adhesive disc which, in large numbers, is efficient in resisting the drag forces of the flow. The larvae of blackfly (O. Diptera: F. Simuliidae) (Figure 7.5b) spin a small adhesive silk net onto stone surfaces into which is anchored a posterior circlet of hooks. Most benthic macroinvertebrates avoid strong flows by selecting more sheltered microhabitats and many move into the interstitial spaces in the matrix, these acting as refugia in times of flood and low flows. Certain mayfly larvae (F. Heptageniidae) (Figure 7.5d) are dorsoventrally flattened and can adjust their position to the flow so as to minimize the lift and drag forces. In fast-flowing alpine streams the larvae of *Rhithrogena* sp. increase adhesion to the substrate by the shape of the gills which act as suckers (Figure 7.5c). Some species, e.g. the freshwater shrimp (*Gammarus* sp.) are laterally flattened and this too, allows movement into the interstitial spaces of the substrate.

Macroinvertebrates cannot remain permanently attached or in refugia; for survival, feeding and reproduction, species for the most part, must move. These movements make them vulnerable to the current and large numbers of organisms are displaced downstream in the drift. The

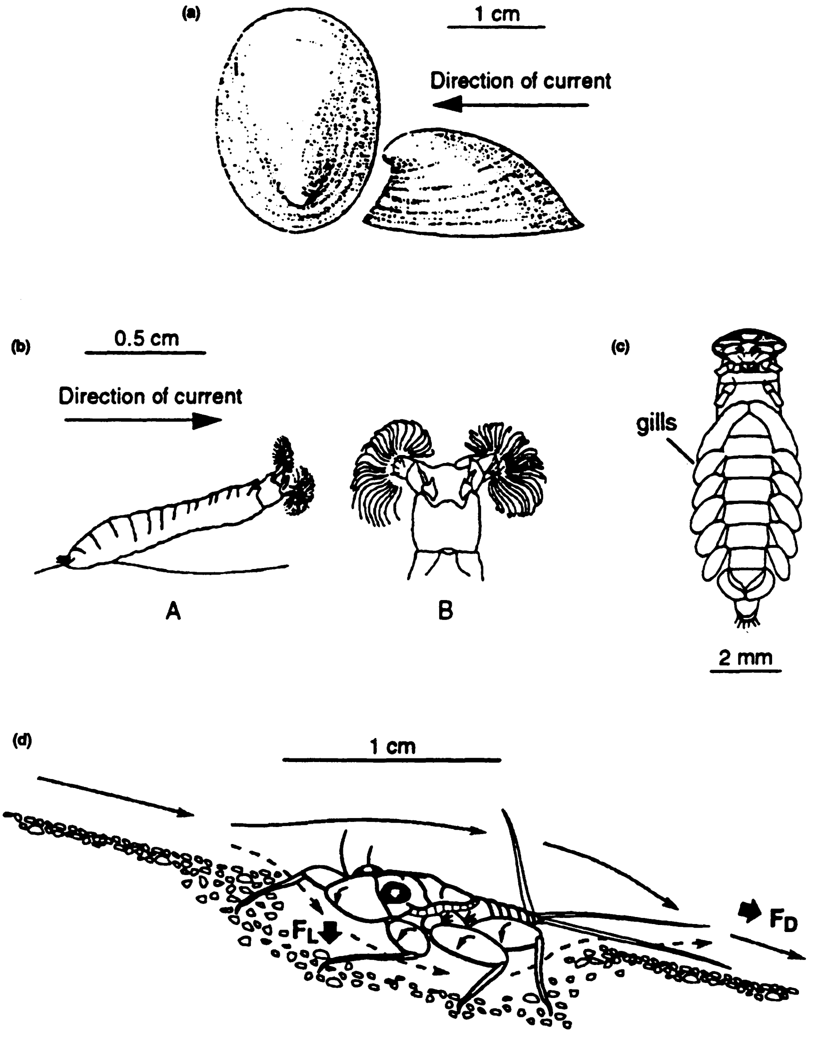

Figure 7.5 Structural adaptations to running water. (a) Shell of *Ancylus fluviatilis*, from above and in profile (after Girod *et al.*, 1980). (b) Simuliid larvae attached to the substrate (A), and detail of the two cephalic fans used as filters (B) (after Hynes, 1970). (c) Abdomen of *Rhithrogena* sp. (Ephemeroptera) from below, showing modified gills for attachment (after Campaioli *et al.*, 1994). (d) Nymph of *Ecdyonurus venosus* (Ephemeroptera) on substrate showing structural adaptations used to withstand lift (F_L) and drag (F_D), forces (after Weissenberger *et al.*, 1991).

phenomenon of drift may also be an active (behavioural) response to competition for food and for space, and is observed in all streams. In large rivers the drifting organisms account for a substantial energy loss

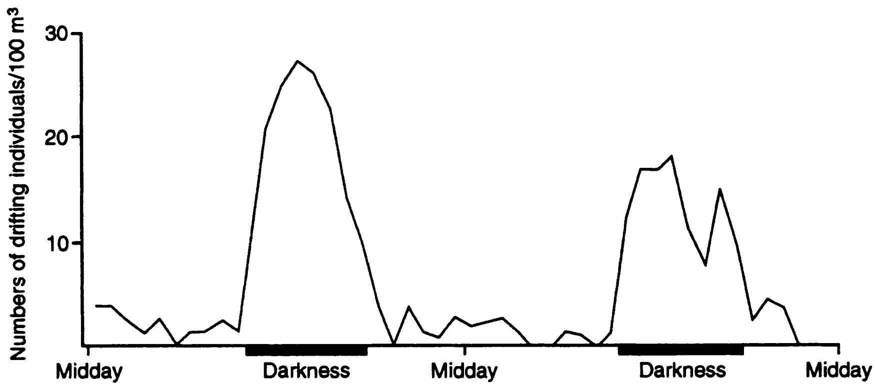

Figure 7.6 Diel patterns of drift density of *Ephemerella ignita* (Ephemeropera), from the Upper Rhône (after Cellot, 1989b).

to the system. For example, Cellot (1989a) estimates that 44 million individuals with an annual biomass of 9631 kg (dry wt), pass through a cross-section of the Rhône at Lyon in 24 h; 64 million drift in the Missouri (Berner, 1951 in Hynes, 1970) and 13.6 million from the Danube in Austria (Anderwald *et al.*, 1991). Many species follow a diel rhythmic pattern with some Ephemeroptera adhering closely to light and dark cues (Figure 7.6). Total drift densities may be three times greater at night than during the day, which is the active period for most species (Cellot, 1989b). The absence of a drift pattern is often a feature of large rivers. In the Danube the watercolumn (of 3.5 m) carries a suspended particle loading of 10–20 mg l^{-1}. Such turbid waters absorbs 99% of the light with only low intensities reaching the benthic inverterbrates. With the light cue weakened, any behavioural rhythmn appears to be eliminated and drifting reduced (Anderwald *et al.*, 1991). The downstream displacement in the drift is partly compensated for by upstream movements of late instar nymphs or by the upstream flight of gravid females. Adult caddis-flies emerge from the pupal case, swarm, mate and with mature eggs, fly upstream to lay their eggs in headwater habitats. This cycle sustains colonization and compensates for the downstream losses (Müller, 1982).

The current velocity and flow forces, not only control the microscale distribution of invertebrates but also play an important role in determining the food supply. Large amounts of CPOM are processed, transported and passively collected by attached filter feeders (e.g. bivalve molluscs). Other collectors, e.g. the larvae of *Hydropsyche* sp., construct a silken net. This acts both as a tubular retreat for the animal and also has a central filtering area taking both plant and animal material from the flow (Figure

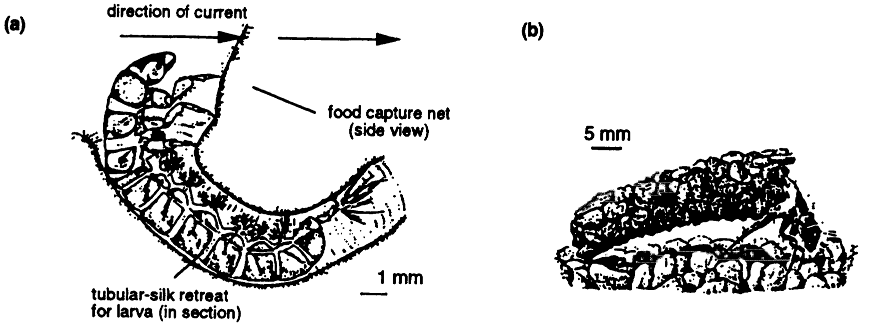

Figure 7.7 Larva of Trichoptera: (a) *Hydropsyche* sp. in net (after Pierrot, 1984), (b) *Micropterna testacea* in case of sand grains (after Prodon, 1976).

7.7a). The larva holds itself in position by the anal appendages, the meso- and metathoracic legs, while the prothoracic legs are held close to the underside of the head which is then moved rapidly from side to side, over the central area of the net. Any particles are rapidly seized by the mandibles and prothoracic legs (Philipson, 1953). The larvae of blackfly found in turbulent reaches, orientate their bodies in such a way that the two cephalic fans filter particles from the flow (Figure 7.5b). The flow also removes the fine sediments which may cover the perilithon growing on stones. This provides a resource for grazers (the limpet, *Ancylus* sp.) and scrapers (F. Heptageniidae) each with mouthparts designed for rasping and scraping surfaces.

7.3.1 SECONDARY CHANNELS WITHIN BRAIDED REACHES

The secondary channels within a braided system are relatively narrow, shallow and of low velocity; spatial niches are numerous and there is a variety of food resources. Species found here are more generalist in their morphological adaptations and resist changes in flow using behavioural responses. Net-spinning Hydropsychiidae, protected by silk nets, coexist with case-building caddis-fly larvae. Species such as *Micropterna testacea* (Figure 7.7b), protect their abdomen with a case made of sand grains which also acts as ballast. Each instar will use sand grains of a different size and is to be found in areas where a preferred particle size exists. Changes in flow velocity produce changing patterns in the granulometry of the substratum and results in the macroinvertebrates being distributed in a mosaic of spatial patterns. A similar strategy is adopted by the large freshwater mussel (*Unio* sp.), which has a thick, heavy shell: this resists drag forces and prevents crushing by movement of pebbles in the flow. Substratum heterogeneity increases niche space and provides a variety of trophic resources. Sedimentation creates a shallow depth and light penetrates the water column resulting in a greater primary production than in the main channel.

7.3.2 CHANNELS CUT-OFF UPSTREAM

Channels may be abandoned by the mainflow by the processes of lateral migration and neck cut-off (Figure 5.7), or by avulsion – a sudden shift in course, typical of aggrading (especially braided) sectors. In many cases, cut-off involves the formation of a sediment 'plug' at the upstream end of the abandoned channel, leaving the downstream end open to the main flow. Over time the downstream end is also 'plugged' and the cut off channel becomes increasingly isolated from the parent river. These cut off channels may be flushed during high floods but for most of the time their flows depend on springflow from the alluvial aquifer or tributary inputs. They become stores for fine sediments and organic matter.

(a) Braided channels

Such old channels are ecologically very diverse. The channels are often lined with dense stands of macrophytes (*Sparganium* sp, *Glyceria* sp.), which provide an important allochthonous source to the system. The wide variety of habitats helps to explain a high species richness. The number of species may be five or six times higher than in the main channel (Table 7.1). Species typical of calm water and the riparian fringe coexist together with free-swimming, open water species. In places where slow flows are maintained, species typical of lowland streams (e.g. *Caenis* sp.) are found together with a wider diversity of limnophilic species (e.g. *Cloeon* sp.). In the Crustacea, densities of actively swimming species (e.g. *Gammarus* sp.) decline, giving way to crawling detritivores, such as *Asellus* sp. The accumulated detritus is an important food source for the shredders. Within the Trichoptera, rheophilic species with cases of mineral particles, are replaced by species whose cases are constructed from stem fragments and cut leaf material (e.g. *Phryganea* sp.). Among the Mollusca, *Ancylus fluviatilis* is only found in flowing sections and is replaced by genera typical of calm and slow flow. Both *Acroloxus* sp. and *Ferrissia* sp., feed in summer on the periphytic algae on emergent plants and in winter on dead leaves and fragments of vegetation. Burrowing species are also numerous in sandy areas. In a comparison of two secondary channels of the Mississippi (Table 7.2), the one still retaining connections both upstream and downstream with the main-channel, was dominated by species living on coarse and solid substrates. The other secondary arm, connected only at the downstream end, was dominated by burrowing species typical of softer substrates. The heterogeneity of

Table 7.1 Comparison of the number of species in the main channel and a former braid arm isolated at the upstream end of the River Rhône (after Castella *et al.*, 1984)

	Main channel	Former braid arm	Species common to both
Mollusca	6	23	3
Crustacea	4	3	3
Ephemeroptera	8	6	2
Coleoptera	5	37	1
Trichoptera	13	14	1

Table 7.2 Comparison of the biomass of benthic and burrowing species in two contrasting habitats on the Mississippi, USA (after Neuswanger *et al.*, 1982)

	Mean biomass (mg m^{-2})	
	Benthic fauna	Burrowing fauna
Secondary channel	7880	1960
Channel isolated at the upstream end	636	5040

the substrate, diverse habitats and large stands of vegetation provide favourable conditions for many predatory species (e.g. dragonflies).

(b) Meanders

These isolated waterbodies are reaches of the main channel cut off by natural avulsion or human activities and distinguished from braided channels in being deeper and with a pronounced curved outline. Once cut off from the main flow, most rheophilic species typical of the main channel disappear. In lower flows, vegetation stands colonize the sand and gravel bars on the convex bank of the river and provide shelter and food for a range of limnophilic species. Fine sediment and organic debris are no longer washed by the current and accumulate in the old channel. The soft substrate is colonized by many burrowing species (Oligochaeta: F. Tubificidae) and molluscs, typical of slow-flowing rivers. *Lithoglyphus naticoides*, for example, reaches densities of 1300 individuals m^{-2} in an ancient meander of the Rhine (Schmid, 1978). These old meanders were once part of the river course and it is not surprising to find that many are still fed with water from tributaries. They are usually found at the base of a terrace on the edge of the floodplain and may be supplied with groundwater from seepages and lateral springs. Occasional floods create tracts of sand and gravel substrate within this large still-water habitat which increase habitat diversity and species richness. Burrowing predatory species colonize the clean, sandy areas and feed on species found in both low velocity areas (rheophiles) and those associated with still water (limnophiles) and adjacent depositional habitats. Stream-dwelling molluscs of the genus *Unio* with robust shells, are found in the faster-flowing regions, but are replaced by *Anodonta* sp., with thin, fragile shells in slow-flowing areas. Upwellings of cold groundwater allow colonization by stenothermal species, such as the pulmonate mollusc, *Physa fontinalis* whereas *Radix auricularia* (Lymnaeidae) is found localized on vegetation away from the flow.

7.3.3. CUT OFF CHANNELS ISOLATED FROM THE RIVER

(a) Braided channels

Cut off from the controls of the main flow, the process of terrestrialization within former braided channels, leaves only small pools which are vulnerable to extremes of flooding from the main channel and to periods of drought. Most water loss is by evaporation and seepage into the underlying permeable gravels. Extremes of flooding and of drought, together with the unpredictability of the timing of these events, are the principal factors controlling the development of the macroinvertebrate communities. There are often small inputs from tributaries and groundwater but any exchange may be impeded by accumulations of decaying organic matter within the substrate. In such cases the pools are supplied by rainwater and periodic floodwaters. In the unsilted parts, the channel bed is supplied with upwellings from groundwater sources. With high flow conditions in the main channel, seepage water raises the water table and the channel pools are replenished by interstitial flow. Under low flow conditions the opposite effect takes place: the bed may dry out as groundwater levels fall but some capillary action within the gravels keeps the substrate moist. Flooding flushes the invertebrates from the habitat and a period of time is required for recolonization to take place. Clearly, the time taken for restoration must be less than the time interval between two flood events. In this type of habitat the supply of groundwater enables species, typical of springs to become established and a specialist subterranean fauna with blind, unpigmented speices such as *Niphragus* sp. (Crustacea), is often found. Rheophilic species are absent from these pools. Primary production is also often limited by the low nutrient status of the groundwater and the shading effects of riparian vegetation. Allochthonous debris provides the organic input used by many insect larvae for food and case-building (*Leptocerus tineoides*). The majority of species are non-specialist feeders. In the river Rhône the mollusc, *Galba corvus* is found along channel margins and during periods of low flow they are able to survive beneath the deposited, moist debris. The absence of flow excludes the filtering collectors with the exception of the small pea-mussels (*Pisidium* sp. and

Sphaerium sp.), which take advantage of the slight water movements created by groundwater seepages.

As siltation progresses in these waterbodies, desiccation becomes an important process. Communities are species-poor with only a few resistant species able to survive the effects of desiccation. Some molluscs, e.g. *Bithynia* sp., *Valvata* sp., maintain internal humidity by closing the aperture of the shell with a waterproof operculum and survive in moist litter. Other species adopt elaborate mechanisms to ensure survival. In the limpet *Ferrissa* sp. (Ancylidae), only immature individuals survive drought periods by partially closing the shell aperture with a thin calcareous layer. This occurs just before the onset of drought when the substrate is still covered with a thin film of water: metabolic processes slow, the animal aestivates and is protected for long periods in the sediments. With the return of favourable conditions, it is this immature cohort that has survived, protecting the reproductive potential of the species (Richardot, 1978).

Many taxa are unable to colonize these temporary habitats (e.g. Ephemeroptera, Trichoptera) but some aquatic beetles (e.g. *Haliplus lineatocollis, Helochares* sp.) migrate to colonize more permanent waterbodies, nearby. Some species overcome drought using both physiological and behavioural strategies. Within life cycles, e.g. Odonata, development may be arrested and can occur at the egg, the larval and in some species, at the adult stage. This process of diapause helps the species to synchronize its development with seasonal fluctuations. On the Danube floodplain, Waringer (1989) records *Sympetrum* spp. as able to withstand periods of drought, by entering diapause at the egg stage. Other species of the Odonata (e.g. *Lestes* sp.) lay eggs on the emergent riparian vegetation. In autumn, when the water level rises, the nymphs hatch and fall into the pools where the life cycle continues. Other species adopt behavioural responses to avoid extreme conditions by seeking refuge within the hyporhoeic zone.

(b) Meanders

Isolated from the main channel, cut off meanders form large stagnant waterbodies surrounded by a marginal zone of macrophytes. Within large river systems such as those of the Danube and Rhine, they may have a surface area of several hectares and show many functional characteristics of lakes. The amount and nutrient status of the groundwater input, as a proportion of total volume, determines the trophic status of these habitats. A large discharge of groundwater may result in slight flows through the system and the occurrence of small outlets. The community structure is determined, principally by two interdependent factors: the area of open water and its trophic status. These deeper waterbodies are more autotrophic and show little response to any changes occurring in the main channel. On the floodplains of the Danube and Mississippi the wind-generated currents mobilize the fine sediments and increase turbidity. Light is limited, phytoplankton production is reduced and establishment of macrophytes is restricted. Invertebrate diversity is low but for those animals adapted to such conditions, densities are high. Botnariuc (1967), in studies of the Chironomidae, records larval densities of 500 individuals m^{-2}. Each larva constructs a fragile tube of silt particles and algal cells cemented together with a salivary secretion. The tube is open at both ends and undulations of the larva create a current of water which brings food particles and oxygen, towards the animal. These high densities of larval Diptera support a high fish production. Conditions also favour those species of the mollusca adapted to the fine, silty sediments. Filtering collectors such as *Anodonta* sp. are found together with *Valvata piscinalis, Lithoglyphus naticoides, Viviparus* sp. and *Fagotia* sp., all of which feed on small phytoplankton. These species have opercula, are gill breathers and are typical of large lowland rivers. Densities are high and reflect the high productivity of these habitats: 2.5 kg m^{-2} of molluscs have been recorded.

In smaller systems, e.g. the river Rhône, a wide macrophyte belt protects the free water surface from disturbance by winds. With clearer water there is high phytoplankton production and a diverse grazing assemblage of zooplankters, each with their predator. An intricate food web is established with a diversity of functional groups. Under eutrophic conditions, the oxygen gradient in the water column falls sharply, leading to anoxic conditions at depth. This limits the macroinvertebrate distribution to surface waters, to stems and leaves of floating vegetation, or to the riparian macrophyte belt. Assemblages of invertebrates associated with this vegetation can be quite characteristic. Within the Coleoptera (F. Chrysomelidae), species of *Donacia* are associated with specific food plants. On the floating leaves of open water plants *Donacia crassipes* is associated with *Nymphaea alba* (white waterlily) and *D. versicolora* with *Potamogeton natans* (broadleaved pondweed). Of the riparian macrophytes, *Donacia clavipes* feeds on *Phragmites communis, D. cinerea* on the leaves of *Typha latifolia, D. dentata* on *Sagittaria sagittifolia, D. sparganii* on *Sparganium emersum, D. marginata* on *Sparganium erectum* and *D. semicuprea* on *Glyceria maxima.*

Deep water, gently sloping banks, open water habitats, macrophyte stands, zones of both stagnant and slow flows and substrates of gravels and silts, are all found in the ancient meanders of the Rhine. With such specific insect–plant associations and diversity of microhabitat, a rich species assemblage is to be found in these ancient meanders. In one study site, 20 species of Hemiptera have been recorded (Voigt, 1978) together with 30 species of the F. Dytiscidae (Coleoptera); this high

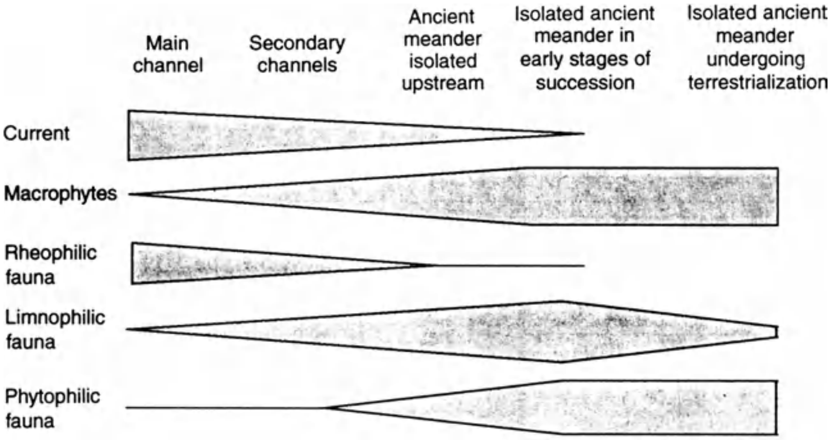

Figure 7.8 Responses of invertebrates to changes in the ecological variables (flow rate, vegetation) found in the different aquatic habitats on the floodplain; arranged according to the degree of connection with the main channel.

diversity coming from a total catch of 167 individuals. Water beetles of the F. Hydrophilidae are also abundant; Gladitsch (1978) recording 33 species from a sample of 169 individuals. In a study of the Rhine, the main channel yielded 11 species of mollusc, whereas 38 species were recorded in a former meander (Schmid, 1978).

7.3.4 SPATIAL VARIABILITY WITHIN THE FLOODPLAIN

The variety of aquatic habitats on the floodplain shows differing degrees of connectivity with the main channel and can be arranged on a gradient to reflect the level of isolation from main flows (Figure 7.8). From running water habitats, successional processes produce a sequence of habitats where water flow is slow but renewed, giving way finally, to those with standing water. With decreasing flow velocities, macrophytes can become established and reach maximum densities in the isolated braided channels and former meanders. As a response to this successional sequence, the structure of the macroinvertebrate community changes: rheophilic species give way to those of standing water (limnophilic) and phytophilic assemblages associated with plant communities, develop. In a sector of the Austrian Danube the assemblage of Mollusca describes and characterizes the degree of connectivity with the main flow; each successional habitat having a unique combination of species (Table 7.3). An analysis of the variety of habitats found on the floodplain suggests that, in a braided system, a zonation across the floodplain is somewhat analogous to the longitudinal zonal patterning of rivers as proposed by Illies and Botosaneanu (1963) and that of a continuum, as proposed by Vannote *et al.* (1980). A community describing the potamon is found in the lower depositional sectors of the longitudinal profile but is replaced by a community typical of shallow, more faster flowing rhithron; such communities are found on the floodplain in the secondary channels. Communities from those channels isolated upstream are somewhat analogous to those of the epirhithron and the small waterbodies supplied by upwellings of groundwater might be considered similar to those of springs and seepages (the crenon). Analogies can also be seen for the functional feeding groups. The abundance of allochthonous organic matter in isolated channels provides favourable conditions for shredders but gives way to communities dominated by filtering collectors as connectivity increases. In meandering sectors, the greater the degree of isolation, the greater is the degree of trophic autonomy showing many of the functional processes found in lakes. Stands of aquatic macrophytes enhance macroinvertebrate diversity. Filtering collectors (bivalve molluscs) are still found in these habitats but coexist with numerous scrapers, shredders, gathering collectors and grazers. In the more open habitats where allochthonous inputs are low, shredders (detritivores) exploit the autochthonous organic debris. Such high diversity is analogous to the epipotamon zone of the main channel.

A simple model has been developed above which in reality is often more complex due to differing geomorphologies, fluvial form, transition zones and local conditions. Macroinvertebrate assemblages have the potential through life-cycle strategies, to respond quickly to both structure and the changes taking place on the floodplain. Distributions will reflect local conditions but a fundamental spatial heterogeneity and temporal order exists within floodplain ecosystems, which can be described and compared using the communities present.

7.4 SPATIAL VARIATION WITHIN EACH FUNCTIONAL UNIT: *MICROSCALE*

7.4.1 MICROHABITATS WITHIN THE MAIN CHANNEL

Despite the apparent unifying role of the current, variable conditions exist within the river bed which create a mosaic of microhabitats for the macroinvertebrates. When observed at this scale, patterns of distribution appear to be continually changing thus highlighting the dynamic nature of the habitat. The mosaic of patches is linked to characteristics of the catchment but reflects the specific hydraulic conditions, geomorphology and particle size distribution of the substrate at any one point in time. At a scale of kilometres, patterns of riffles and pools are observed. These contrasting habitats; riffles with faster, more turbulent flows, and deeper pools in which fine sediments accumulate, shelter different communities.

Table 7.3 Zonation of aquatic molluscs in former channels on the floodplain of the Danube, arranged according to degree of connectivity with the main flow (after Foeckler, 1990); the length of line is proportional to population density

	Secondary channels	Channels recently isolated	Older isolated channels	Temporary waterbodies
Radix ovata	——			
Pisidium supinum	—			
Lithoglyphus naticoïdes	—			
Dreissena polymorpha	——			
Sphaerium rivicola	—			
Unio pictorum	———	—		
Anodonta anatina	———	——		
Valvata piscinalis	——	———	—	—
Radix auricularia–	——	————	——	
Gyraulus albus		————	——	—
Sphaerium corneum	——		—	
Planorbis carinatus		—	———	
Bathyomphalus contortus			——	
Physa fontinalis			——	
Viviparus contectus			—	
Hippeutis complanatus			——	
Valvata cristata			———	—
Sphaerium lacustre			——	—
Valvata macrostoma			—	———
Anisus spirorbis				——
Aplexa hypnorum				————
Pisidium casertanum				——

In the rivers Wye and Elan (Mid-Wales), the Trichoptera (*Rhyacophila dorsalis, Hydropsyche siltali*), the Plecoptera (*Protonemura meyeri*) and the Ephemeroptera (*Baetis muticus*) are found only in riffles, whereas the Dytiscidae (Coleoptera), the Plecoptera (*Nemoura* sp., *Amphinemura sulcicollis*) and the Trichoptera (*Polycentropus flavomaculatus*), are present only in pools (Scullion *et al.*, 1982). Specific distributions often occur within these habitats, and many species take up positions in areas where there is a stable substrate or where thresholds exist, e.g. at the head of the riffle. Certain species may move from patch to patch as their life cycle progresses, for example the larvae of *Hydropsyche* sp., migrate from riffle to pool just before metamorphosis (Boon, 1979). This temporal phenomenon highlights the need for a precise knowledge of the ecological requirements of each species. Instars may coexist on the river bed by being at different stages of development and as such have different requirements of flow and food resource. In the North Tyne (UK), *Hydropsyche siltali* and *H. pellucidula* coexist. Each species has its own pattern of development and during the winter months the third instar of *H. siltali* coexists with the more advanced fifth instar of *H. pellucidula*. Patterns are continually changing as adjustments to numbers and to species diversity, are made between neighbouring communities.

Along the banks and margins, the water level and shape of the channel section create a variety of habitats. Unlike the mainstream flows, the currents along each bank may show complex configurations with reverse flows and deadwater zones. In a study of the cross-sectional profile of the Rhône (width 80 m) macroinvertebrates were distributed in three zones. Two zones (10 m wide) with high species richness and diversity occur on each bank separated by a central zone which has a restricted fauna (Figure 7.9). There is also an asymmetry in the distribution of species along the two banks which differ in the nature and size of the substrate: *Polycelis* sp. and *Dreissena polymorpha* were dominant species of the right bank, with *Sphaerium* sp. and leeches, found on the left. The paucity of the fauna from the centre of the channel is illustrated from a study of the Rhône at Lyon. Here, densities of 3500 ind m^{-2} belonging to 46 species, are estimated from the central part of the channel (depth, 2–5 m) whereas 38 000 ind m^{-2} representing 91 species, have been collected from the banks (Berly, 1989; Cogerino, 1989). The differences between the central channel and the banks, a feature only found in the cross-sectional profiles of large rivers, illustrates the link between faunal densities, species richness and microhabitat. In the channel, pebbles, gravels and sands dominate the particle type but along the banks a more diverse habitat has developed due to falling coarse woody debris, to roots, macrophytes and bryophytes, all of which trap sands, silts and mud.

The development of microhabitat available to the fauna, is itself linked with the structure of the bank, to direction of flow, to the pattern of riffles and pools and to the riverine vegetation which acts as a food source. Bank structure and the consequent nature and variety of microhabitats, differ according to the degree of erosion and deposition within the channel. In the Austrian Danube (width 330 m), populations of Oligochaeta, Crustacea, Diptera and Trichoptera are abundant in habitats on the erosional side of the channel, whereas only Oligochaeta and Diptera are found in depositional habitats, on the opposite bank. These asymmetric patterns in distribution are most obvious in large meander bends with strongly eroded concave banks and opposing convex banks made up of deposited sediments. Finally, at the interface between flow and the substrate, the macroinvertebrates are those able to withstand the forces of lift, drag, shear–stress etc., as well as being suitably adapted for collecting food. A careful analysis of microcurrents shows that many species take up positions on the river bed so as to optimize the source of food (Figure 7.10). Blackfly larvae (Simuliidae) locate and angle their

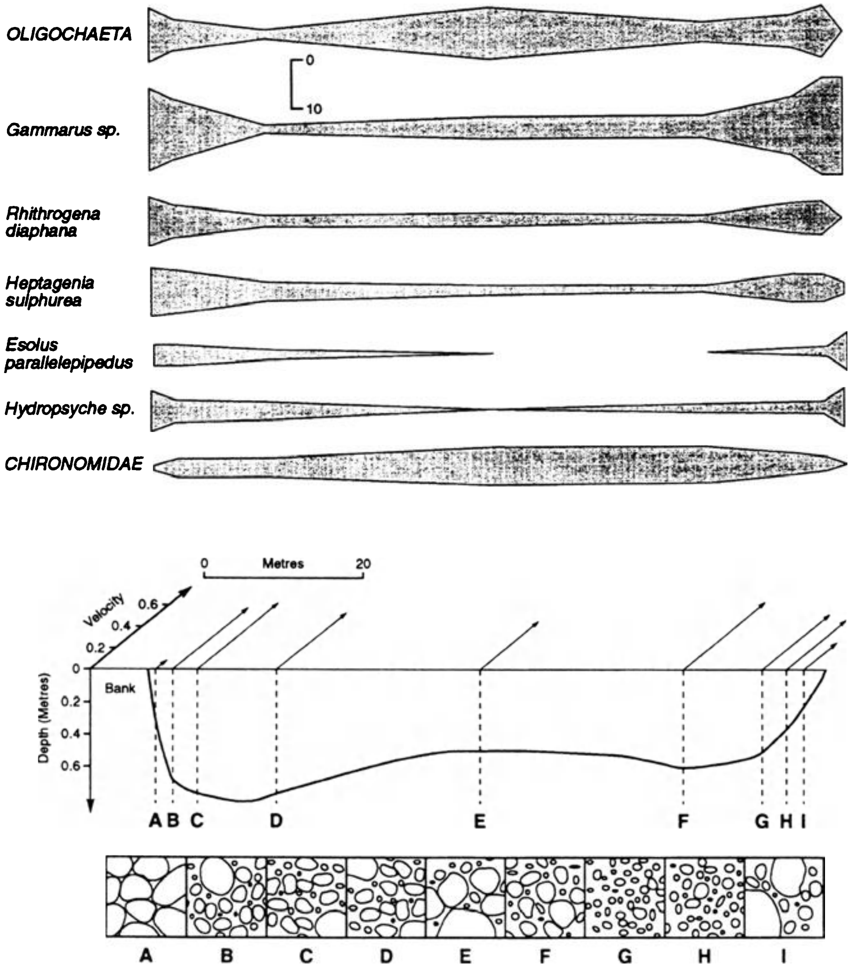

Figure 7.9 Distribution of benthic invertebrate taxa and substrate heterogeneity in a cross-section of the Rhône, upstream of Lyon. A-I are sampling stations where velocity (arrows), depth (m) and substrate heterogeneity have been measured (after Gaschignard *et al.*, 1983).

body in such a way that the cephalic fans are held in flows carrying food particles of an appropriate size.

7.4.2 MICROHABITATS WITHIN BRAIDED CHANNELS CUT-OFF UPSTREAM

With the direct connection to the main channel severed upstream, these narrow, shallow habitats become vulnerable to drying out. A longitudinal

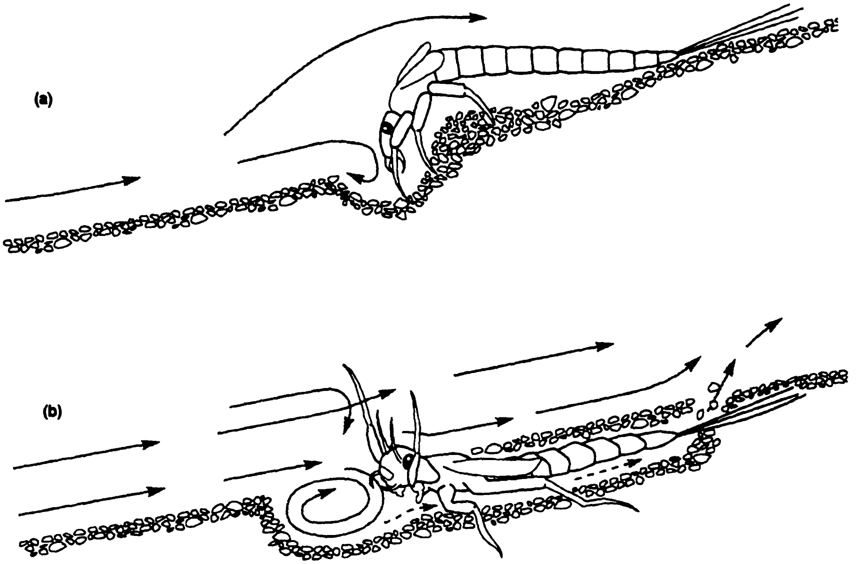

Figure 7.10 Ephemeropteran nymphs, (a), *Pseudiron centralis*, (B), *Ametropus neavei*, using microcurrents to obtain food. (after Soluk and Craig, 1988).

set of conditions can be identified with terrestrial habitats at the upper end, gradually giving way to those still strongly influenced by the main channel. At the upstream end, the channel becomes narrow and is colonized by riparian forest: this provides large amounts of organic debris to the system. Further downstream groundwater inputs increase, the channel widens and conditions resemble those of a small river with open water and aquatic macrophytes at the riparian edge. At the junction with the main channel, depth increases and reverse flows transport fine sediments into the cut-off channel. The transparency of the water column is reduced which affects phytoplankton production. The communities from such an ecosystem on the Rhône show this effect with a changing pattern of distribution from upstream to downstream. Species with precise ecological niches are replaced by others and the more ubiquitous species show a gradient in their abundance (Table 7.4). Upstream, species typical of springs coexist with standing-water species, whereas downstream, species typical of running water habitats are found, e.g. *Haliplus fluviatilis, Hydraena riparia.* Two species of Crustacea also indicate a zonation within these habitats. Numbers of *Asellus aquaticus,* a species typical of organically rich standing water decline downstream and are replaced by increasing densities of *Gammarus fossorum,* a species of running water.

Table 7.4 Changes in population structure of a braided channel isolated upstream, in the floodplain of the French Rhône (after Castella, 1987)

		Upstream sector	Mid-sector	Downstream sector
M	*Hippeutis complanatus*	——		
E	*Caenis robusta*	——		
M	*Sphaerium corneum*	——		
CO	*Agabus bipustulatus*	——		
CO	*Haliplus obliquus*	- - -		
CO	*Hyphydrus ovatus*	- - -		
CO	*Hydrophilus pusillus*	- - -		
M	*Acroloxus lacustris*	——	——	
M	*Bithynia tentaculata*	——	——	
M	*Valvata cristata*	——	——	
M	*Planorbis carinatus*	——	——	
M	*Anisus vortex*	——	——	
E	*Cloëon dipterum*	——	- - -	
M	*Pisidium*	——	- - -	
CO	*Stictotarsus duodecimpustulatus*	——	- - -	
C	*Asellus aquaticus*			
C	*Gammarus* sp.			
CO	*Ilybius fenestratus*	- - -		
CO	*Riolus subviolaceus*		——	
CO	*Hydroporus palustris*		——	
T	*Limnephilus gr. lunatus*		- - -	
T	*Limnephilus decipiens*		- - -	
T	*Limnephilus flavicornis*		- - -	
T	*Limnephilus flavospinosus*		- - -	
T	*Anabolia nervosa*		——	——
M	*Lymnaea stagnalis*		- - -	- - -
M	*Gyraulus albus*			——
M	*Lymnaea truncatula*			——
E	*Caenis macrura*			——
CO	*Hydraena riparia*			- - -
CO	*Haliplus flavicollis*			- - -
CO	*Haliplus immaculatus*			- - -

—— Species abundant - - - Species less abundant

Densities of *Asellus aquaticus* and *Gammarus* sp. are represented diagrammatically M, Mollusca, E, Ephemeroptera, CO, Coleoptera, T, Trichoptera, C, Crustacea.

In these old channels a number of boundaries meet, expressing the idea of an ecotone at the interface between habitats. Terrestrialization upstream gives way to aquatic conditions; groundwater gives way to surface-water dominance and at a different scale, the backwater interfaces with the main channel. Certain species are found which characterize these transition zones (Figure 7.2). *Galba corvus* (Mollusca), is an indicator species which dominates assemblages in zones where the processes of terrestrialization are most active. Upstream, where the groundwater emerges, spring-like conditions are found with white, blind species of Crustacea, more commonly found in the interstitial subsurface habitats. These species form part of a diverse hyporhoeic fauna which, as water levels fluctuate, appear periodically at the surface. Such species survive where groundwater emerges and often coexist with the riffle beetle (*Esolus parallelepipedus*). The adult stage of this species is characteristic of flowing water but the nymphal stages live hidden in the highly porous sediments. Finally, near the confluence, the effects from the main channel mix with those of the former channel. Species are found which exploit both sets of condition. The rheophilic nymphs of the whirligig beetle (*Orectochilus villosus*) settle in the banks of the main channel, whereas the adults are commonly found as surface dwellers of still-water. The heterogeneity of these habitats is not fixed. At times of high flows the bed can be scoured creating a harsh, more homogeneous habitat only colonized by especially adapted species.

7.4.3 MICROHABITATS WITHIN MEANDERS CUT OFF UPSTREAM

The reduction or lack of flow occurring as the meander is cut off enhances, as in the previous case, a longitudinal zonation of macroinvertebrate assemblages. Transversally, any suspected asymmetry in the species distributions from the steep concave bank to the opposing, more gently sloping convex bank, is less obvious. However, in these former meanders the results of upstream isolation differ from those of braided channels, as a function of the difference in the size of each system. At the upstream end of the meander the terrestrialization processes are more progressive and there is, to a greater or lesser extent, a marginal swamp to the open water edge. The standing water, fringed with macrophytes, is connected to the main flow by a channel, the width of which governs the degree of influence of the main flow. Water movements occur between the meander and the main channel: of particular importance is the water flowing from the main channel as this is a source of fine sediment.

Longitudinal heterogeneity is reduced in this type of habitat when compared with those of former braided channels. In an ancient meander of the Danube the large filter-feeding Mollusca are found throughout and coexist with the zebra mussel in its more limited habitat, downstream (Foeckler, 1990). However, species of pulmonate (air-breathing) Mollusca are only found in the shallow conditions upstream, whereas operculate species and those using respiratory gills (*Bithynia tentaculata*), are more prevalent downstream.

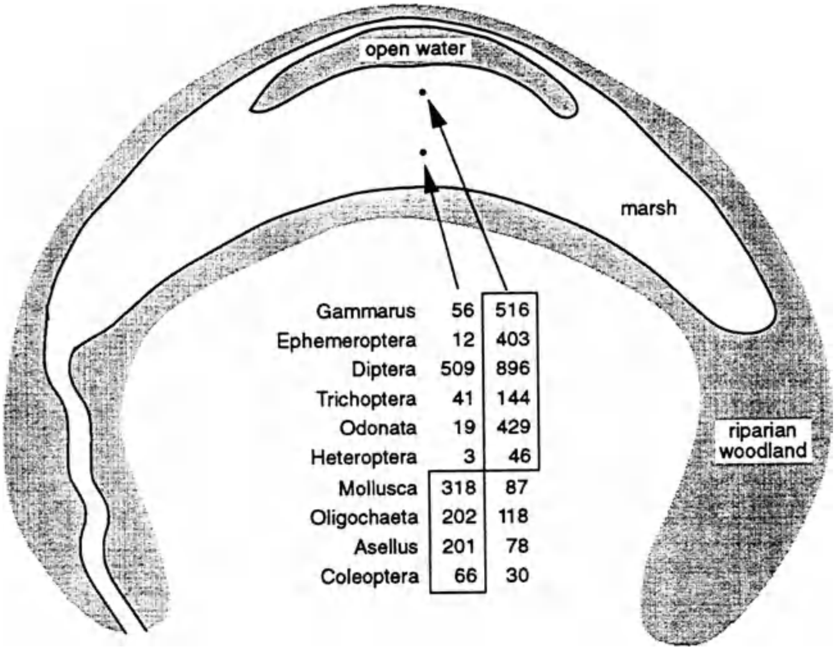

Figure 7.11 Zonation along a transect across an ancient meander of the French Rhône. Number of individuals for major groups is given at two points on a transect aligned with the most convex section of the bank (after Richardot-Coulet *et al.*, 1986).

7.4.4 MICROHABITATS WITHIN ISOLATED CUT OFF MEANDERS

Once totally isolated from the main flow the processes of terrestrialization take place throughout the meander, longitudinal heterogeneity diminishes and an extensive swamp develops. Open water remains in the deepest point of the channel, i.e. on the concave bank, and macrophyte stands (of reeds) colonize the water's edge, spreading extensively on the gently sloping convex bank. With a more radial geometry, a distribution of species can be identified in zones along a transect from the open water to fully terrestrialized habitats. The high densities and species richness of aquatic insects found in the open water, give way to an assemblage of shallow water Mollusca, Oligochaeta and species of Coleoptera, typical of temporary habitats. When situated at the lateral edge of the floodplain, groundwater flushes and springs may produce flows within the meander. Such local conditions are illustrated by the opposing density gradients of *Asellus* sp. (limnophilic Crustacean) and *Gammarus* sp. (rheophilic Crustacean), found in these habitats (Figure 7.11). Also present in these groundwater habitats are populations of small bivalve molluscs (*Pisidium* sp.) which migrate vertically within the substrate and form part of a rich hyporhoeic fauna. Species which migrate to and from the surface, such as *Pisidium* sp. (Mollusca) and *Siettitia* sp. (Coleoptera) use the interstitial microhabitat as shelter for larvae and young stages but a rich, more permanent groundwater fauna (*Niphargus* sp., Crustacea), also exists. Sixty litres of groundwater pumped from an ancient meander on the Rhône floodplain, at a depth of 50 cm, yielded 3500 individuals of 60 different species (Reygrobellet and Dole, 1982).

7.5 TEMPORAL DYNAMICS

The evolution and successional development of the floodplain is a dynamic process taking place over a range of time-scales (Chapter 10). For a seasonal focus, a time-scale of one year will be considered. The flow regime of the river, the seasonal nature of flooding, of low flows and of discharge, play a significant role in the structure of macroinvertebrate communities, in both the main channel and within floodplain habitats. With an increase in discharge, seepage is amplified and provides a groundwater flow. A time lag will exist between changes in flow regime of the main channel and the effects of upwelling on the floodplain habitats. The seasonal patterns of flow, characteristic of the catchment offer a temporal picture to which the life cycles of many species have evolved. The mayfly, *Leptophlebia cupida* is univoltine (laying one batch of eggs year^{-1}). Eggs are laid in early summer in the main channel when flows are low and the water is warm. Nymphs hatch, grow through a number of instars and eventually colonize riffle habitats in the autumn. In the cold winter months, the nymphs migrate to deeper pools. In the spring, the rise in water level flushes the nymphs from the pools; they move to the sheltered edge and migrate upstream. On reaching side-arms, still connected to the main channel, the migratory movements take the nymphs into the wetland habitats which offers protection and from which the life cycle is completed (Figure 7.12). The sequence and periodicity of inundation is a principal determinant of the floodplain mosaic, together with the geomorphological origins of these ecosystems; for example, ancient braided channels are more sensitive to these effects than are the ancient meanders.

7.5.1 TEMPORAL CHANGES IN THE MAIN CHANNEL

Detailed studies of the Rhône, have shown that variations in the number of macroinvertebrates throughout the year, follow patterns of discharge (Bournaud *et al.*, 1987). Certain species withstand strong currents by adhering to stones (*Ancylus* sp., *Dreissena polymorpha*) with rheophilic species remaining within the substrate (*Rhyacophila* sp., *Baetis fuscatus*).

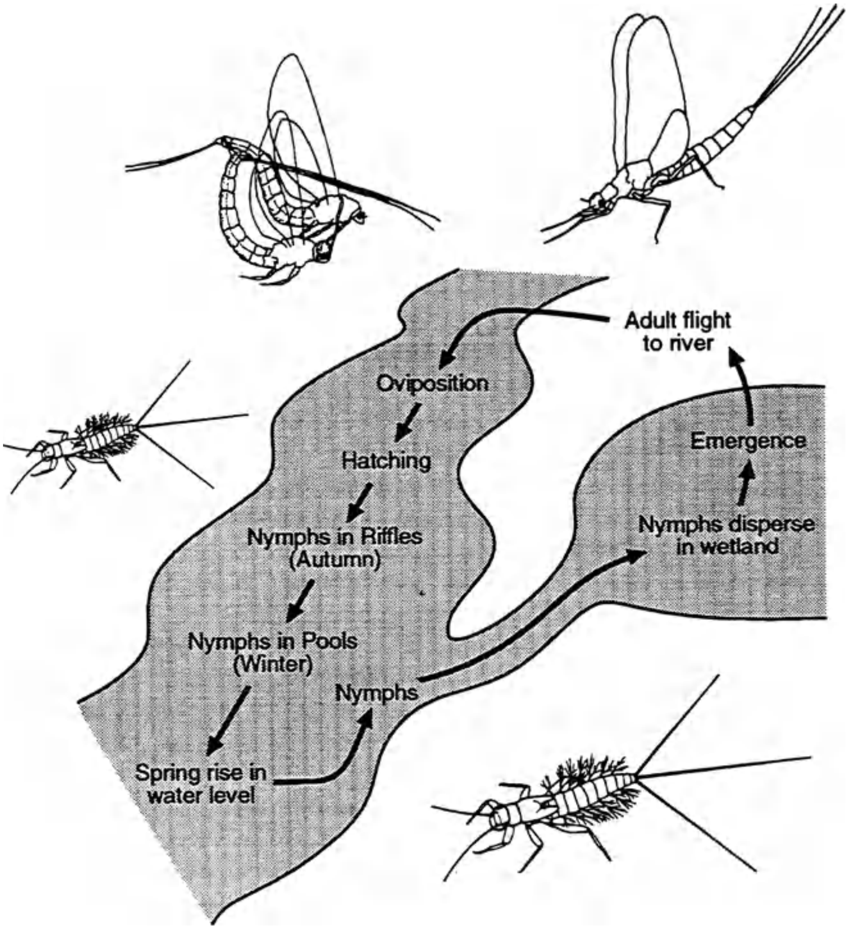

Figure 7.12 Riverine-wetland migration of *Leptophlebia cupida* (Ephemeroptera) over an annual cycle (after Ward, 1989b).

The insects using filter-capture methods (*Hydropsyche* sp.) benefit from a supplemented food supply and other more vulnerable species, have evolved a life-cycle strategy whereby they avoid periods of maximum discharge and the dangers of being swept away (*Leptophlebia cupida, Ephemerella ignita*). Many macroinvertebrates are sensitive and respond quickly to environmental change: many are able to recolonize habitats following drought and low-flow conditions. Some species of Chironomidae (Diptera), are opportunistic and with a fast growth rate, establish populations between two successive disturbances (Wevers and Warren, 1986). Such an adaptive strategy is shown by the bivalve mussels (*Unio* sp., an r-strategist) which can withstand such fluctuations in the main channel. The breeding period occurs between April and mid-August during which time each individual will release larvae at intervals to ensure some survival. Other species (*Anodonta* sp.), more adapted to the buffered effects found in more isolated channels, have a long reproductive season from late summer until the spring, during which time each individual has one larval release. At times of spate and drought many species of Plecoptera (*Leuctra major*) burrow and seek refuge in the interstitial spaces of the substrate. At low flows the macroinvertebrates move from bankside habitats into the pools remaining in the channel bed. The shallow, warmer water and more stable substrate allows for the development of a rich periphyton which is exploited by grazers. The warm, summer temperatures may also increase growth rates and stimulate early reproductive activity (*Erpobdella octoculata*, Hirundinea). Following such conditions, the autumn rainfall and high discharge have a severe effect on the drift. Cellot and Bournaud (1986) collected drift samples from the River Rhône, under low flow conditions in September, then in October when there was a sudden increase in discharge. The two collections were very different, with the October sample having a high biomass and invaded by wetland species (limnophilous Coleoptera and Trichoptera), washed in from the adjacent floodplain. Although able to recolonize quickly, losses of taxa and instars are closely linked with both the individual life cycles and the seasonal variations in discharge.

7.5.2 TEMPORAL CHANGES CUT OFF MEANDERS

The ancient meanders, still with narrow connections both upstream and downstream are less exposed but are still vulnerable to, fluctuations in water level in the main channel. In certain cases the meanders are isolated from the main channel except during periods of flooding. The community structure in these water bodies is strongly dependent on the length of time it is disconnected from the main flows. In a meander of the Danube, as the period between two flood events increases, the zooplankton community develops and populations of Oligochaeta and Chironomidae, reach high densities (Table 7.5).

Braided channels isolated from the main channel at their upstream end are particularly vulnerable to flooding as they are close to the main

Table 7.5 Abundance of zooplankton and zoobenthos in a cut off meander of the Danube as a function of the time interval (in weeks) between flood events (after Bothar, 1972)

Average number of weeks between floods	23	6	13+3+2
Zooplankton abundance (no. m^{-2})	1558	23	579
Zoobenthos abundance (no. m^{-2})	11549	5622	4063

channel and flow in a similar direction. These periodic inundations deposit fine sediments which are rapidly colonized by macroinvertebrates. The receding floodwaters, however, accelerated by a downstream connection to the main channel, can impoverish these habitats by sweeping away many limnophilic species. As noted previously (section 7.3.2(a)), when totally isolated from the main flow, the fauna of these braided channels is controlled by the frequency and periodicity of flooding. In contrast, periodic flooding has a lesser effect on the communities found in the ancient meanders. The effects of any flood event are buffered by the size, volume and marginal position on the floodplain. Such an event may temporarily enhance the community by the provision of nutrients and greater primary production. In a former meander of the Rhône following the renewal of water by flooding, there was an initial decrease in plankton, followed later, by algal blooms (Carrel and Juget, 1987). The seasonal variations shown in community structure in habitats of this type, are influenced by the phenology of the aquatic plants which offer shelter, food (periphyton), sites for egg laying and as a nursery for the development of many species.

7.6 CONCLUSION

In its natural or seminatural state, the floodplain may be viewed as a mosaic of habitats undergoing succession. Controlling factors, such as catchment runoff, flooding, the role of groundwater and rates of eutrophication, are all interlinked in influencing each ecosystem. Macroinvertebrates respond to this spatial and temporal variability by changes in the structure of their communities. Adaptive strategies may be morphological, behavioural or concerned with life history; all used to exploit the available space and trophic resource.

If the various types of aquatic ecosystem associated with braided channels are arranged according to the degree of isolation from the main flow, it is possible to illustrate how the flows and impact of flooding affect each system (Figure 7.13a). From each macroinvertebrate assemblage, the food availability can be deduced, based upon the trophic grouping to which each species belongs, the early suggestion of Illies and Botosaneanu (1963) that a longitudinal zonation of rivers is reflected in the patterns of macroinvertebrate distribution, together with a continuum of trophic

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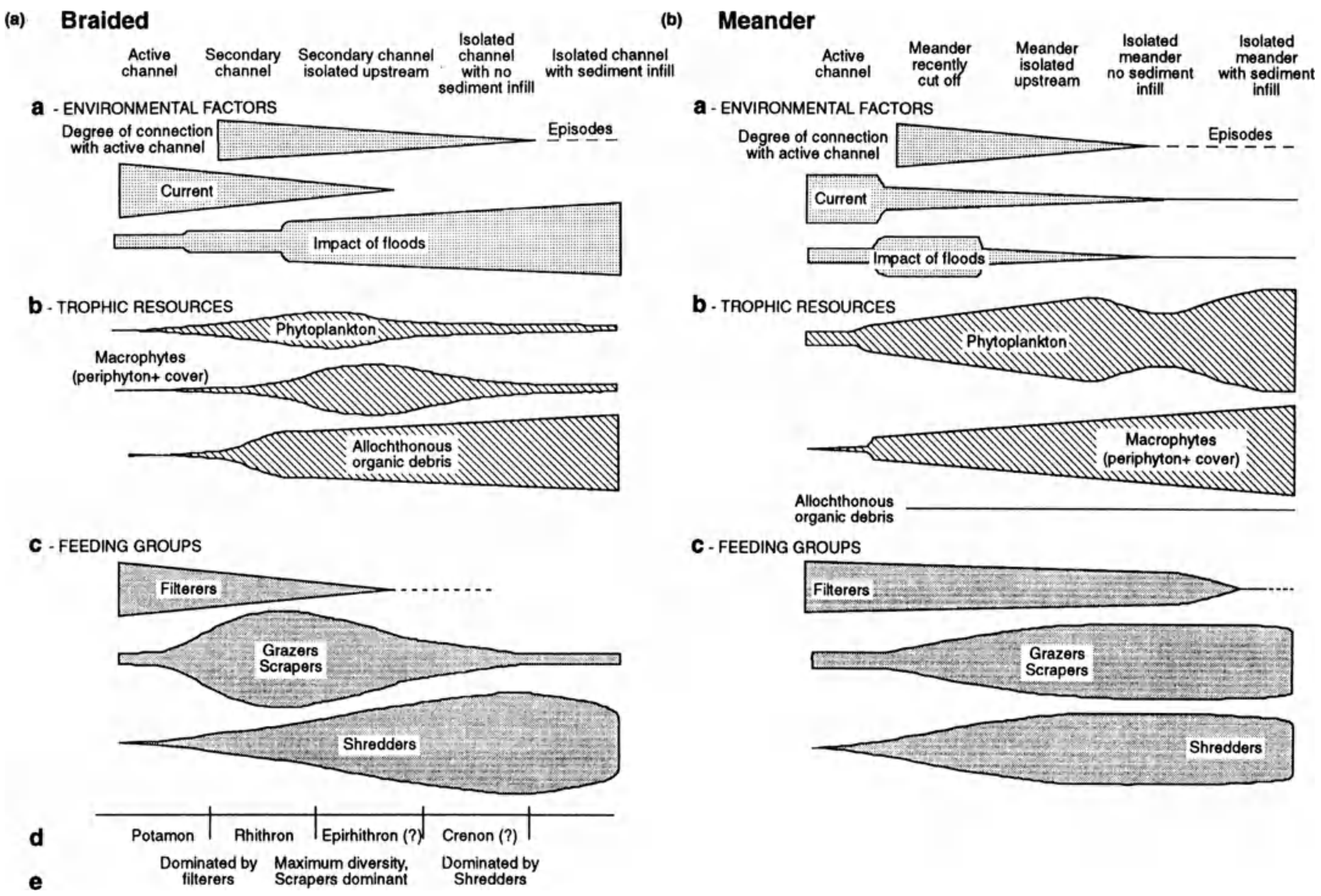
Figure 7.13 (see facing page) Variation of the main ecological parameters (a), trophic resources (b), responses of the different trophic groups (c), fitted to the model of zonation as proposed by Illies and Botosaneanu (1963) (d), and the River Continuum concept of Vannote *et al.* (1980) (e), in the different habitats of the braided (a) and meandering (b) sectors.


(a) Braided
Active channel
Secondary channel
Secondary channel isolated upstream
Isolated channel with no sediment infill
Isolated channel with sediment infill
a - ENVIRONMENTAL FACTORS
Degree of connection with active channel
Episodes
Current
Impact of floods
b - TROPHIC RESOURCES
Phytoplankton
Macrophytes (periphyton+ cover)
Allochthonous organic debris
c - FEEDING GROUPS
Filterers
Grazers Scrapers
Shredders
d
Potamon
Rhithron
Epirhithron (?)
Crenon (?)
e
Dominated by filterers
Maximum diversity, Scrapers dominant
Dominated by Shredders
(b) Meander
Active channel
Meander recently cut off
Meander isolated upstream
Isolated meander no sediment infill
Isolated meander with sediment infill
a - ENVIRONMENTAL FACTORS
Degree of connection with active channel
Episodes
Current
Impact of floods
b - TROPHIC RESOURCES
Phytoplankton
Macrophytes (periphyton+ cover)
Allochthonous organic debris
c - FEEDING GROUPS
Filterers
Grazers Scrapers
Shredders

resource, proposed by Vannote *et al.* (1980). In a meandering system (Figure 7.13b), the aquatic ecosystems of the floodplain correspond to reaches of the main channel which have been isolated from active flows. Here the controlling parameters differ from those found in the braided system. Along the successional gradient under these conditions, trophic resources and the distribution of trophic groups differ: the main channel contrasts with the younger cutoff meander which represents the first stage in the process of terrestrialization.

Fish populations in rivers

8

A. L. Roux and G. H. Copp

8.1 INTRODUCTION

Of all aquatic organisms, fish are among those that possess the greatest mobility, thus offering the possibility of rapid occupation and exploitation of the various biotopes in the fluvial mosaic. For those fishes that migrate in order to reproduce, the longitudinal course of the river represents the principal means of access to spawning grounds. Long-distance migrants may ascend the entire length of the river to reach its headwaters; whereas non-migratory species, such as some cyprinids, use the longitudinal course of the river merely as part of the fluvial network to move between various transversal parts of the hydrosystems (e.g. side channels, ox-bows) for different periods in their ontogeny.

The vertical dimension of river channels is also an important spatial aspect in the repartition of fish. The depth at which riverine fish are observed is generally a reflection of their level of development, the time of day and/or the season of the year. Generally speaking, fish tend to occupy progressively deeper layers of the water column as they increase in size and age. Although some mixing occurs, there tends to be notable segregation within the water column. The establishment and recruitment success of fish populations in large rivers are thus influenced by the diversity of channel types present in the hydrosystem and accessibility of these biotopes to the fish.

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8.2 THE LONGITUDINAL ZONATION OF WATERCOURSES

As demonstrated in Chapters 1, 2 and 4, river courses have classically been perceived and presented as linear systems with a pronounced longitudinal gradient in terms of environmental conditions as well as the corresponding invertebrate and fish assemblages. This linear perspective has naturally led to the development of zonation paradigms to describe the longitudinal distribution of flora and fauna within river systems. The longitudinal zonation of streams and rivers dates back to the middle of the last century (Nowicki, 1868), with certain species of fish being identified as characteristic for each zone (Table 8.1). Subsequent investigations in both Europe and North America (e.g. Carpenter, 1928; Huet, 1949; Sheldon, 1968) endeavoured to elucidate these zones, thus substantiating the notion that certain species are characteristic of each successive zone. Hence, the longitudinal distribution of fish was defined through the correlation between the composition of fish assemblages and physical factors such as river slope and depth (Huet, 1949), stream order (Sheldon, 1968) or chemical and biological variables (Holcik and Hensel, 1972). Historically, the designation of fish zones was preceded by that for invertebrates, which eventually led to the well-known and often-used zonation developed by Illies and Botosaneau (1963). More recently, Vannote *et al.* (1980) proposed a summary paradigm of previous invertebrate-based zonations known as the River Continuum Concept (Chapter 7), which emphasized the progressive changes undergone by a river from its source to the sea with respect to its physical/chemical character, its trophy and thus its invertebrate assemblages. However, despite its limitations, the longitudinal zonation proposed by Huet (1959) is the most often used paradigm in western Europe (Figure 8.1).

Table 8.1 Examples of river zonation schemes and their proposed integration (adapted from Holcik *et al.*, 1989)

Source	Zones							
Thienmann (1925)[a]	Spring	Spring brook	Trout		Grayling	Barbel	Bream	Brackish
llies (1962) Illies and Botosaneanu (1963)	Crenon		Rhithron		Potamon			
	Eucrenon	Hypo-crenon	Epi-	Meta-	Hypo-	Epi-	Meta-	Hypo-
Cummins (1972)	Erosional zone				Intermediate zone		Depositional zone	
Schumm (1977)	Production zone				Transfer zone		Storage zone	

[a] Based largely on work by fish scientists in the late 19th century (see Holcik *et al.*, 1989).

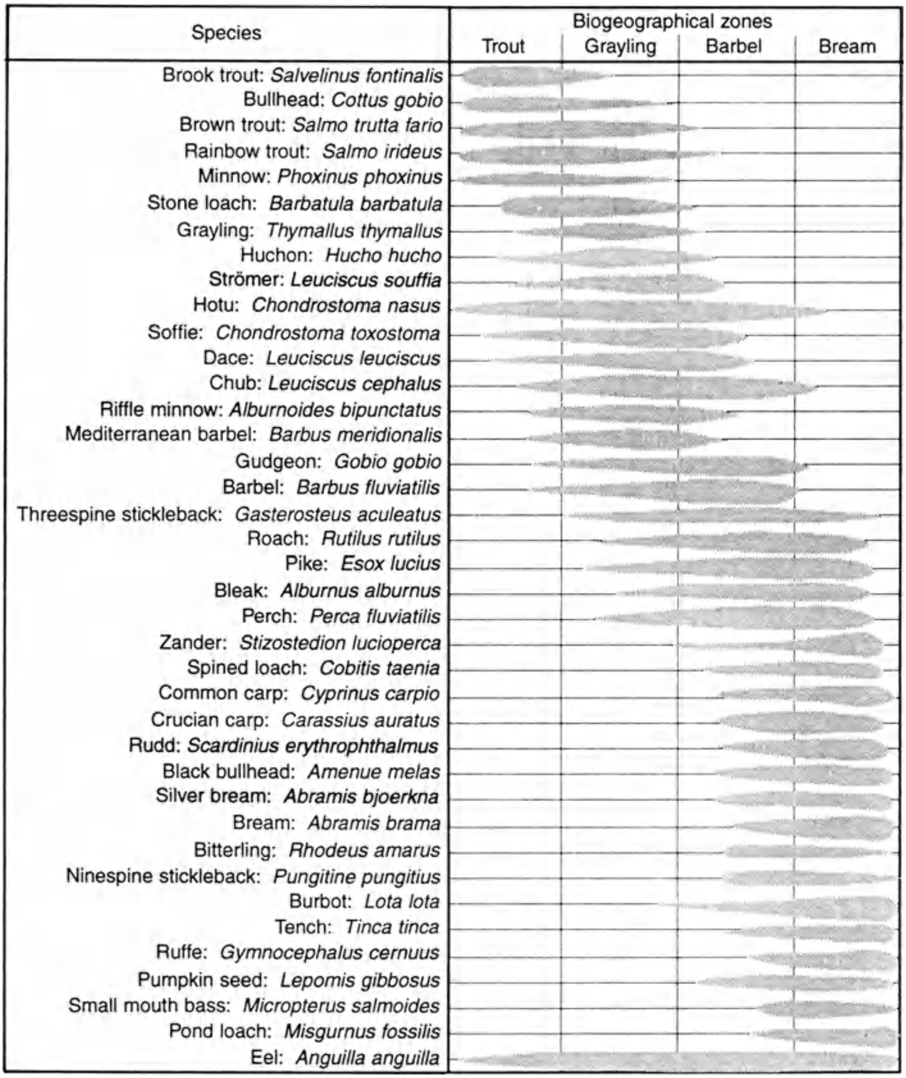

Figure 8.1 Longitudinal zonation of riverine fish populations in western Europe (after Huet, 1959; Arrignon, 1976).

Regardless of the fish zonation considered, a number of general characteristics are apparent. From source to sea, one notices not only the progressive succession of populations characteristic of the various zones, but also a gradual increase in the number of fish species. However, the increase in species richness is due more to the addition of species than to their replacement (Figure 8.1). For example, in the River Danube 59 species are found between its source and Vienna (Austria), whereas, 72 species are known to occur between Vienna and the Iron Gates (Romania) and 73 species between the Iron Gates and the Danube delta (Bacalbasa-Dobrovici, 1989). There are nonetheless exceptions to this general rule, depending on particular local conditions whether they be natural or the result of human activities.

On the River Mississippi, Fremling *et al.* (1989) reported a progressive increase from source to delta (from 49 to 114 species) with irregularities in the middle course. The non-linear relation between river length and species richness was attributed to natural biogeographical factors (north-south changes in fauna) associated with its tributaries (Rivers Missouri and Illinois), but also to the impact of dams, channelization, industrialization and pollution. In any case, there generally exists a direct correlation between species richness and stream order, as revealed by Horwitz's (1978) comparison of 15 river courses in the USA. Similarly, Morin and Naiman (1990) found a positive correlation (0.92) in Québec between the number of fish species and stream orders between 2 and 9. In Europe, similar correlations have been reported, such as that by Blachuta and Witkowski (1990) in Poland. A positive correlation has also been found between species richness and drainage basin size.

The increase in numbers of species as a function of the size of watercourse, its stream order and the size of drainage basin, corresponds to the increase in habitat diversity, particularly with respect to flood plains (Chapter 5). This diversity of biotopes and microenvironments is due most notably to the different types of contacts existing between the water and the land, not only with respect to the main channel but also with respect to the flood plain as an entity. The frequency and intensity of connections between the various floodplain biotopes is also of importance, both the connectivity variations in time and space.

8.3 USE OF FLOODPLAIN BIOTOPES BY FISH

8.3.1 CHANNEL BANKS: THE LAND–WATER INTERFACE

On the large scale, the environmental diversity of a river catchment, or subsector thereof, can be appreciated using a simple index based on the ratio between the total length of bank and the linear length of the river course. This ratio integrates the potential diversity of environments with respect to the land–water interface and the development of floodplain annexes. For example, Pont and Persat (1990) found a highly significant positive correlation between this ratio and the mean abundance of fishes in the French River Rhône (Figure 8.2). Closer examination of this data set revealed that the mean abundance was markedly influenced by the

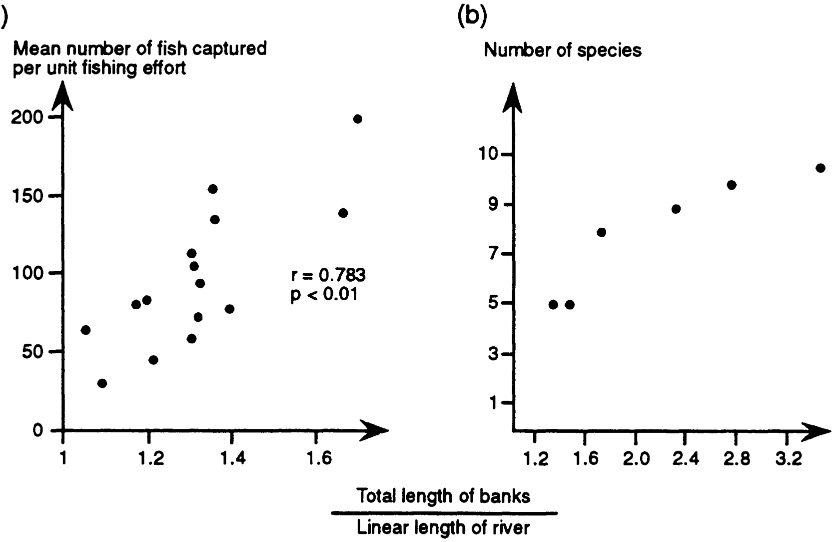

Figure 8.2 Fish abundance on the Rhône (a) and number of species on the Danube (b) as a function of river margin heterogeneity defined as bank length per unit length of channel (after Pont and Persat, 1990 and Schiemer *et al.*, 1991).

numbers of young-of-the-year fish (henceforth 0+ fish), emphasizing the importance of habitat diversity to fish reproduction.

Often underestimated is the importance of river channel banks, which in natural river systems can present a wide range of environmental conditions favourable as fish spawning and nursery areas. As on the Rhône, a good correlation has been observed on the Danube (Schiemer and Spindler, 1989) between 0+ fish species richness and the ratio of bank length-to-river length (Figure 8.3). A similar relationship has been described in tropical rivers by Gossé (1963), who reported a correlation between the 'bank coefficient' and fish production in the central basin of Zaire. In addition to spawning habitat, channel banks can also represent important areas of refuge for fish during floods or spates.

8.3.2 FLOODPLAIN ENVIRONMENTS

It is now well known that the biomass and the production of fish, and also invertebrates (Chapter 7), are greater in biotopes of flood plains than in the flowing channels of the river. Thus, Holcik *et al.* (1981) found a ten times greater fish biomass per hectare in secondary arms than in the main channel of the River Danube in Slovakia, downstream of Bratislava. The respective contributions of the main channel and its floodplain

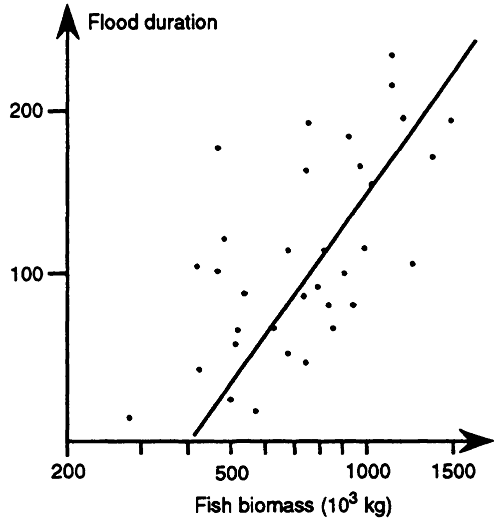

Figure 8.3 The 'flood-pulse advantage': fish biomass related to the duration of the annual flood on the River Danube (after Stankovic and Jankovic, 1971).

annexes to fish production in a hydrosystem become clearly evident when examining their relative importance with respect to length of bank and water surface area. For example, in the 231 ha, 5.2-km long 'Baka' stretch of the River Danube floodplain downstream of Bratislava, the secondary arms and abandoned channels represented 28.5 km of bank and 331 ha of water surface area, or 490% and 143% of that provided by the main channel, respectively.

Similarly, on the lower 2000 km of the River Mississippi, downstream of water retention structures, the surface area of floodplain annexes is 110% (186 000 ha) of that provided by the main channel (170 000 ha) during low water, but 2360% of that in the main channel during high water (4 372 000 ha/185 000 ha). According to Richardson (1921, cited in Guillory, 1979), fish production in the River Illinois drops from 199 kg ha^{-1}, when the annexes represent 90% of water surface area, to 146kg ha^{-1}, and then to 83 kg ha^{-1} when the surface area represented by annexes drops to 83% and 63%, respectively. A similar type of drop in productivity can be observed when comparing fish species richness and abundance before and after river regulation schemes, which generally constrict the flood plain and reduce the number of annexes. Such examples are unfortunately numerous both in Europe and North America (Pennington *et al.*, 1983; Stanford and Ward, 1986; Bacalbasa-Dobrovici, 1989; Fremling *et al.*, 1989; Schiemer and Spindler, 1989.

8.3.3 HYDROLOGY AND HYDRAULICS, FLOODS AND SPATES

Hydrology and hydraulics represent key factors in the ecology of large river systems (Statzner *et al.*, 1988). Life in rivers and near their floodplains are conditioned by the intensity and duration of drought and especially spates in the annual hydrological cycle; this is not only apparent in tropical rivers but also in the temperate regions, where their importance has been recognized only relatively recently. It is important to distinguish between exceptional spates, which in their intensity and frequency occur in a random manner following episodic climatic events, and the regular floods or periods of high water that result from seasonal fluctuations of the region of drainage basin. The role of floodplain annexes in these two types of situation is obviously different.

During strong spates, which represent true perturbations, a river's aquatic annexes constitute important refuges from which fish recolonize the main channel following the spate. Some refugee fish remain in the annexes to feed or perhaps to replace conspecifics eliminated from the annexes during an exceptionally strong spate. Floodplain annexes play a similar role as refuges in the case of pollution events, such as the toxic spill into the River Rhine downstream of Bail, Switzerland, during November 1986. Contrastingly, during periods of extreme drought the main channel of a large watercourse can function as a temporary refuge for fishes of the river's floodplain and smaller tributaries.

The importance of regular floods and spates to the biological cycles and productivity depends both on the frequency, intensity and especially the duration of the hydrological event. The precise moment of reproduction in many species of floodplain fishes corresponds to the rise in water levels, which allows them to enter the floodplain annexes where the spawning and nursery of progeny takes place. The abundance of fish larvae and juveniles is much greater in the annexes than in the main channel, being that the former channels are much more productive than the main channel, thus resembling the littoral zone of lakes. The abundance of 0+ fish rises correspondingly at the confluence of the main channel and its annexes, where some rheophilous fishes spawn just before or during the flood in order to ensure the maximum dispersion of their progeny throughout the floodplain (Bayley and Li, 1992; Vasquez and Wilbert, 1992). For example, Sheaffer and Nickum (1986) reported a 2.8 times greater abundance of fish larvae and 1.5 times higher number of 0+ juveniles at the confluence of the main channel and its annexes than along the banks of the channel just upstream of the confluence. This discrepancy can result both from the migration of fish larvae and juveniles from the annexes towards the main channel and from the drift of zooplankton from the annexes, which combined with the favourable semi-lotic conditions, attracts 0+ fishes from the main channel towards the confluence area for feeding.

Numerous investigations on the River Danube have corroborated the postulate originally put forward by Antipa (1928), that annual fish production is positively correlated with the intensity and duration of flooding. This differential rise in production is due to the demographic expansion brought on by the increase in spawning and nursery environment. For example, based on data over a 38-year period, Stankovic and Jankovic (1971) demonstrated that a production level of 500 tonnes from 20 days of inundation increases to 1500 tonnes when flooding lasts 200 days (Figure 8.3). Also, the increase in production manifests itself not only during the year of increased duration of flooding, but in the following years. This was demonstrated in the Slovak sector of the Danube by Holcik *et al.* (1981), who reported that each 1 cm rise in the mean annual water level resulted in a 500 kg increase in production for that year and a 300 kg increase in the following year.

Elsewhere, such as on the River Atchafalaya, fish biomass has been reported to be greater after a year of high water than after a year of low water (Fremling *et al.*, 1989). Indeed, the quantity of commercially exploited fish species is lower during years of low water than that of forage fishes, which are five times more abundant. According to Bryan and Sabins (1978), primary production increases and the influx of allochthonous matter is reduced during years of low water, thus favouring primary consumers such as forage fishes, which are exploited by predatory fishes in the following year.

Numerous authors have described a similar relationship between the intensity of flooding and fish production for tropical rivers, though the drought suffered in many African countries does result in reduced catches for fishermen. For example, Lae (1992) reported flood intensity and duration to be the factors determining the abundance of fish stocks in the central delta of the River Niger; the effects are immediate, as a weak flood results in a diminished yield of fish in the current year, whereas a return to normal flood levels permits fish populations to recover with little or no delay.

The examples given above illustrate well the ecological effects of spatial and temporal variability on the production of ecosystems, and fish production in particular. The notion of variability, and that of 'perturbation', contrast the dogma of ecosystem stability and equilibrium, which has long preoccupied ecology. As a consequence of the alternating phases of inundation and desiccation that result from hydrological fluctuations, the land–water interface in alluvial plains varies in height, length and surface, constituting a 'moving littoral' (Junk *et al.*, 1989). The more or less regular change between flood and desiccation permits a rapid recycling of organic matter and nutrients, leading to an overall greater productivity than found in either entirely terrestrial or entirely aquatic environments. The displacement of the moving littoral should, however, not occur with a frequency or speed too elevated to permit the recycling and utilization of the nutrients. Such conditions co-occur when a hydrosystem is subjected to regular inundations over time, where the frequency of inundation permits the floodplain populations to adapt themselves to the exploitation of the resources of the land–water interface.

Thus, variability at one scale of perception induces a certain 'stability', or predictable pertubation, at another scale. In the case of brutal and irregular spates, which are more frequently observed in headwater streams, the fish populations often present a lower level of adaptation, as the unpredictability of the short, sharp spates impedes development. In this way, the differences in hydrological and hydraulic regime induce functional differences between lower order streams (without flood plains) and higher order streams or rivers that possess inundation zones. Note that in tropical rivers, where changes in temperature are insufficient to induce the seasonal population cycles observed in temperate areas, the seasonality of tropical populations is induced by the hydrological cycle. In some rivers, seasonal changes in both temperature and hydrology combine to influence population cycles.

8.3.4 MIGRATIONS BETWEEN FUNCTIONAL UNITS OF THE HYDROSYSTEM

It is rare that a species of fluvial fish reproduces and feeds exclusively within the same habitat, and thus fish populations in rivers generally undertake either longitudinal or transversal migrations, and occasionally a combination of both, as part of their annual cycle. Thus, the ability to move freely between the various aquatic components, i.e. functional units, of a hydrosystem is required if fluvial fish populations are to survive and reproduce. Circulation is thus required not only up and down the longitudinal course of the river, but also transversally between the main channel and its various annexes.

In the River Parana, species of potamodromous fishes can migrate hundreds of kilometres up the river, and then return to the downstream main channel one or two years later (Bonetto *et al.*, 1989). The migration is induced at the beginning of a spate, with the greatest migration occurring during the peak discharge. The fish larvae and juveniles drift down to the aquatic annexes of the flood plain, where they undergo their larval and juvenile development; later, the adults move downstream progressively, though erratically, living in the main channel, its tributaries and floodplain annexes until the next annual spate (Figure 8.4). Migrations of similar amplitude and importance have also been reported for fluvial systems elsewhere, such as the River Murray in Australia (Cadwallader,

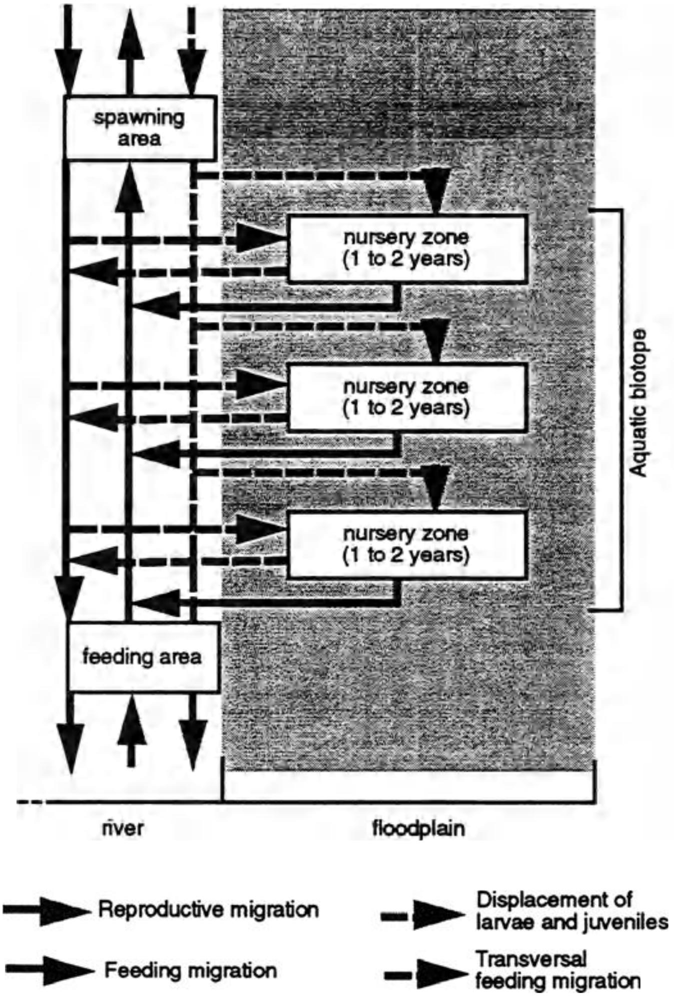

Figure 8.4 Schematic representation of the principal fish migrations in the Parana river (after Bonetto *et al.*, 1981).

1986) where the migration of Percidae is induced by both temperature and the onset of annual spates, leading to displacements of up to 2000 km distance.

The repartition of fish larvae and juveniles within the various functional units of the upper River Rhône in France clearly demonstrates the fundamental role of connections between the main channel and the backwaters of the flood plain (Copp, 1989; Copp *et al.*, 1991; Penáz *et al.*, 1991). In lotic braided channels and along the banks of the main channel, fish reproduction is generally limited to lithophilous species of fish (terminology after Balon, 1985), i.e. those that deposit their eggs on gravel bottoms, such as the barbel *Barbus barbus*, chub *Leuciscus cephalus* and nase *Chondrostoma nasus*. Ecosystem succession, leading to a transformation from lotic to semilotic environment (or domain of attraction), induces a progressive change in the species composition of the reproducing fish assemblage due principally to temporal fluctuations in the hydrological regime. As a channel is progressively isolated from adjacent lotic channels by the alluvial plug forming at the upstream end of a channel, variations in the hydrological regime allow some species of aquatic plant (e.g. mosses, water starworts and crowfoot) to colonize the side channel.

During the initial phases of the abandonment process, the channel is generally lotic during strong floods and spates, such as in spring when some rheophilous fishes are able to reproduce. Once ebbing of the flood has given way to lentic conditions, the channel is then favourable to the reproduction of semirheophilous species such as bleak *Alburnus alburnus* and bream *Abramis brama*, which spawn on either plants and/or alluvia (phytolithophilous). Reproduction by strictly phytophilous (plant spawning) species such as silver bream *Abramis bjoerkna* and rudd *Scardinius erythrophthalmus* also takes place if the necessary species of aquatic plant are present. This progressive series of reproductive events over the course of the spring and summer, due in large part to hydrological and climatic variability, explains the relatively greater fish species richness of these partially abandoned channels as compared with entirely lotic and entirely abandoned channels.

Definitive blockage of a channel's upstream end, which is accentuated by the colonization of the alluvial plug by pioneer species of semi-aquatic plants, leads to permanently lentic conditions (except for exceptional flood or spate events). The increasingly stagnant character of the partially abandoned channel favours reproduction of the phytophilous species (e.g. tench *Tinca tinca*, rudd and silver bream) as well as that of nest-guarding species such as pumpkinseed *Lepomis gibbosus* and black bullhead *Amerus melas*. Complete abandonment of a channel occurs with the near total blockage of its downstream end, though a narrow, temporary connection may continue to persist even during periods of mean water level. Abandoned braided channels, being relatively shallow and narrow, generally succeed towards a terrestrial state at a much faster rate than do abandoned meander channels, which are generally wider and deeper.

Abandoned braided channels are often within closer proximity to existing lotic channels and thus are more prone to inundation during floods and spates, but tend to dry out in the summer. As a result, fish reproduction in abandoned braids is generally characterized by phytophilous species able to exploit the temporary periods of inundation (e.g. pike *Esox lucius*, rudd and silver bream), with hybridization between the cyprinid species not uncommon. It should be noted that when reproduction of pike occurs in such relatively small abandoned braids, it is rare that the progeny of any reproducing cyprinids survive the season, as intensive predation pressure results in the total eradication of other species and perhaps even cannibalism of the pike progeny if the parents remain in the biotope.

Abandoned meander or anastomose channels, on the other hand, possess greater inertia and 'stability' by virtue of their greater depth, width and distance from the parent main channel. Thus, a much more gradual change over in the composition of reproducing fishes takes place, with reproduction of the phytolithophilous fishes eventually ceasing whereas the reproduction of lithophilous species flourishes. However, even former meander channels eventually give way to terrestrialization processes, and the range of reproducing fishes decreases drastically as the former channel is gradually clogged with the profuse growth of submerged macrophytes (e.g. *Nuphar lutea, Nymphaea alba*). Strictly phytophilous species, such as rudd, are the generally the last cyprinids to cease reproduction, with only those species physiologically adapted to anoxic conditions (e.g. pond loach *Misgurnus fossillis*) able to continue reproducing thereafter.

In summarizing the succession of fish reproduction in floodplain channels as they are progressively abandoned, one notices that the lotic channels, which possess little aquatic vegetation and organic matter, are characterized by reproducing fish assemblages of predominantly lithophilous and psammophilous (sand spawning) species (Figure 8.5). Whereas fish reproduction in the semi-lotic conditions of partially abandoned channels, which have moderate amounts of aquatic vegetation and organic matter, is predominated by phytolithophilous, though a range of reproductive styles may be encountered (lithophilous, phytophilous, nest-guarding), depending on the channel's level of ecological succession. Fish reproduction in abandoned channels, where organic matter and aquatic macrophytes are in greatest abundance, tends to be dominated first by both phytophilous and nest-guarding species, with the number of reproducing species gradually decreasing until only the most resistant phytophilous species continue to regenerate themselves. In the same vein, species richness in the various floodplain biotopes decreases in relation to the reduced frequency and intensity of communication with the lotic components of the hydrosystem (Chapter 9) and also decreases as the channel progresses in terms of ecological succession towards terrestrialization (Chapter 10).

Similar patterns have been observed with respect to biomass and production. For example, on the River Rhine, Kieckhafer (1977) demonstrated that fish biomass in a side-channel directly connected to the main channel is greater (524 kg ha^{-1}) than that of an abandoned channel

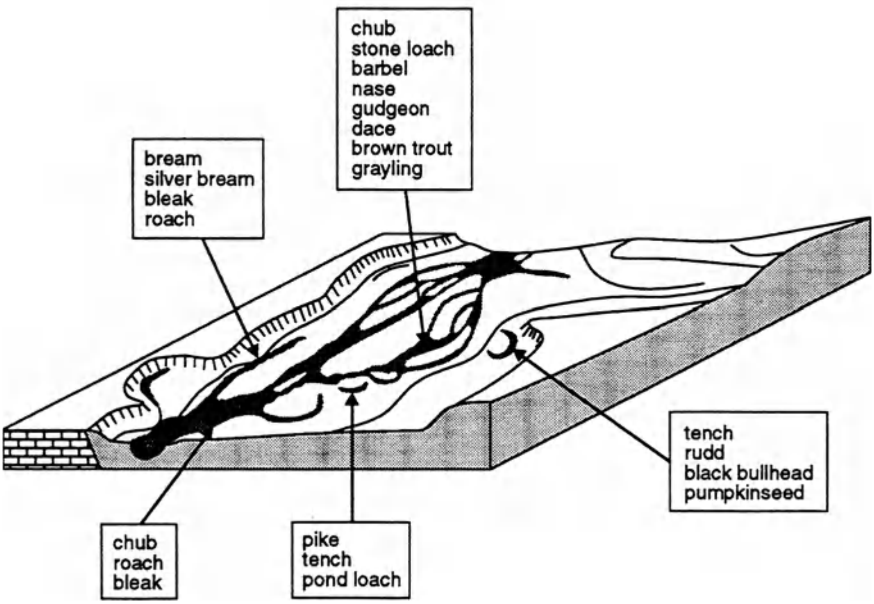

Figure 8.5 Examples of spawning habitat separation by fish on the French Upper Rhône river.

entirely isolated from the main water course (321 kg ha^{-1}). It is thus apparent that a fundamental requirement for the reproduction, larval and juvenile nursery, development and thus long-term success of fishes in rivers is the existence of numerous floodplain channels at the various levels of ecological succession. These complementary roles of floodplain channels require that a maximum level of connectivity exists between the various components of a hydrosystem if fish populations are to maintain themselves.

8.3.5 INFLUENCE OF HYDROLOGY ON THE DISTRIBUTION OF LARVAL AND JUVENILE FISHES

The hydrological regime of a river plays an important role at each level of ecological perception with respect to riverine fishes, influencing not only the reproduction and displacement of fishes between the various components of a hydrosystem, but also the distribution of larval and juvenile fishes within any given biotope. If one first examines reproduction itself, the first step in fish recruitment, it is quickly apparent that reproduction takes place over a large part of the year, with species reproducing in the season of the year to which they have adapted themselves, thus ensuring successful propagation of the species. For each species, an ensemble of environmental variables determines the exact moment (day length, water temperature, flood intensity) and location (current speed, shearing force, type of substrate or vegetation, depth of water, width of channel) for spawning. Although conditions can change progressively during the incubation of eggs, in European fishes the environmental character required for a species to spawn is generally similar to that required by its larvae and 0+ juveniles (Kryzhanovsky, 1949). Thus, the progeny of lithophilous fishes generally demonstrate a preference for gravel and sand banks (Schiemer and Spindler, 1989; Copp, 1992a, 1993b), whereas the young of phytophilous species are normally associated with beds of aquatic macrophytes (Copp, 1992b, 1993a). However, most if not all forms of refuge (branches, vegetation) normally found in lotic channels can be left above the water line when river discharge decreases at the end of summer, forcing the non-piscivorous species of juvenile fish to co-exploit the only remaining potential refuge, the shallow waters of weakly sloped banks (Copp, 1992a). Whereas, with abandoned channels, such seasonal decreases in discharge can isolate the biotope completely from adjacent channels and limit the amount of favourable microhabitat for progeny of many species of non-piscivorous fish. Excessive growth of macrophytes combines with the drop in water level to reduce the amount of open water within the abandoned channel, forcing the non-piscivorous juvenile fishes to utilize the same limited amount of available open water (Copp 1993a). In the event of extreme desiccation, fish assemblages of abandoned channels can suffer increased, if not total, mortality. When connectivity between floodplain biotopes is not reduced by human activity, then such local extinction is often reversed through recolonization during the next flood event. However, the precise impact of the vast majority of river management schemes is in fact a reduction in connectivity between the functional units of a river, as well as the destruction of important floodplain biotopes.

8.4 THE IMPACTS OF RIVER MANAGEMENT SCHEMES

River management is not a recent human endeavour, despite the fact that their number and size has increased exponentially during this century, and most notably in the last few decades. Channelization is an ancient practice, the first forms undoubtedly being levees and dykes to impede the inundation of inhabited lands and to regulate flood waters. Similarly, in the floodplains of braided geomorphological origin, the river tends to separate into a number of small channels during low flow and water retention structures are used to redirect the river's flow into one channel in order to maintain a navigable lane. The development of irrigation practices and the increase in demand for energy has led to a

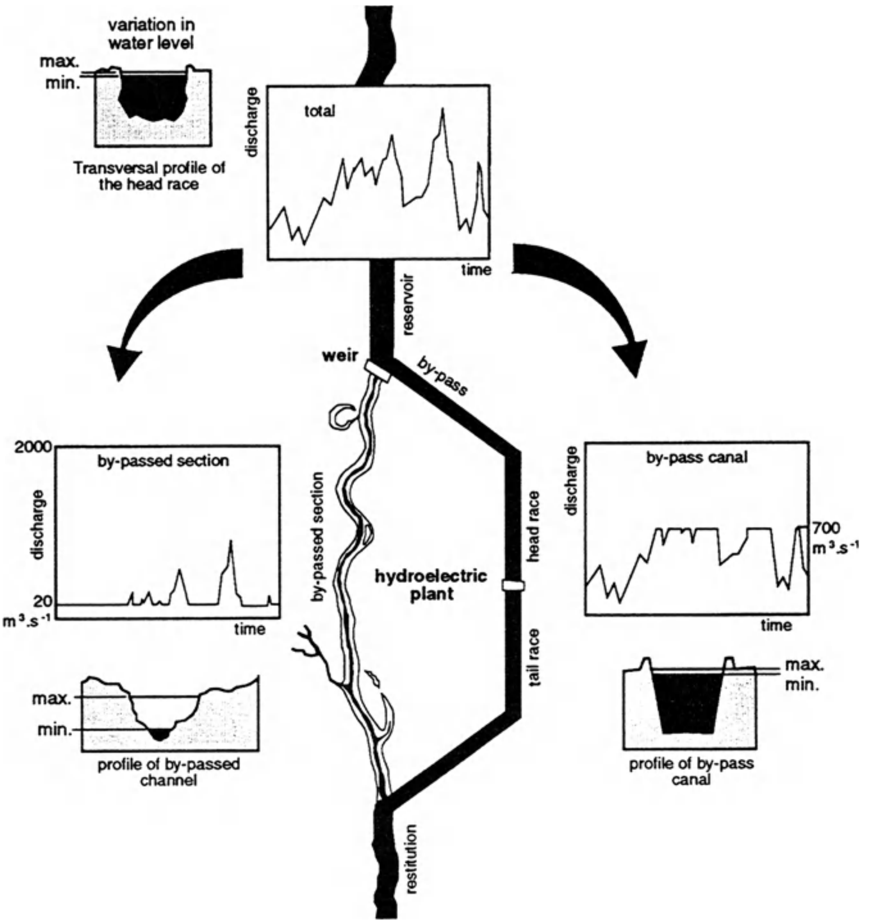

Figure 8.6 Presentation of a hydroelectric power scheme on the French Upper Rhône river (after Bravard *et al.*, 1992).

rise in the number of dams and hydropower schemes constructed on rivers. In the case of floodplain sectors, a system of dam-reservoir, which by-passes the original flood plain, is frequently used to overcome the lack of steep river gradient (Figure 8.6; also Chapter 11). Thus, the transversal constriction of river corridors by flood embankments and dykes combines with the longitudinal segmentation of the river systems by way of dams and reservoirs, a phenomenon encountered in virtually every industrialized nation. To cite but a few examples, only 25 km (5%) of the 522 km of the French River Rhône have not been regulated; similarly, only 40 km (1%) of the River Missouri's 3768 km have been spared from regulation.

The direct impacts of the physical regulation of rivers are related to the ruptured connectivity between the functional units of a river system, with dams disrupting the longitudinal migration and dykes the transverse movement of fishes. For example, migration of the allis shad in the River Rhône is now limited to the lower 70 km, up to the first dam (Vallabrègues) upstream of the Mediterranean Sea. Prior to river regulation, this species migrated up the Rhône as far as Lakes Bourget and Seyssel, a distance of approximately 500 km (Pattee, 1988). Similarly, before dams were constructed on the River Volga, sturgeon and allis shad migrated up to Kalinin, approximately 3000 km, whereas they are now limited to the lower 500 km of the river (Poddubnyi, 1979). The same type of consequences are evident in the large rivers of North America, such as the Mississippi, Missouri, Columbia and Tennessee. The construction of fish ladders and fish lifts does not always compensate for the problems created by the dams. Such by-pass structures must attract the fish away from the river outlet downstream of the dam, and they must function not only for the upstream migration but also for the downstream drift of progeny. Given the different life-history strategies in the various species of migrating fish, it is obvious that a fish ladder appropriate for one species may not necessarily provide the attributes required by other species. In the most favourable cases, where migration is indeed possible, fishes have been observed to concentrate either downstream or upstream of the by-pass structure in the anticipation of its use. Such concentrations of fish do not go unnoticed by potential predators, and elevated mortalities due to predation can be observed. At the same time, the delay caused by the fish being forced to 'wait their turn' for entry into the by-pass structure can result in retardation of the species' normal life cycle. Once the obstacles have been surmounted, the upstream spawning areas must still exist if the species is to reproduce successfully. Often, other human activities affect the character of upstream tributaries, with excessive silt or clay deposits on the river bed making it impossible for lithophilous species to reproduce.

Dams also have indirect impacts on the physical and chemical character of the water. The river becomes lentic upstream of the dam, bringing most of the well-known implications associated with lacustrine environments, such as thermal and chemical stratification to name a few. Downstream of the dam, the discharge of reservoir water presents different consequences, depending on whether the discharge originates from the reservoir's surface, whose warmer waters favour cyprinid species, or from its bottom strata, which favours salmonids. Thus, a salmonid river can be adversely modified by a dam that discharges warm water from the reservoir's surface, as cyprinid species will eventually predominate.

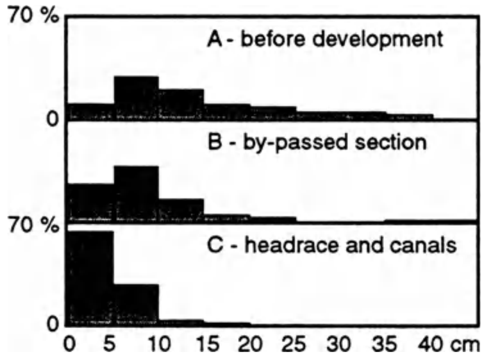

Figure 8.7 Modification of the size distribution of fish following introduction of a hydroelectric power scheme on the French Upper Rhône river (see Figure 8.6, after Persat *et al.*, in press).

Conversely, a river predominated by cyprinids can be 'rejuvenated' to the salmonid watercourse by a dam that discharges cooler water from its reservoir's lower strata (Penáz *et al.*, 1968). Note, however, that if water from the lower strata of a reservoir is anoxic, such as those incorporating sediment traps, the conditions downstream of the dam will be inhospitable to almost every fish species. This latter problem is exacerbated in the warmer months, when problems of eutrophication are most acute.

The by-pass type dam systems, such as those on the Rhône (Bravard *et al.*, 1992), consist of a long reservoir channel (Figure 8.6) that presents little risk of change to the physical and chemical character of the water but results in the radical alteration of the environment within the channel itself and in the by-passed floodplain sector. The drastic reduction in river discharge through the by-passed flood plain transforms the river into a small water-course characterized by riffle and pool sequences, similar to that found in lower order rivers and streams. The composition of the fish assemblages is altered, with small-bodied species predominating and with the populations of large-bodied species being skewed in size distribution towards the smaller size classes (Figure 8.7). In such regulated systems, the larger individuals of a population often occupy the deeper channels, mainly the artificial reservoir channel and its adjacent seepage canals, the latter of which may in some places be rather shallow and thus favour smaller-bodied species. In conclusion, the by-pass type of regulation schemes tend to affect fish assemblages in a by-passed flood plain by favouring small-bodied species, and by shifting the population size structure of large-bodied species towards smaller size classes than existed prior to the scheme's construction.

Interactions between units of the fluvial hydrosystem

9

C. Amoros, J. Gibert and M. T. Greenwood

9.1 INTRODUCTION

The distribution of the different units within a hydrosystem is related to the geomorphological mechanisms involved in their creation (Chapter 5). In addition to the effects of the environmental constraints specific to each unit (Chapters 6, 7 and 8), the composition of the populations in each unit also depends on their spatial relations because of exchanges and interactions between them. Some species need to be close to different complementary units for their development, or for re-establishment after disturbance. The hydrosystem as a whole has a resilience, with some units within it acting as refugia or foci for recolonization.

The previous three chapters have considered flows of materials and energy within each unit of the hydrosystem. This chapter is concerned with flows which may or may not pass between one unit and another. These flows take the form of exchanges of energy, materials (water, alluvium, dissolved or particulate organic matter) and living organisms. Both the flows themselves (their nature, direction, magnitude, variations) and the role of boundary areas (interfaces between units of the hydrosystem), which may encourage the transfer of some components, or restrict or prevent them, will be considered.

9.1.1 INTERACTIONS AND INTERCONNECTIONS

Two concepts can be used to take into account what happens in boundary areas. These are the concepts of the ecotone and connectivity.

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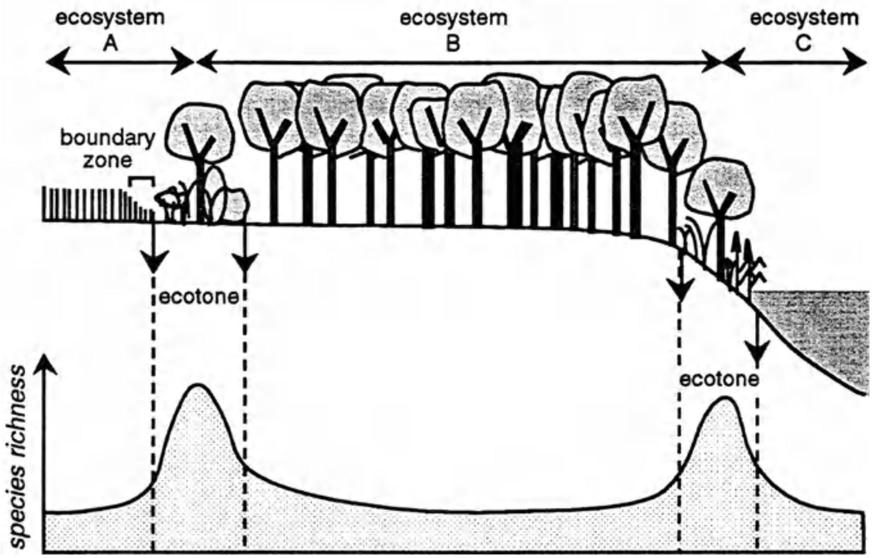

Figure 9.1 Ecotonal boundary and biodiversity.

The ecotone concept was defined as early as 1897 by Clements, and then Livingston (1903), as a boundary between two plant associations or communities where processes of exchange or competition between adjacent formations could be observed. A high density and variety of communities is typical of boundary areas, this has been called the edge effect (Leopold, 1933). The edge effect is associated with a maximum biodiversity. This is explained by (a) the coexistence of species from two adjacent ecosystems, (b) the presence of other species which need the two adjacent ecosystems and (c) the presence of species which discover special environmental conditions in the transition zone. The influence of an ecotone may extend beyond a structural 'edge' because of the influence of the boundary on environmental and biological processes (e.g. competition and predation). Thus, in Figure 9.1 a boundary zone at the edge of the ecosystem A may be defined where poor growth of maize plants results from the competition for water and light with the adjacent forest.

More recently, the ecotone concept has been reformulated (Holland, 1988; Naiman *et al.*, 1988; Hansen *et al.*, 1988) on the basis of a set of features which are uniquely defined by the scales of time and space and by the strength of the interactions between adjacent ecological systems. This applies in particular to earth–water ecotones (Naiman and Décamps, 1990) (Figure 9.1). However, different ecotones may be defined at different spatial scales of observation. For example, within a river corridor, at

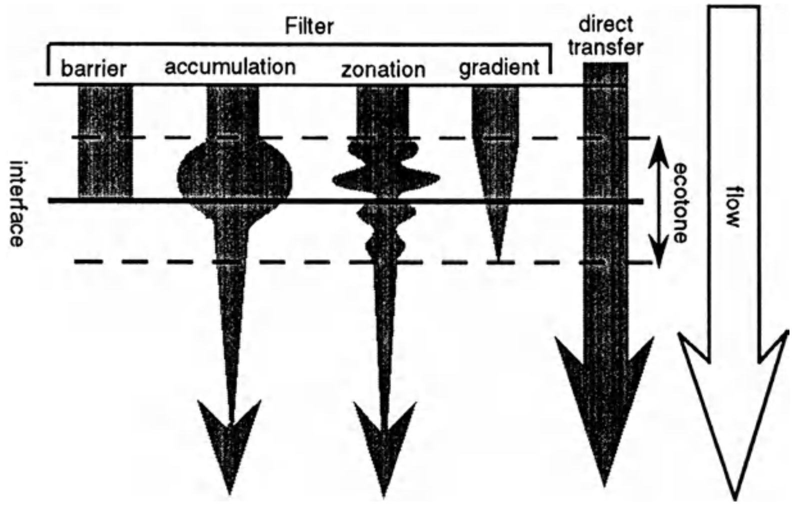

Figure 9.2 Patterns of flow across an ecotone.

the landscape scale the alluvial plain may be regarded as an ecotone; at the scale of units, the transitional zone around a spring, the surface water–groundwater interface with a floodplain pond, and the riparian fringe along the river channel may also be considered as ecotones. Ecotones are regarded as membranes between ecological systems controlling the quality and magnitude of exchanges between systems. Five types of interface may be defined (Figure 9.2). First, flows can pass directly through several different units of the hydrosystem without being affected. An example of this are fish which reproduce in cut-off channels remote from the main river, but which are normally to be found in the main channel. In other cases, the interface acts as a filter. This may produce four different effects:

1. gradient effect occurs where there is a progressive reduction in the number of components, e.g. the reduction in the number of grassland insect species on the edge of the alluvial forest;

2. zonation effect occurs where there is an irregular distribution of flows and concentrations in particular regions, e.g. the distribution of bird species along the transverse dimension of a river corridor;
3. the effect of accumulation through the retention of a majority of components, e.g. organic matter across the river/aquifer interface;
4. the effect of an insuperable barrier – flows are completely halted, e.g. strictly subterranean species are physiologically stopped by the boundary of the day/night alternation and permanent darkness.

9.1.2 THE CONCEPT OF CONNECTIVITY

Connectivity is a fundamental parameter which determines whether the subpopulations of each type of unit can be interconnected to form a demographic whole called a 'metapopulation' (Merriam, 1984). Each subpopulation has a number of characteristic features, such as the spatial distribution of individuals; density, structure, natality and mortality coefficients; interdependent relationships between individuals, etc. Subpopulations have their own organization but, as a result of extrinsic (environmental) factors and/or intrinsic factors (factors intrinsic to the subpopulation), they can establish links of a spatial and/or reproductive order between them, giving rise to the effects of genetic mixing and species dispersion. High connectivity is reflected by less isolation between populations and thus greater demographic stability. One case of this is the aquatic Coleopteran *Gyrinus marinus*. Only Van Der O Eijk (1987) has shown that when a metapopulation consists of five subpopulations, 38% extinction occurs after 25 years, whereas if a metapopulation consists of 20 subpopulations there is no extinction at all,

The concept of connectivity in this functional sense, must be distinguished from that of a structural connectivity, which involves permanent or episodic physical connections between units (Figure 9.3). Non-adjacent components of the landscape may have a high or low connectivity depending on circumstances, regardless of their structural connections. Particles which are dispersed by the wind, such as the seeds of willows, poplars or ash trees, are examples of this. This also applies to dispersion by water. Observations of bank colonization by *Impatiens capensis* show that the species is common when the watercourse passes from a wood in which *Impatiens* is present but not common, but absent when the stream flows from grassland towards a wood. In the first case the connectivity is high, in the latter it is low or zero.

The lack of structural connections between components of the landscape (e.g. woods) and corridors (e.g. hedgerows) does not always reduce connectivity. A 5 m break in a corridor may stop the dispersion of a plant, but have little effect on a bird or a flying insect. Connectivity thus depends on both structures and the nature of the flows and vectors; it

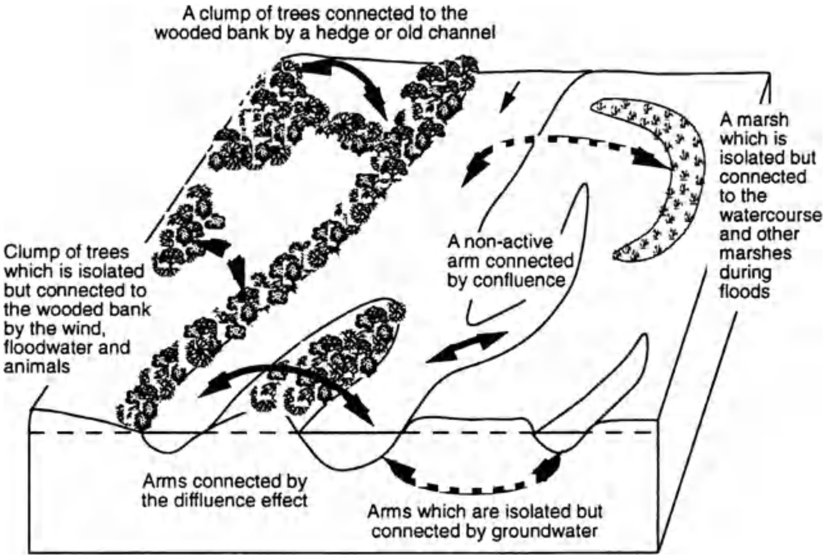

Figure 9.3 Some permanent or episodic connections in a fluvial hydrosystem.

reflects the process by which the various components of a landscape are functionally incorporated into an ecocomplex as a whole, in this case the fluvial hydrosystem. The concept is of much wider scope than that of the ecotone, but it incorporates the effect of the different types of ecotones which can be found in an alluvial plain.

9.2 NATURE AND EFFECT OF EXCHANGES AND INTERACTIONS

9.2.1 TRANSFERS

The transfer of an abiotic or biotic component from one unit of a hydrosystem to an adjacent unit represents the simplest form of interaction. The transfers of water, nutrients, organic matter, sediments and living organisms are closely interlinked, but considered separately for ease of discussion.

(a) Transfers of water

Water is the component which is most frequently exchanged between the units of a hydrosystem, in the longitudinal, transverse and vertical dimensions. Flow characteristics such as duration, frequency and timing of inundation; strength of surface-water and groundwater interactions; and retention times, influence the distributions of biota. Plant species,

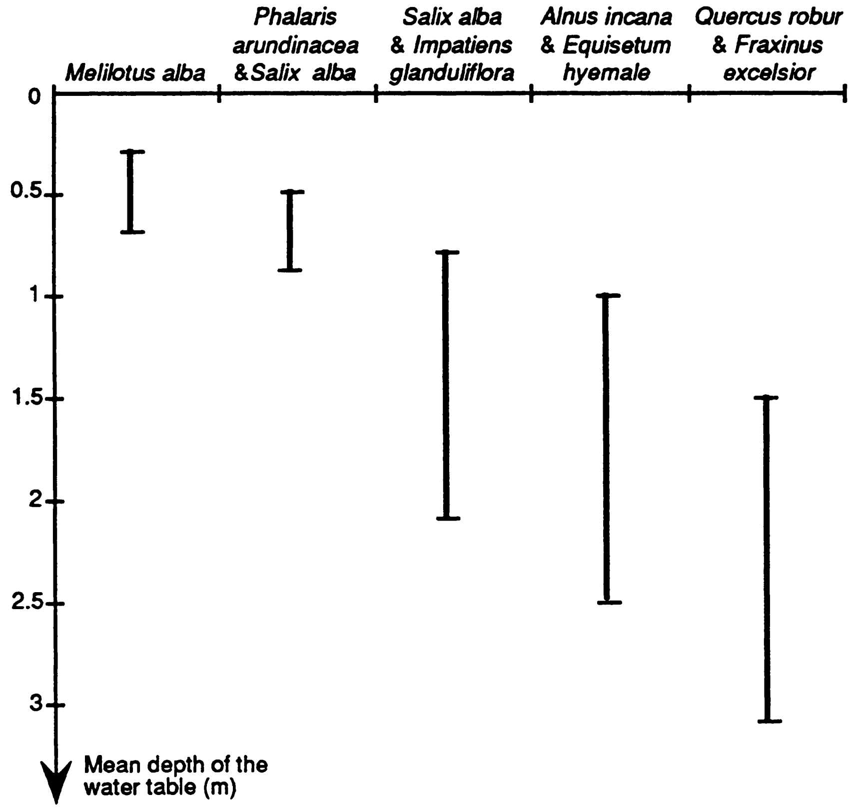

Figure 9.4 Distribution of plant groups on the sand/silt alluvium of the Upper Rhône flood plain, in relation to water-table depth (after Pautou 1984; Bravard *et al.*, 1986).

for example, distribute themselves over the alluvial plain according to the length of their root systems, a feature based on the distance between the surface of the soil and the level of the water table (Figure 9.4).

However, differences in particle size give rise to different rates of flow in the movement of groundwater. Such differences in the rate of renewal of groundwater are responsible for differences in surface populations for a given average water-table depth. Thus, on the plains of the Upper Rhône and the Rhine, populations of black alder (*Alnus glutinosa*) colonize impermeable fine-grained soils (clay and peaty soils) whereas the hoary alder (*Alnus incana*) only grows on permeable substrates with a coarse particle size (sandy silts on gravel). Previous chapters have shown how water transfers from the alluvial aquifer to old arms of a river can

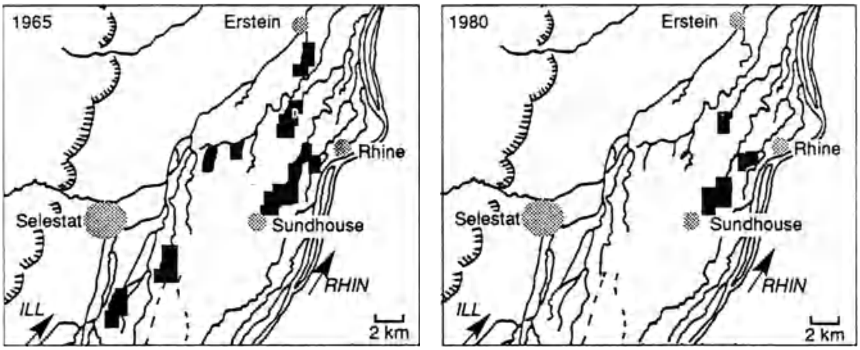

Figure 9.5 Distribution of *Potamogeton coloratus* (solid squares), 1965 and 1980, in old braided arms of the River Rhine (after Carbiener, 1983).

influence both the primary productivity of these environments (Chapter 6) and the composition of animal populations (Chapter 7).

(b) Transfer of nutrients

The input of nutrients such as nitrates and phosphates to floodplain ponds by surface water during floods accentuates nitrification. Less obviously, but equally effectively, inputs of groundwater can have a similar effect. Thus, in the alluvial plain of the Rhine, cut off braided channels are fed by the water table. Until 1965 this groundwater contained little nitrate and phosphate. Most of the arms were oligotrophic, as indicated by the presence of *Potamogeton coloratus* (Figure 9.5). During the last few decades the growth of agriculture and in particular the more intensive use of chemical fertilizers has caused an increase in nitrate and phosphate concentrations in the groundwater. Even when their immediate terrestrial environment has not been altered, the cut-off channels fed by groundwaters developed signs of eutrophication, reflected by a reduction in the surface area occupied by *P. coloratus* and associated species.

(c) Transfers of organic matter

All wooded banks provide watercourses with dissolved and particulate organic matter (dead leaves, twigs, etc.). The importance of this has been clearly demonstrated in the Fluvial Continuum Concept (Cummins et al., 1983; Minshall *et al.*, 1985; Naiman *et al.*, 1988), particularly in the case of narrow headwater forest watercourses whose functioning depends essentially on these allochthonous inputs. Imports of a terrestrial origin have a very important part to play in narrow cut-off and secondary channels, some of which may be completely covered by the branches of adjacent trees. In such cases, the aquatic unit operates heterotrophically and depends entirely on inputs of organic matter provided by adjacent woodland. Dead leaves may be degraded quickly in the aquatic environment, depending on the nature of the species from which they originate (Kaushik and Hynes, 1971; Suberkropp and Klug, 1976). The higher the nitrogen content of the leaves, in the form of amino acids or proteins, the greater the nutrient value for terrestrial herbivores and aquatic detritivores. Irons *et al.*, (1988) evaluated the nutrient value of dead leaves from four species common in Alaska (*Alnus crispa, Betula papyrifera, Salix alexensis* and *Populus balsamifera*) for the larvae of Trichopteran insects (*Hydatophylax variabilis*). The chemical composition of the dead leaves varied in relation to the species in question and to any treatment with fertilizers. *Alnus* leaves were richer in proteins and the use of fertilizer generally increased the protein content of leaves. Trichopteran larvae preferred to consume the leaves of trees which had been given nitrogen and phosphate fertilizer (with the exception of *Populus* leaves). For a given type of fertilizer use, *Alnus* leaves were the most readily consumed.

The fall of dead leaves into an aquatic environment and their decomposition may also give rise to deoxygenation of the water. This effect, which is immediate (a few hours), and strong in the case of dead leaves of certain species like poplar and ash, is the result of a biochemical deoxygenation process caused by polyphenyl oxidase–polyphenol systems (Trémolières and Carbiener, 1981). It precedes the medium term fall in oxygen content (2–3 days) due to the consumption of oxygen following microbiological litter-decomposing activity.

(d) Transfers of mineral sediments

During floods, suspended sediments may be deposited across the alluvial plain (Chapter 4). Thus, in two old meanders of the Pembina River (Central Alberta, Canada), which are permanently connected to the main course, Van der Valk and Bliss (1971) measured silt deposits 3 and 4 cm thick after only three days of flood. In addition to smothering submerged aquatic plants, water transparency was reduced for 10 days. The flora of these channels was restricted to shade-tolerant plant species.

Flood deposits on terrestrial units cause the level of the ground to rise (from 0.9 to 1.2 m of sand and gravel deposited locally in a flood in the Republican River, USA, in 1935 after Schley, 1940, quoted by Bellah and Hulbert, 1974), and changing the ecological conditions in these units and driving population successions (Chapter 10). The deposits of fine sediments represent a source of exchangeable cations for vegetation. Layers of fine sediments deposited by spring floods form a bare damp ground which is essential for the germination of some species such as *Populus deltoides* in North America (Bradley and Smith, 1986). It should be noted that, although there is a net transfer of particulate organic matter from terrestrial units to aquatic units, net transfers of mineral sediments are from aquatic units to terrestrial units.

(e) Biotic transfers

Many animal species need to live and develop in at least two different units. Their movements between these units give rise to transfers of material and energy within the hydrosystem. These movements are caused either by the need to seek food resources, or habitats appropriate for reproduction, or again shelter to withstand extreme variations in the environment (floods and droughts).

In Europe for example, the pike (*Esox lucius*) is found in both the stagnant waters of cut-off channels, in the flowing waters of secondary channels or the main river and reproduces in flooded meadows and reed beds. The common heron (*Ardea cinerea*) is a large bird which nests at the tops of the trees on river banks but obtains its food in the shallow parts of the stagnant waters of cut-off channels. Beavers import very large quantities of plant material gathered from adjacent terrestrial units into the aquatic environment of secondary channels. Naiman and Melillo (1984) have calculated that a colony of six beavers (*Castor canadensis*) introduced 10 g m^{-2} year $^{-1}$ of nitrogen into a small water body in Canada, which was equivalent to an increase of 145% in relation to other sources of nitrogen. This covered only food needs and must be supplemented by the amount of wood introduced for the construction of lodges and the dam.

Hayden and Clifford (1974) have demonstrated that the larvae of an Ephemeropteran (*Leptophlebia cupida*) in a Canadian river move upstream by swimming along the banks as soon as the water first rises following snow melt in spring. Following the bank, they move up the outflow channels from floodplain marshes where they complete their development, protected from the high water levels in the river. The adults emerge at the end of summer and return to lay eggs in the river where the larvae overwinter, avoiding drying out or freezing in the marshes (Chapter 7).

Stanford and Ward (1988) collected Plecopteran larvae from interstitial environments in the floodplain of the Flathead River, Montana, USA, up to 2 km from the watercourse. Many small invertebrates (molluscs, crustaceans, insect larvae) also take refuge in interstitial water to avoid temporary desiccation when water levels are low, and recolonize them rapidly once they rise. Thus, Imhof and Harrison (1981) observed that Trichopteran larvae survived for 2 weeks under natural conditions in a small dried up channel in southern Ontario, and up to 4 weeks under experimental conditions. Reygrobellet and Castella (1987) collected young Odonate larvae up to a depth of 2 m in the alluvium of the plain of the Upper Rhône in France. It is now known that up to 80% of the benthos in rivers and streams can live within the sediments, whether as juveniles or adults. Flows of biota from underground ecosystems to surface ecosystems thus reinforce the possibilities for homeostasis within hydrosystems.

9.2.2 FILTER EFFECTS

Interfaces may stop or reduce the flows of energy, materials or living organisms which are likely to enter a unit. Interfaces can also act as physical filters, chemical filters or biological filters.

(a) Physical filter effect

The physical filter effect generally depends on the structure of a unit, which enables it to act as an obstacle to a transfer of energy or material. For example the growth of trees along river banks can give rise to complete cover over narrow aquatic environments, like old braided arms, and thus by shading, reduce the penetration of solar energy into these aquatic units. In these aquatic ecosystems which are shielded by the leaves of river-bank trees, autochthonous primary production will be extremely low, with the result that the ecosystem will function heterotrophically.

Discontinuities in surface roughness, for example, at the edge of a wood, lead to the deposition of woody debris and suspended sediments. Thus, scrub vegetation which gains a hold on alluvial plugs retards flood flows into old channels, causing most of its alluvial load to be deposited and clear water to reach the central portion of the old channel, encouraging light penetration and increased primary production.

(b) Chemical filters

The passage of flows of water through some interfaces or some units may give rise to a change in the concentrations of some chemical substances. The self-purification capacity of flowing water is long established. Concentrations may decrease due to either absorption and uptake of the chemical substance by living organisms, or by conversion. For example, in surface waters, aquatic plants play a major role in reducing nitrate concentrations. Some absorb nitrates as nutrients for their metabolism and production; the high plant biomass which is produced in nutrient-charged waters very often accumulates *in situ* and its decomposition gives rise to anaerobic conditions in the sediments which encourage nitrification processes (Figure 9.6). Thus the reduction in nitrate concentrations in water leaving a sewage works appears to be greater when it passes through a *Phragmites* reed bed, than in open water (Figure 9.7a). similarly, in an old channel of the Waal (the southern branch of the Rhine in the Low Countries), Brock *et al.* (1983) observed a substantial fall in nitrate concentrations during the growing season after winter flooding by the nitrate-laden waters of the Rhine (Figure 9.7b)

River margins, especially woodlands and wetlands, act as filters with regard to nutrient or toxic substances carried towards a river by groundwater. The effect becomes noticeable beyond wooded edges or meadows some 30 m wide. In Maryland, Peterjohn and Correll (1984) measured the rate of nitrogen retention, at 80% in the alluvial forest, but only 8% in the adjacent cultivated fields (Figure 9.8), About 75% of the losses occurred by denitrification in the groundwater under river-bank woodland. In the highly productive alluvial forests of the Garonne, Pinay (1986) measured denitrification capacity at 50 mg of nitrogen m^{-2} day $^{-1}$. These buffer zones between terrestrial and aquatic ecosystems thus offer real protection for the quality of groundwater and surface waters (Chapter 12).

The banks of a river have a very important role to play in relationships between the ground water and a river. This ecotone is the site of many physical and chemical reactions which slow down, stop or fail to stop the transfer of pollutants from a river to the alluvial aquifer. In fact major changes in the physical and chemical conditions of the environment (change in pH, fall in oxygen content, etc.) alter chemical equilibria and produce precipitation or adsorption onto solids. Trace metals and remobilization into solution (iron, manganese) are frequent, and many molecules can be carried through banks in the form of colloids.

(c) Biological filters

The biological filter effect depends not only on the contrast between the environmental conditions on either side of the interface, but also on the ability of individual species to withstand these differences in conditions. For species which do not have these abilities the interface will act as an impenetrable barrier.

For example, the land–water interface does not represent a barrier for the spread of plants having hydrochoric seeds (*Alnus, Oenothera, Polygonum*) or plants which are capable of multiplying by natural propagation (*Salix, Tamarix*). The aquatic environment often represents a favoured route for the transport and propagation of these plants. Conversely, species with barochoric seeds (*Corylus, Quercus, Juglans*) cannot survive crossing the land–water interface. In the same way, many terrestrial animals cannot penetrate aquatic environments, but others are quite capable of making use of both types of environment, e.g. ducks,

Nitrification : nitrogen compounds present in the organic matter produced in aquatic environments or of terrestrial origin are decomposed and mineralised essentially by aerobic bacteria (e.g. *Nitrosomonas, Nitrobacter*).

Denitrification : nitrates resulting from the process of mineralisation are converted in a reducing medium as they enter the system by anaerobic bacteria (e.g. *Pseudomonas, Achromobacter, Bacillus*) into gaseous materials such as nitrogen dioxide (NO_2) or molecular nitrogen which can escape into the atmosphere. During the denitrification process nitrates are used by anaerobic bacteria as electron acceptors instead of oxygen. The vigour of this bacterial activity is proportional to the amount of organic matter present.

Nitrogen fixation : blue algae (e.g. *Oscillatoria, Nostoc, Anabaena*) and to a lesser extent some facultative anaerobic bacteria (e.g. *Azotobacter, Clostridium*) can absorb molecular nitrogen directly and fix it in the form of ammonium and then amino acids.

Uptake of nitrates : plants absorb nitrates through their roots and reduce them to ammonium before using it to synthesise amino acids and proteins. This uptake of nitrates of course occurs during the growth period.

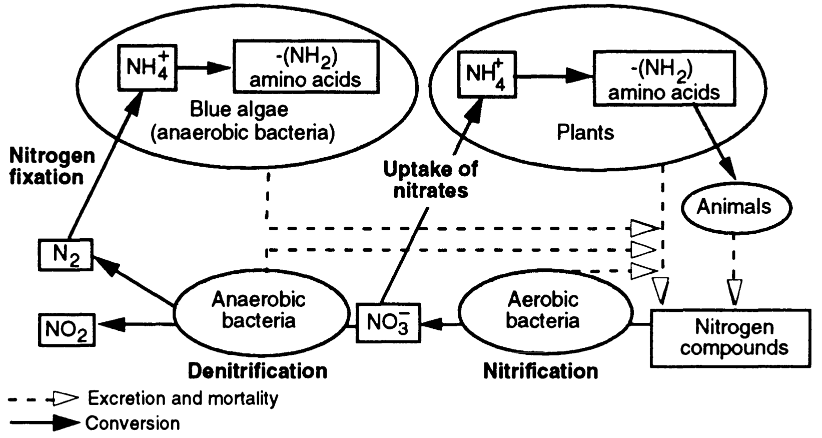

Figure 9.6 The process of conversion of nitrogen compounds. **Nitrification**: nitrogen compounds present in the organic matter produced in aquatic environments or of terrestrial origin are decomposed and mineralized essentially by aerobic bacteria (e.g. *Nitrosomonas, Nitrobacter*). **Denitrification**: nitrates resulting from the process of mineralization are converted in a reducing medium as they enter the system by anaerobic bacteria (e.g. *Pseudomonas, Achromobacter Bacillus*) into gaseous materials such as nitrogen dioxide (N_2O) or molecular nitrogen which can escape into the atmosphere. During the denitrification process nitrates are used by anaerobic bacteria as electron acceptors instead of oxygen. The vigour of this bacterial activity is proportional to the amount of organic matter present. **Nitrogen fixation**: blue algae (e.g. *Oscillatoria, Nostoc, Anabaena*) and to a lesser extent some facultative anaerobic bacteria (e.g. *Azotobacter, Clostridium*) can absorb molecular nitrogen directly and fix it in the form of ammonium and then amino acids. **Uptake of nitrates**: plants absorb nitrates through their roots and reduce them to ammonium before using it to synthesize amino acids and proteins. This uptake of nitrates of course occurs during the growth period.

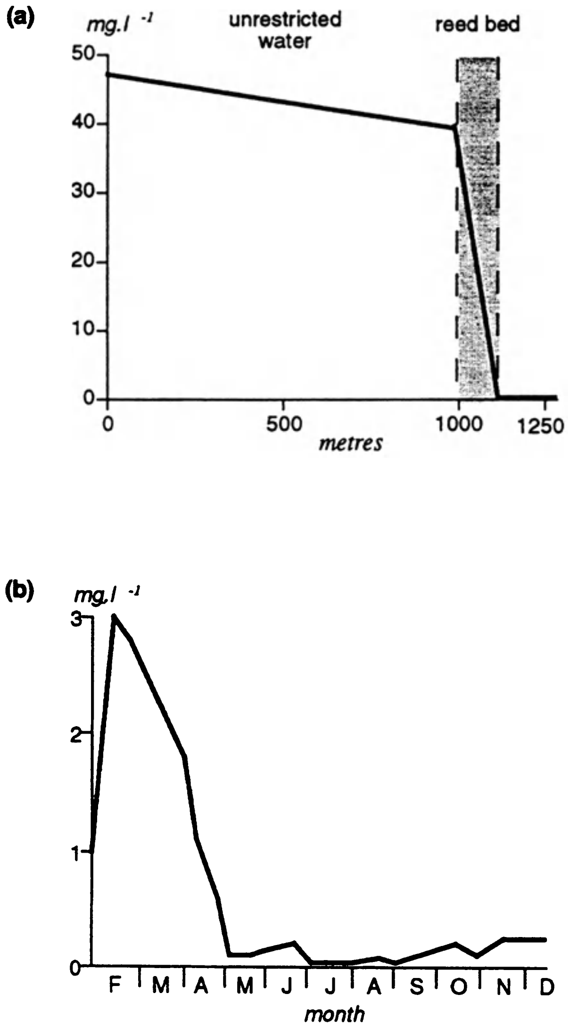

Figure 9.7 Reduction in nitrate concentrations; (a) during flow across a reed bed of *Phragmites australis* (after Klötzli 1967), and (b) in the waters of an old channel of the Waal after inputs during winter floods (after Brock *et al.*, 1983).

coot and moorhen among the birds, and shrew, beaver, coypu and otter among the mammals.

At the interface between surface water and groundwater there are many lotic animals which can bury themselves in the interstitial environment and thus survive disturbances in the surface environment (section 9.2.1(e)). This interface also acts as a filter. Although these are two aquatic units, the narrowness of the spaces available in the interstitial

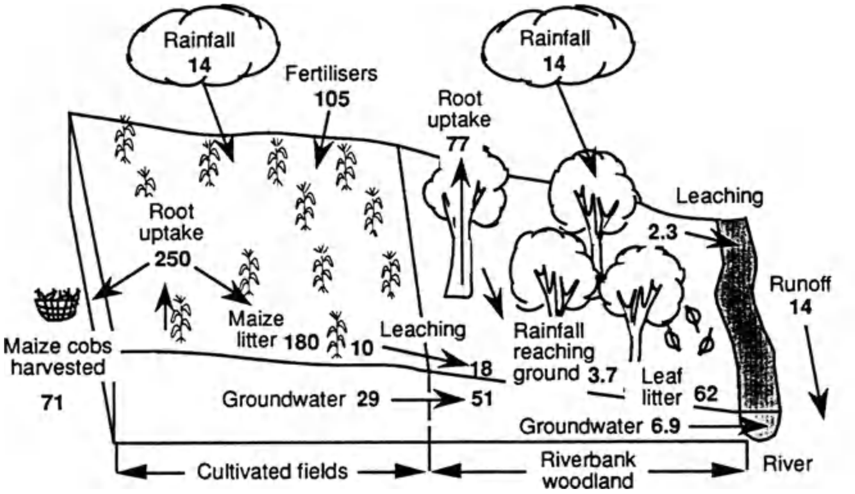

Figure 9.8 Inputs, pathways and release of nitrogen (kg of N $ha^{-1}y^{-1}$) from the catchment of the Rhône (after Peterjohn and Correll, 1984).

environment selects for animal size and morphology. Some larger animals, such as salmonid alevins (*Salmo, Thymallus*) can live in the interstitial environment as a result of special behaviour (Chapter 8). Relationships between species create very effective biological filters at the surface water – groundwater interface as a result of competition and predation. For example, in cut-off channels fed by limnocrene springs, the lack of hypogeal invertebrates which could easily drift downstream from the springs, is explained by the vulnerability of these animals when they reach epigeal environments (Plenet *et al.*, 1992).

A biological filter may also be formed between two surface aquatic units. One example is the interface between the stagnant water of a cut-off channel and the flowing waters of an active channel. When high production and extensive decomposition reduces the dissolved oxygen content of the water in the cut-off channel, the fauna will be restricted to species which can tolerate low dissolved oxygen concentrations.

9.2.3 BORDER EFFECTS

The contact zone between two different units may give rise to special conditions that are highly favourable, to or even necessary for, some species in one of the two units, or which are unfavourable to some organisms. This border effect can be observed in interstitial springs in surface aquatic environments. The border formed by the mixture of underground and surface communities develops within the sediments of the spring.

The biological ecotone is therefore beneath the surface and creates a zone of influence in the surface environment, a border effect which extends for several metres beyond the emergence of the groundwater. It corresponds to quantitative changes in species of Crustacea, in particular Ostracods of the genus *Pseudocandona*, for which numbers are very high around the spring but decrease in areas further downstream (Plenet *et al.*, 1992).

At the interface between two surface aquatic units, e.g. at the downstream confluence between an isolated channel cut-off upstream, and the main channel, the backflow of turbid river water into the cut-off reduces light penetration leading to a fall in the productivity of planktonic algae and submerged water plants.

At the river margin, fluvial processes create a range of unique habitats. New sand banks which have not been colonized by terrestrial vegetation represent a suitable environment for the nest holes of sand martins (*Riparia riparia*). This bird, which lives in dense colonies, feeds on airborne insects, but has an absolute need to reproduce in this special environment along the edge of the channel.

The form of a river bank is related to the riparian plant community. If this is old hardwood woodland, dominated by *Fraxinus excelsior* or *Quercus robur*, the deep roots form an obstacle to erosion, encouraging scour of the channel bed creating pools with cover provided by the roots. This provides shelter for fish and substratum for invertebrates.

In addition to the border effects which occur at the boundary between units, the juxtaposition of some units greatly favours some animals. The otter, for example, an amphibious mammal which essentially feeds on fish, makes good use of the thickets of young willows on the banks to establish rest areas. However, it only uses cavities excavated at the foot of adult trees, whose roots go vertically down into the ground, essentially between the roots of oaks, ash or maple, as dens for reproduction. Riverbank woodland dominated by trees with roots which extend mainly horizontally (e.g. willows), seem to be little used as sites for reproduction (Andrews, 1989).

9.3 TOPOLOGICAL EFFECTS

The distribution of functional units in a hydrosystem is not random, but structured by geomorphological processes (Chapter 5). The arrangement of units is of ecological significance because the spatial configuration of the hydrosystem governs the interaction between units and the overall functioning of the hydrosystem.

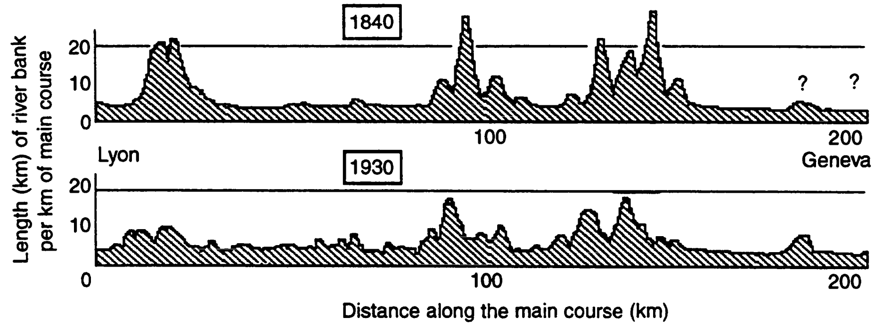

Figure 9.9 Total bank length for all the channels of the Upper Rhône for each kilometre of the main course before (1840) and after (1930) the embankment work carried out in 1880–1890, to assist navigation (modified after Bravard, 1987).

9.3.1 LENGTH OF ECOTONES

Given all the processes which take place at interfaces, it is obvious that the quantity of exchange will depend on the length of the ecotones present in each sector of a hydrosystem. For example, the length of river margin depends on the number of channels and their sinuosities. Under natural conditions, anastomosing sections show the greatest length of land–water interface because the large number of channels are also sinuous (Chapter 5). Embankment work for navigation has considerably reduced the length of land–water interfaces in braided sections, for example on the Upper Rhône (Figure 9.9) (Bravard, 1987). On a 25 km stretch of the Willamette River (Oregon), Sedell and Froggatt (1984) demonstrated that length of river bank decreased from more than 250 km in 1854 (an average of more than 10 km of ecotone for each linear 1 km of watercourse) to 64 km in 1967 as a result of human intervention.

9.3.2 FRAGMENTATION OF UNITS

Fragmentation of units increases the length of the ecotone but also reduces the surface area of each unit, and this may have significant ecological consequences. It is only at the centre of a unit that the environmental conditions specific to that unit develop (zone a in Figure 9.10a). As the size of the unit decreases, this central zone becomes smaller and may even disappear if the unit becomes too small.

The relationship between the edge effect and unit size is particularly clear in the case of vegetation patches. For animal populations, territoriality is an additional factor; animals require a certain living space over which they can find their food resources or in which they can reproduce.

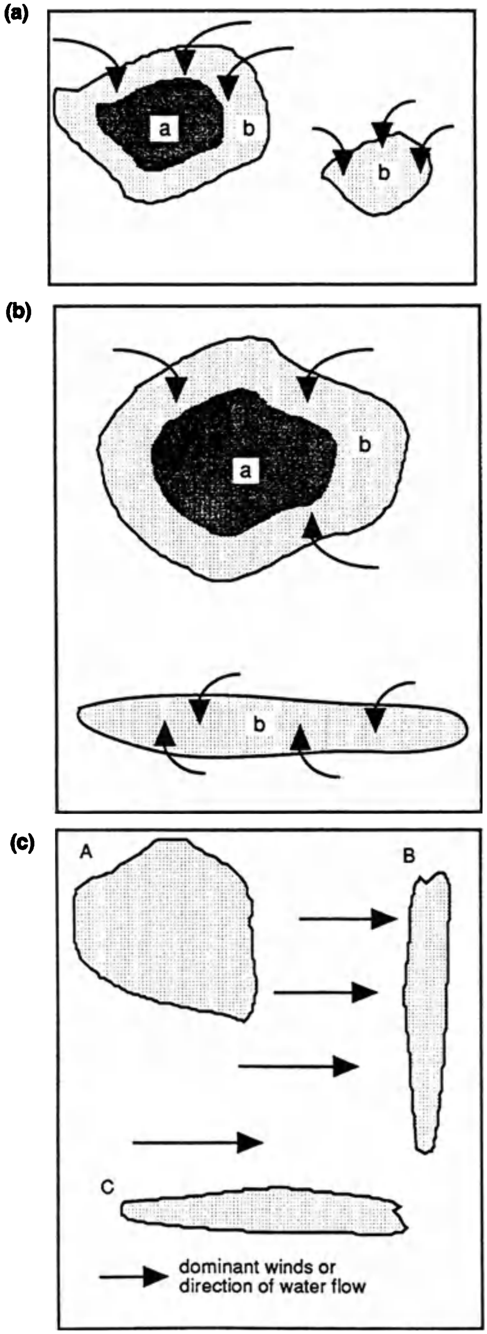

Figure 9.10 The effect of (a) unit size, (b) unit shape (a = interior, b = border) and (c) position of units (the likelihood of receiving components from A is much greater for B than for C).

In many higher vertebrates reproduction is accompanied by behaviour to defend the territory occupied by each pair (from 1 to 150 000 m^2 for some bird species, other than for birds of prey). Furthermore, in order that an animal population may sustain itself for several generations, several pairs of the same species must live within a given area so that genetic mixing can take place. According to Décamps *et al.* (1987) such biological connectivity between wooded units of the hydrosystem largely explains why bird populations in units of the river-bank woodland of the Garonne do not seem to be affected by the surface area of the units.

9.3.3 SHAPE OF UNITS

In addition to surface area, the shape of units influences their functioning and the nature of their populations. For a given surface area the relative portion represented by the border area will be greater the more extended the unit (Figure 9.10b) because the perimeter/surface ratio is higher for elongated shapes. In the extreme case a unit of linear shape would be entirely subjected to border effects. Thus, narrow braided channels may be entirely covered by the canopy of adjacent woodland and their ecosystems function heterotrophically, while wider meandering channels are more autotrophic (Chapter 7).

In addition to this, linear forms are frequently connected to a greater or lesser extent and form networks along which animals can easily move or plant propagules can be disseminated (Figure 9.10c). For example, within a landscape dominated by wetland and aquatic environments, the relatively dry sandy–silty raised levees of the banks are emergent, and many terrestrial mammals can move along these. Conversely, old braided channels filled with fine moist sediments form a network which encourages the propagation of plant species such as *Fraxinus excelsior, Quercus robur* or *Ulmus minor* (Pautou, 1988).

9.3.4 THE POSITION OF UNITS

Exchanges between units are obviously encouraged by their proximity. The orientation of units of an elongated shape can also have an effect on the magnitude of exchanges. Thus, elongated units whose major axis is perpendicular to dominant winds or directions of water flow will have a greater probability of receiving components transported by one or other of these vectors than units whose major axis is parallel to the preferred trajectories of these vectors (Figure 9.10c).

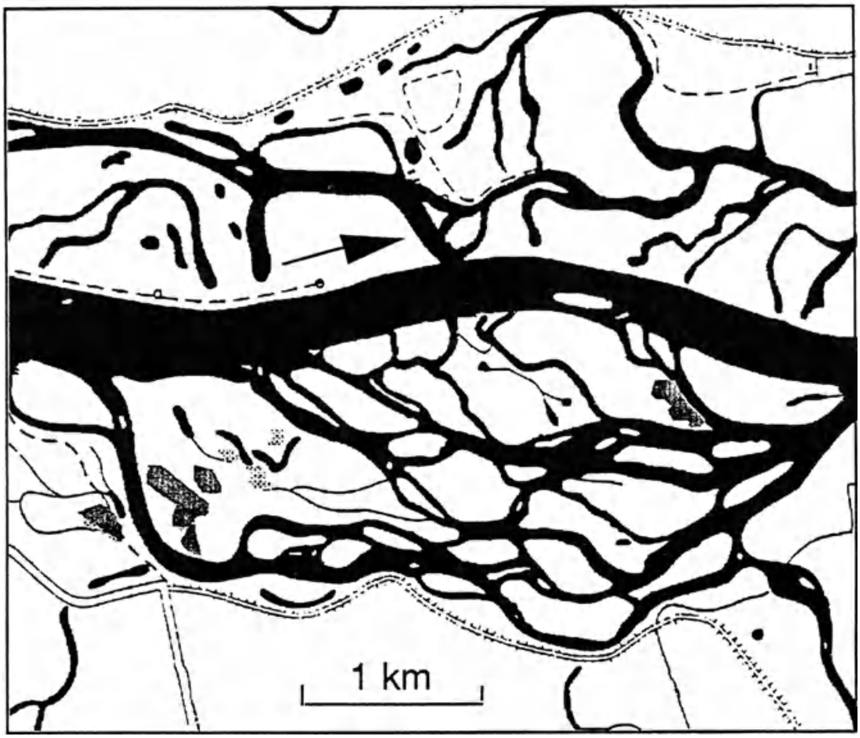

Figure 9.11 The River Danube at the Hungarian–Czechoslovak border: an example of a system consisting of interconnected linear forms.

9.4 CONNECTIVITY AND TEMPORAL VARIATIONS

The methods for exchange and interaction between units of the hydrosystem fluctuate not only in space but also in time. Temporal fluctuations, are above all determined by variations in the flow of the river, as well as by variations in levels of the water table. A rise in the level of a river places different surface units in connection by restoring water to old beds. Raising of the water table connects surface with underground units. The frequency with which these connections occur has important consequences for biological functioning both at the scale of the units concerned and at the scale of the hydrosystem as a whole.

9.4.1 CONNECTIVITY BETWEEN GROUNDWATER AND SURFACE WATER

Along a major upstream–downstream drainage axis a whole organization of water connections is established, providing an integral whole (Chapter 3).

Within the hydrosystem, flows within the alluvial aquifer are not uniform. The nesting of old alluvial terraces and lower terraces of recent alluvium gives rise to perched water tables. In the plain of the Rhône at St Fons to the south of Lyon, the water table, which is 15 m deep, flows in three very different layers – two highly permeable layers 5 m deep which flank a central layer which is a hundred times less permeable. Similarly, upstream of the confluence with the Isère, the permeability of the alluvial aquifer, which is estimated as 5×10^{-3} m s^{-1}, is higher than the permeability of the allluvium in the plains located further downstream, where the mean permeability coefficient has been measured at 3×10^{-1} m s^{-1} because the Isère is heavily laden with fine sediments (Creuze des Châtelliers, 1991).

There are two-way relationships between surface waters and groundwater, sometimes with an alteration of flows in time and also in space. Within aquifers there is hydraulic continuity, but the heterogeneous nature of the formations gives rise to zones of preferential flow which form a mosaic of subsystems with non-synchronous dynamics which are responsible for delays in exchanges. Nevertheless, underground ecosystems are dependent on surface ecosystems, and the essential transport of organic materials and minerals from epigeal production sites to hypogeal consumption sites. This allochthonous replenishment therefore depends on rhythms of vegetation growth, rhythms of component decomposition and of hydrological regime. Conversely an aquifer underlying a river and its alluvial plain influences the metabolism of surface aquatic, semi-aquatic and terrestrial ecosystems. Through its hydrological function the interstitial medium makes a quantitative contribution to the maintenance of wetland zones. Qualitatively it brings water which is frequently oligotrophic but sometimes very rich in nutrients (especially nitrates) to the surface. Groundwater also has an effect in the supply and development of surface environments by slowing down or accelerating ecological successions (Chapter 10). Through its role of retaining, storing and converting organic material it acts on the metabolism of surface waters. Finally it has a considerable part to play in the maintenance and dynamics of benthic populations (Table 9.1).

The heterogeneous framework within which surface and underground influences act has the result that the structures of interstitial communities (a mixture of the benthos and underground organisms) vary considerably from one site to another. Permanent populations of epigeal organisms live in the upper layer of the water table. This explains why the number of individuals and biomass in this zone is considerable. For example in the alluvial domain of minor Canadian watercourses. Williams and Hynes (1974) estimated the density of organisms in the subfluvial interstitial environment at between 185 000 and 800 000 individuals m^{-3}. In the Rhône, water and sediment samples obtained at -0.5 m in the

Table 9.1 Summary of the interactions between surface and groundwater units within the hydrosystem

Functioning of surface ecosystems	*Consequences for underground ecosystems*
• Primary production	Source of materials and energy
• Water flows	Supply of water to aquifers
• Flows of organic material	Spatial structuring and productivity
• Biotic flows	Colonization of the underground environment
• Natural disturbances	Increase in the complexity of functional systems, development of new structures (forms of resistance and protection)
Functioning of underground ecosystems	*Consequences for surface ecosystems*
• Water flows	Maintenance of water in aquatic ecosystems and waterlogging of the ground
• Physical and chemical flows	Source of nutrients (oligotrophication versus eutrophication, denitrification, slowing and acceleration of ecological successions)
• Zones in which organic materials are trapped	Recycling of materials
• Locations where aquatic organisms (benthos) are stored	Reservoir for life – diversification of ecological niches, maintenance of diversity
• Refuge areas in the event of hydraulic disturbances or surface pollution	Ecosystem resilience
• Compulsory living environments for some aquatic organisms (eggs and young stages of fish, insect larvae)	Species survival and maintenance of biodiversity

alluvium, at the interface between the substrate and the free water, can yield more than 700 000 individuals m^{-3}, essentially crustaceans. Species richness is also high. For example in the river alluvium there are 112 species, of which 99% are epigeal, in the inactive arms connected to the river there are 157 species, of which 80% are epigeal, and in the inactive arms which are disconnected from the river 107 species, of which 53% are epigeal (Dole, 1983). These examples emphasize the role of storing living matter, which benefits watercourses. Regardless of what the surface conditions may be, organisms can recolonize surface ecosystems at any time.

In addition to this, surface ecosystems are subjected to disturbances which give rise to changes in the structure of communities (richness, biomass and production). Rapid events taking place at the surface such

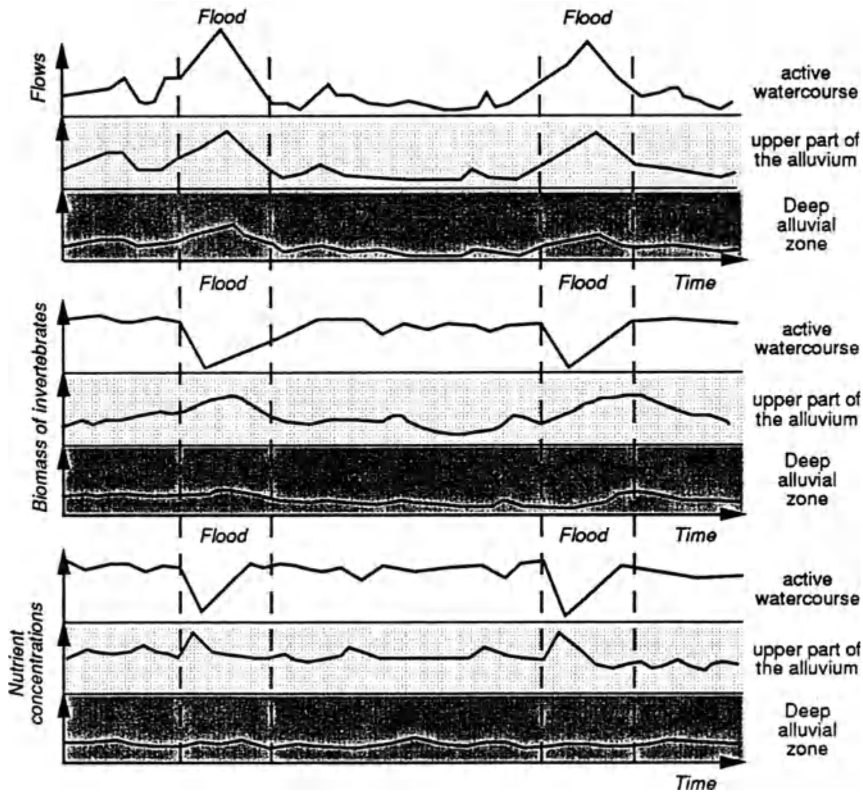

Figure 9.12 Dampening of surface fluctuations and regulating function of the alluvial aquifer.

as short period hydrological episodes (floods) or the sudden arrival of pollutants, are greatly dampened in the alluvial domain (Figure 9.12). Vertical movements of the benthos take place from the channel bed to the upper zones of the alluvial deposits. This temporary colonization of an environment for which the organisms are not adapted, is short lived; the refuge is abandoned after the disturbance has passed.

9.4.2 CONNECTIVITY BETWEEN SURFACE WATERS

From a functional point of view there appears to be complementarity between calm stagnant waters, which are the site of organic recycling and production, and flowing waters, which are the site of consumption and transfer (Figure 9.13).

The production of fish in a sector of the hydrosystem appears to be proportional to the quantity of calm or stagnant water in the cut-off channels in the sector. Thus, Richardson (1921) demonstrated that the fish biomass in the Illinois reached an average of 199 kg ha^{-1}, 146 kg ha^{-1} and 78 kg ha^{-1} in the sectors where the surface area of the cut-off channels represented 90%, 83% and 63% of the water surfaces, respectively. This is explained by the joint action of a number of phenomena.

Thus, the cut-off channels of the Danube, which are connected to the main course by their downstream ends, Vranovsky (1974, 1975) measured zooplankton biomasses of 6000–10 430 mg m^{-3} (fresh weight), 14–22 times more than that in the main channel. In a cut-off channel of the Danube which is only connected when water levels are high, the number of planktonic crustaceans is 200 times greater than in the main channel (Bothar, 1968). The difference in productivity also applies to fish: Holcik *et al.* (1981) estimate the mean biomass in the cut-off channels of the Danube in Czechoslovakia at 37 kg ha^{-1}, against only 35 kg ha^{-1} in the main river.

When abandoned channels are connected to a river at times of high water level, the organisms which are poor swimmers (plankton, some macroinvertebrates, alevins and juvenile stages of fish) may be carried away by the current, providing a food resource for organisms in the main river. Thus, in the Upper Mississippi the number of macroinvertebrates derived from cut-off channels is three to eight times higher than that measured in the main channel upstream of the connection (Eckblad *et al.*, 1984). On the Upper Rhône, Cellot and Bournaud (1988) have shown that a small increase in flow can carry off a large number of invertebrates from connected backwaters. For example, the number of *Asellus aquaticus* (a typical crustacean of calm stagnant waters) drifting in the river water increased by 379 times when the flow increased from 400 to 630 $m^3 s^{-1}$ (mean annual flow in this stretch is 450 $m^3 s^{-1}$).

In addition to the proportion of production which they transfer to the main channel through drifting, cut-off channels are used by fish in the river as areas for reproduction and feeding, and as refuges during natural disturbances (violent floods) or anthropogenic disturbances (accidental pollution)

Thus, Stankovic and Jankovic (1971) demonstrated a positive correlation between the annual number of days of flooding and fish biomass, for the main course of the Danube over 38 years (Figure 8.3).

The changes of flow in a river govern the magnitude of the exchanges between the various aquatic units of the hydrosystem. Because of this the hydrosystem functions in a pulsed manner, with a rhythm which is governed by hydrological oscillations, as illustrated in Figure 9.14. Thus, when the waters are low, nutrient salts which were introduced into the cut off channels during the previous period of high water are consumed by primary producers such as planktonic algae, which are thus able to

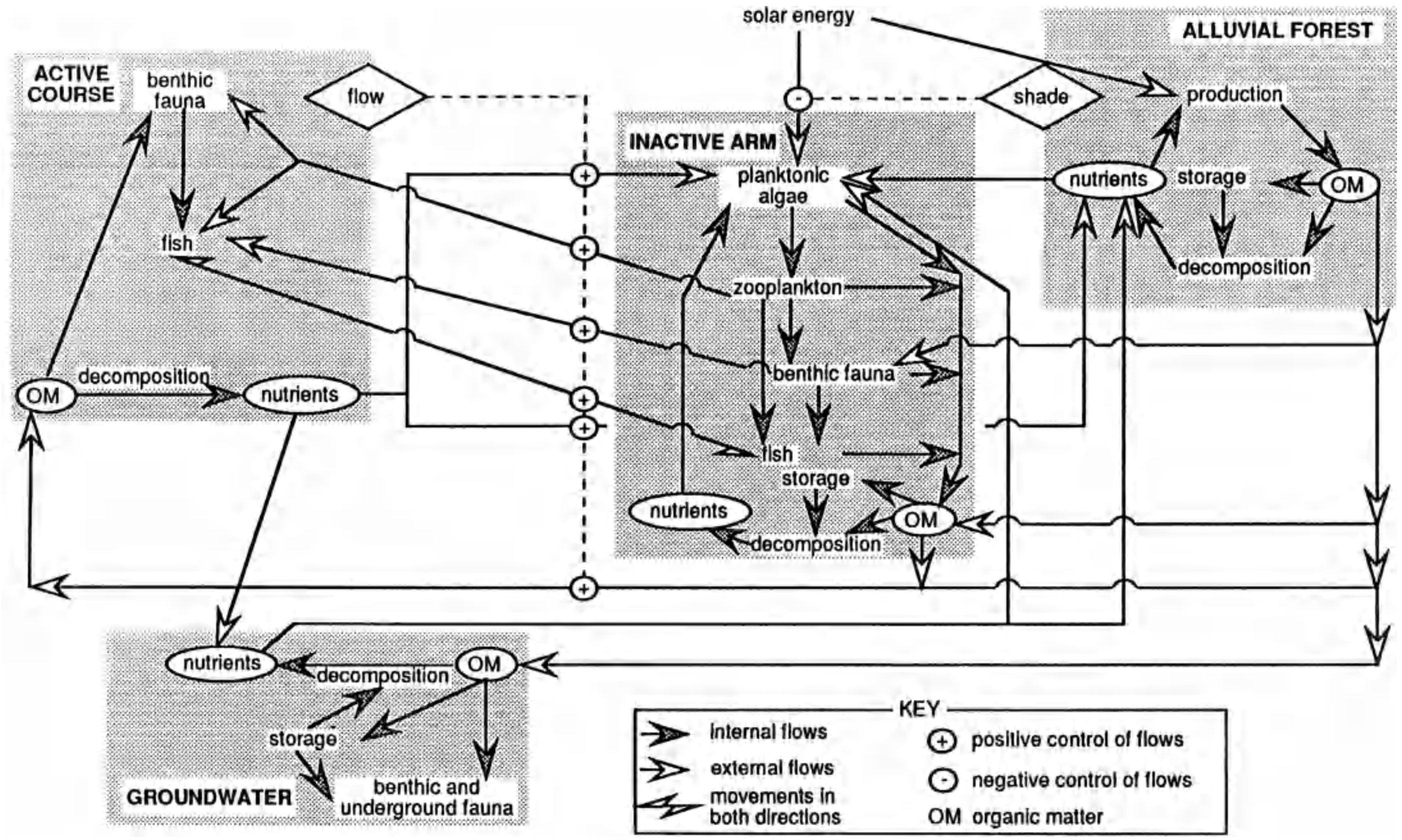

Figure 9.13 Examples of connections and exchanges between and within units of the fluvial hydrosystem; many interactions are not shown, such as exchanges of benthic fauna between the active watercourse and groundwater, or between inactive arms and groundwater.

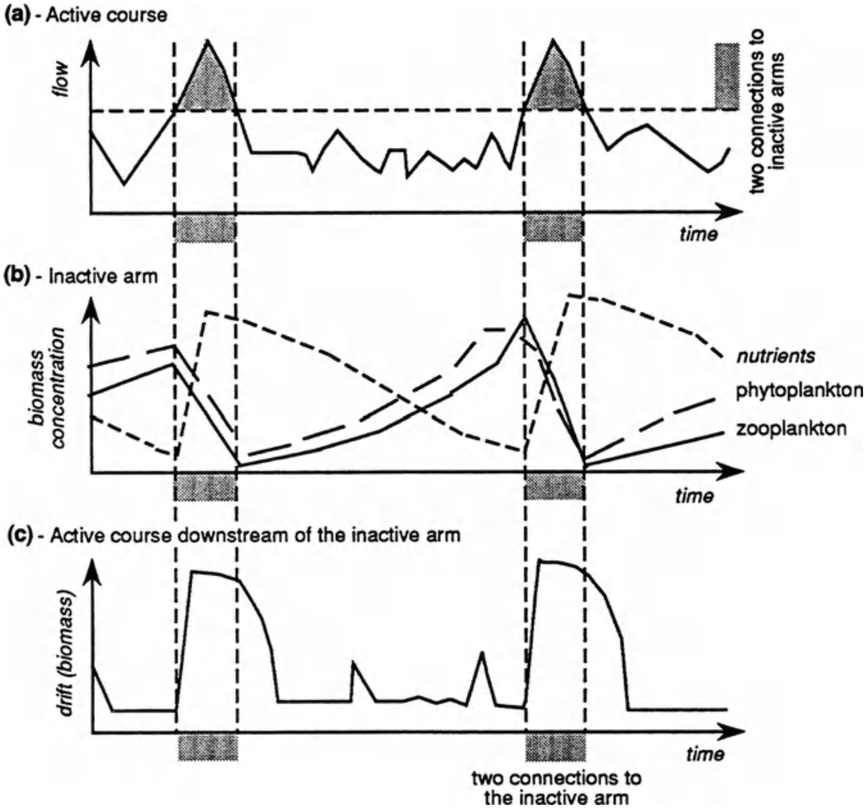

Figure 9.14 Relationships between the flow of the active course (a), fluctuations in concentration of nutrient salts, phytoplankton and zooplankton biomass, in inactive arms during and between phases of double connection (b), and fluctuations in the drifting biomass in the main channel (c) (see text).

increase their biomass (Figure 9.14). This biomass is in turn consumed by the zooplankton which feeds the other links in the food chain. When a flood occurs a large part of the biomass produced in the plain is carried into the main course, where it increases the amount of drifting biomass, a food resource for the fauna of the flowing water (Figure 9.14). At the same time flood waters can replenish the stock of nutrients in the aquatic environments of the plain, initiating another stage of intense production in these units.

If the interval between two floods is sufficiently long, several self-induced oscillations may occur. Zooplanktophagic animals (invertebrates, and above all, fish) apply predation pressure which causes a fall in the biomass of zooplankton (particularly in the case of large planktonic species, e.g. *Daphnia longispina*), which permits a further increase in the growth of phytoplankton biomass. The phenomenon appears to be much more complex if phytophilic or benthic macroinvertebrates are taken into consideration. In fact, although generation times for planktonic species are generally very much shorter than the time between two floods (a few hours to a few days for algae, up to a few weeks for crustaceans), this is not the case for macroinvertebrates, whose generation times are frequently of the order of magnitude or longer than the interval between floods. This being the case, the season in which a flood occurs and the interval between floods is of even greater importance (Chapter 7).

The time when the connection is made is particularly important for lotic fish which use associated environments in the hydrosystem for reproduction, as emphasized by Junk *et al.* (1989) when presenting the 'flood pulse concept'. Thus, when connections are established in spring, when the water temperature rises, fish can effectively use these connected environments in order to reproduce. Conversely, if high water levels occur too early, the temperatures are still too low to allow these species to reproduce (Chapter 8). The importance of the season in which the connections are established has also been revealed for vegetation on the plain. The flooding of terrestrial units in winter and early spring favours plant productivity by recharging the water reserves of the soil and the stock of nutrients before the spring resumption of growth (Gosselink *et al.*, 1978). Conversely, flooding during the growth season may have completely the opposite effect by drowning the rhizosphere during its period of activity (Dister, 1983).

Seperation and isolation of units during the low water period also has a part to play in the processes of organic matter decomposition. Some of the organic matter produced during the aquatic phase in land–water ecotones is exposed to oxygen in the air at relatively high temperatures, which appreciably intensifies the processes of mineralization. The nutrient salts released in this way then become available for a resumption of plant growth when high water levels return. This pulsed functioning also relates to exchanges between terrestrial and aquatic units. Dead leaves which accumulate in the terrestrial units of the hydrosphere in the autumn are stored *in situ* during the winter before being carried away by the spring floods. Thus, those leaves represent a very useful food resource for the aquatic communities as biological activity resumes. This time lag appears to be very important for large watercourses on alluvial plains, which have relatively little *in situ* storage capacity, unlike the small watercourses of the headwaters.

Over a longer time-scale more permanent changes in connectivity between surface waters may occur as a result of human interventions such as embanking. Thus, on the Missouri, by reducing the floodable surface area by 60%, civil engineering work has reduced fish production six-fold (Whitley and Campbell, 1974). Isolation of the water bodies on the plain causes an increase in the productivity of the stagnant-water flora and fauna which are no longer disturbed by floods. For example, on the Romanian floodplain of the Danube, Negrea and Negrea (1975) compared two water bodies, one of which had been artificially isolated from the main channel after an interval of ten years. In the isolated channel, the mean annual biomass of Cladoceran crustaceans increased 95 times (from 52 to 4904 mg m^{-3} whereas it only increased six times in the control water body which had only been subjected to the process of eutrophication. The considerable increase in biomass in the isolated environments is mainly due to the growth of aquatic vegetation and the proliferation of phytophilic species.

Natural processes can also reduce connectivity and bring about similar consequences. In fact the formation of alluvial plugs at the ends of inactive arms and the ecological succession which take place there tend to isolate old channels progressively from the main course. These changes, which take place on the scale of historical time (several decades or centuries), but in which some processes may prove to be reversible, will be the subject of the next chapter.

Ecological successions

10

C. Amoros and P. M. Wade

10.1 DEFINITIONS AND CONCEPTS

In the oxbow lakes formed by channel cut-off along meandering rivers, flowing waters become stagnant and then become invaded by submerged aquatic vegetation (hydrophytes), which is itself dominated and then replaced by emergent vegetation (helophytes). These helophyte communities, such as reed beds, will in turn be invaded by marshland shrubs, which themselves may be replaced by hygrophilic forest communities. Likewise, herbaceous plants will become established on a newly deposited sand bar, followed by shrub thickets, which will tend to eliminate them, and these will in turn be replaced by larger trees. Of course, these changes in vegetation are accompanied by changes in the conditions of the habitat (e.g. nature of the soil, water depth) and animal populations. This is a very general phenomenon known as ecological succession.

10.1.1 THE VARIOUS SUCCESSIONS

When a succession begins on a substratum which has never been occupied by a living community (e.g. newly bared rock or a sand bar which has just been deposited) it is described as a 'primary succession'. If the succession begins on a substrate which has previously been occupied by a living community it is called a 'secondary succession' (e.g. a succession occurring following a hurricane, a fire, ground clearance, abandoned cultivation, or a change in water levels). In this case the succession is

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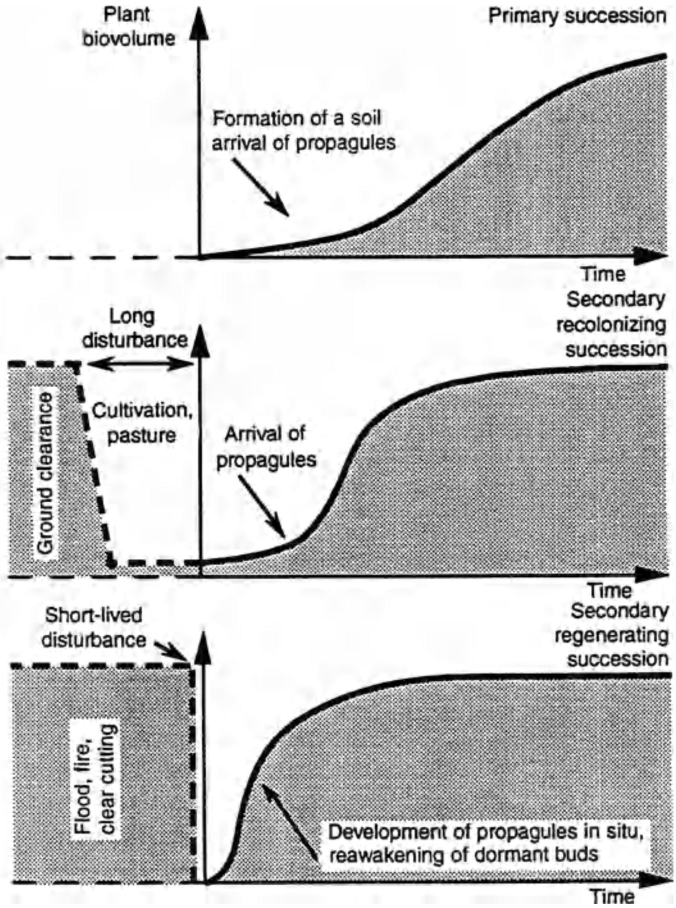

Figure 10.1 Comparison of the dynamics of different types of ecological succession (modified after Prodon, 1988).

generally more rapid, due to the presence of some organisms or their propagules and the existence of nutrients and organic matter.

A distinction may be made between two types of secondary successions (Figure 10.1):

- 'regeneration successions' which bring about very rapid reconstitution of the communities after a sudden short period of disturbance (e.g. a flood, fire, hurricane or clear cutting), which has not destroyed the propagules (e.g. seeds buried in the ground):
- 'recolonization successions' which develop rather more slowly after a longer-acting disturbance. Although the biotope remains favourable for plant and animal life, it is necessary to wait for the arrival of new

propagules, which may originate from sites some distance away. In this type of secondary succession, connectivity is an important factor (Chapter 9).

Any primary or secondary succession which is characterized by the enrichment and growth of living communities from abiotic stages (bare sediment, open water) through stages with low productivity (lichens, mosses, herbaceous formations, subaquatic plants) to more productive stages (marsh, forest) is called a 'progressive succession'. The increase in plant biovolume is a convenient way to assess the progress of such a succession.

A 'regressive succession' corresponds to development in the opposite direction, whether due to natural or artificial causes. For example, an increase in the mean water level following a change in river dynamics, a climatic change or human intervention drowns the marshy vegetation of an old channel and causes a return to a previous open water stage.

The stage which is achieved when the ecosystem becomes more favourable to the species *in situ* than to any other potentially dominant species is called the 'climax'. By definition the climax should be the final stage in an ecological succession, and remain relatively stable. The composition of climax communities should therefore only depend on climatic and edaphic conditions. However, this is not always the case, mainly because of the complexity of ecological successions, changes in biotopes due to natural factors or human activity, or again because of the scale of observation.

A distinction needs to be made between the ecological successions due to phenological changes and fluctuations in ecosystems (Van der Maarel, 1988):

- 'phenological changes' depend directly on seasonal cycles and thus show a regularity on an annual scale as distinct from cyclical succession in which the much longer and irregular stages are the result of completely different mechanisms.
- 'fluctations' are short-term, irregular and essentially quantitative changes due to population dynamics and/or medium or weak disturbances. Fluctuations are characterized by their random aspect and by the absence of any clear trend or direction in the changes.

The mechanisms involved in phenological cycles, like the mechanisms involved in fluctuations, interfere with the processes which govern ecological successions. Some, particularly major fluctations, may even deflect or change the direction of an ecological succession.

Other changes in the composition of the flora or fauna occur over the geological time-scale, or even over the scale of millennia, in connection with large-scale geomorphological changes or climatic changes (Chapter

1). Only changes which occur on the historical scale will be considered in this chapter.

10.1.2 THEORETICAL MODELS

Three theoretical models have been proposed by Connell and Slatyer (1977) to explain changes in the composition of communities.

1. 'Facilitation model': the species in a particular stage of the succession can only establish themselves if the environmental conditions have been altered by the species in the previous stage. In other words, by altering the environment, pioneer species help these vicarious species, in the succession to become established and develop, forming subsequent stages, and these species in turn alter the environment and so on. In doing so the species in any particular stage can make the environment unsuitable for their own reproduction. In most cases these species are eliminated by competition with the vicarious species of subsequent stages, which are themselves favoured by the new conditions in the environment.
2. 'Tolerance model': species of subsequent stages establish themselves independently of the species in the initial stages. The change in dominance within the community is explained by the growth of species: the later the stage in succession, the slower the growth (e.g. trees grow more slowly than grasses), and/or by the greater tolerance of these later species. This theoretical model assumes that the quantity of nutrients available diminishes over the course of time through consumption and storage in the biomass. The more tolerant a species is (the less exacting with regard to nutrients or less exacting with regard to light), the longer it can survive and therefore grow and dominate towards the end of the succession.
3. 'Inhibition model': the species in a given stage prevent the establishment and development of other species. The species in this stage disappear only as a result of disturbance, parasite attack or very intensive herbivory or again through senescence and death.

10.1.3 AUTOGENIC AND ALLOGENIC PROCESSES

The facilitation model applies very well to primary succession while the other two models are more applicable to secondary succession. In point of fact the processes involved in these three models very often act together, but in differing degrees which vary depending on the type of succession and sometimes even the course of one succession. In all three cases these mechanisms are intrinsic to the ecosystem, and are described as 'autogenic processes', the ecosystem bringing about its own transformation. Conversely some changes are caused by external factors which alter habitat conditions (e.g. the filling of a lateral arm by alluvial deposits or the drying out of a soil due to a fall in the average level of the water table). In such cases these are 'allogenic processes'.

The importance of these allogenic processes engendered by the dynamics of the river are reflected in ecological successions which are marked both by special populations and by relatively fast rates of evolution (e.g. the conversion of a water body into a terrestrial environment in only a few decades). On the other hand, in industrialized temperate regions the only situations where primary successions can still take place are alluvial plains with active dynamics, along with the retreating fronts of glaciers, areas affected by landslip and mudflows produced by volcanic eruptions.

10.2 MODES AND MECHANISMS

In temperate environments the final stages of successions are represented by forest communities. There are, however, very clear differences between these communities depending on whether these successions take place on islands or raised alluvial banks, or on old channels which are progressively filled.

10.2.1 SUCCESSIONS ON RAISED ALLUVIAL BANKS

(a) Case studies

Terrestrial successions, which are easy to observe because they begin rapidly once sand or silt bars are deposited, have been known for a long time. Thus Shelford (1954) described the plant successions on the bars and islands of the Mississippi, and on the bank levees:

- Dense thickets of *Salix interior* grow on recently deposited bare sand from seeds carried by the wind or water with *Populus deltoides* growing on the better drained soils. From their second and third years these willow thickets form an obstacle to water flow and thus encourage sand deposition and raise the bar.
- After about 15 years 2–3 m of sand and silt will have accumulated and *Salix interior* is then dominated by *Populus deltoides*. Among the other species in this plant grouping it will be noted that many creepers, are present, for example *Cynanchum laeve. Ampelopsis arborea. Brunnichia ovata* and *Ipomoea lacunosa.*
- Approximately 40 years after the start of the succession, *Acer negundo* becomes the dominant species with *Acer rubrum, Platanus occidentalis, Carya illinoensis, Ulmus americana, Robinia pseudoacacia, Celtis laevigata, Liquidambar styraciflua* and *Fraxinus pennsylvanica* germinating under

the shade of *Populus deltoides* in a soil which has become enriched in organic matter.

- After about 80 years the forest community is dominated by *Celtis laevigata* and *Liquidamber styraciflua*. Other associated species vary from site to site.
- Between approximately 200 and 300 years after the start of the succession, the forest communities become dominated by oaks (*Quercus*) and hickory (*Carya*).
- More than 400 years after the start of the succession, on levels located 12 m or more above the mean level of the water, a forest community containing tulip trees (*Liriodendron tulipifera*) and oak, accompanied by *Tilia heterophylla, Fagus gradifolia* and *Castanea dentata,* is observed.

Similar succession have been described for other hydrosystems. For central European watercourses Figure 9.4 provides a diagrammatical summary of the successions which occur on the Upper Rhône in France. On the Rhine, between Basle and Strasbourg, the softwood forest community which is dominated by *Salix alba* and *Populus nigra* lasts for 30 to 80 years (Carbiener and Schnitzler, 1990). After 100–150 years it is replaced by a community of *Populus alba, Ulmus minor, Alnus incana, Prunus padus, Fraxinus excelsior* and *Betula pendula*. The final hardwood stage is dominated by *Quercus robur, F. excelsior* and *U. minor,* individuals of which can live for 200–400 years in these alluvial forests.

The different descriptions of the sequences provided by the literature show differences but also common factors. An examination of these differences and constant factors makes it possible to understand the mechanisms involved in these ecological successions.

(b) Factors common to ecological successions in fluvial hydrosystems

(i) The herbaceous pioneer stage

By their rapid growth on pebble and gravel bars, herbaceous plants form an obstacle to water flow and thus encourage the deposition of fine sediments on which the woody species of subsequent stages can germinate (Figure 10.2). In addition to this the presence of leguminous plants such as *Glycyrrhiza lepidota, Amphicarpa bracteata* and *Vicia americana* in North America (Johnson *et al.*, 1976) or *Melilotus albus* in Europe (Pautou *et al.*, 1985) contribute to the enrichment of sand bars with mineral nitrogen as a result of their rhizobionts which fix atmospheric nitrogen.

All species in this stage and those of the following stage can tolerate not only periodic submersion but also relatively strong currents during floods.

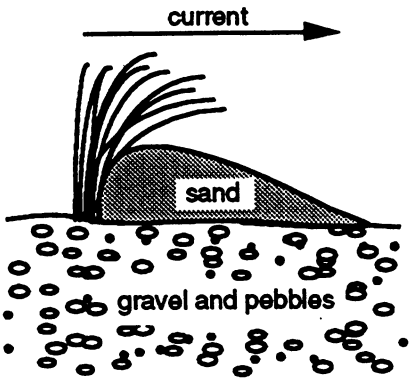

Figure 10.2 Establishment of herbaceous plants, e.g. *Phalaris arundinacea*, accelerates sand sedimentation and favours colonization by woody species.

(ii) The bush and shrub stage

The first woody plants which become established (e.g. *Salix alba* in Europe, *S. interior, S. amygdaloides* or *Populus sargentii* in North America) can only germinate on freshly deposited sediments. In addition to their tolerance to flooding, these species have pioneer features which are remarkably well adapted to the disturbances caused by river dynamics. They have the ability to grow adventitious roots from the entire lengths of their stems and trunks, and thus to resist burial when the soil level is raised. This is particularly important as this increase in level can reach an average of 16 cm year^{-1} during the first 10 years, for example the convex banks of the meanders of the Milk in Northern Montana (Bradley and Smith, 1986). By throwing out lateral shoots these bushes and shrubs can also grow even if they are felled and buried by a flood. Conversely, their inability to grow under shade and their relatively short lives (30–50 years) limit their presence to the initial stages of successions.

The difference between these pioneering species, which by throwing out lateral shoots can rapidly colonize horizontal space, and the species of subsequent stages such as *Populus deltoides* and *Betula nigra,* which produce vertical shoots from the stump when they are damaged by floods (Barnes, 1985), should be noted.

In addition to this high capacity for regeneration, these pioneering woody species are easily disseminated when fragments are broken off by floods and carried off by the current.

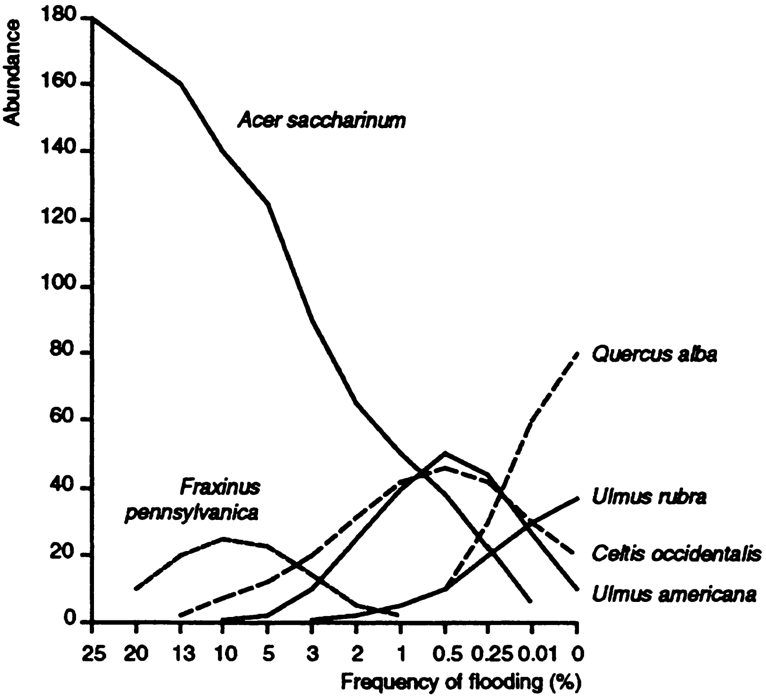

Figure 10.3 Distribution and abundance of the main tree species of the succession on raised alluvial ground on the Sangamon River (Illinois) as a function of flood frequency (adapted after Bell, 1980).

(iii) The tree stage

Whereas the pioneering stages rely on the occurrence of autogenic processes such as the competition for light which prevents a species perpetuating itself, the progress of subsequent stages is essentially dependent on allogenic processes such as raising of the soil surface by sand and silt as a result of flood deposits. These processes are themselves accentuated by positive feedback loops (in that the existence of woody plants slows down flows and encourages further sedimentation). Species then become established on the basis of their biological characteristics, that is their tolerance of flooding, the depth of their roots and their requirements in relation to soil texture. A direct consequence of the raising of the soil surface with respect to the mean water level is a reduction in liability to flooding making it possible for species which are less tolerant to floods to become established (Figure 10.3). Raising the soil surface also increased the distance between the surface of the ground and the mean level of the water table (Figure 9.4). Finally, raising of the ground level is accompanied by a fall in the mean particle size of the deposits (Chapter 5). This refinement in soil texture compensates to some extent for the increase in the distance between ground level and the water table as a result of water being raised up by capillarity. This reduces the number of hydrophilic species and increases the number of mesophilic species, and in particular woody species.

(iv) The rate of succession

When the dynamics of the river are not subject to change, i.e. when the overall functioning of the hydrosystem remains stable, the rate of succession decreases and the life of each stage is prolonged. This decrease is due to both physical and biological factors.

A reduction of the likelihood of flooding tends to reduce the sediment flows which enter the stretch of river under consideration, and thus the rate of rise of the ground surface is slowed. This therefore is a purely physical negative feedback loop.

There are two biological causes. One is the fact that the herbaceous species of pioneering stages have a shorter lifetime than the woody species of the first stages such as willows (*Salix*) which themselves live for a shorter time than the hardwood trees of the latter stages such as ash (*Fraxinus*) or oak (*Quercus*). Also, as we have seen previously, the woody species of the first and intermediate stages are incapable of germinating under shade, unlike the species of the latter stages. The duration of these earlier stages thus corresponds to the lifetime of one generation of the woody species of which they are made up. Conversely several generations of a given species may follow each other during the last stages of these succession.

(v) Complicating the structure of communities

The increase in the number of woody species during succession (on the Rhône there is a change from four species at the *Salix alba* stage to more than 50 species in the later hardwood stages (Figure 9.4) is accompanied by the development of many herbaceous or woody creepers (on the Rhine: *Gallium aparine. Solanum dulcamara, Tamus communis, Humulus lupulus, Clematis vitalba, Hedera helix* some of which grow to 35 m (Carbiener and Schnitzler, 1990)). (For the Mississippi see section 10.2.1(a).) During the latter stages the horizontal heterogeneity resulting from the increase in species diversity is combined with vertical heterogeneity (e.g. woodland bordering the Rhine) due to such components as the woody creepers to form an extremely complex spatial structure (Figure 10.4).

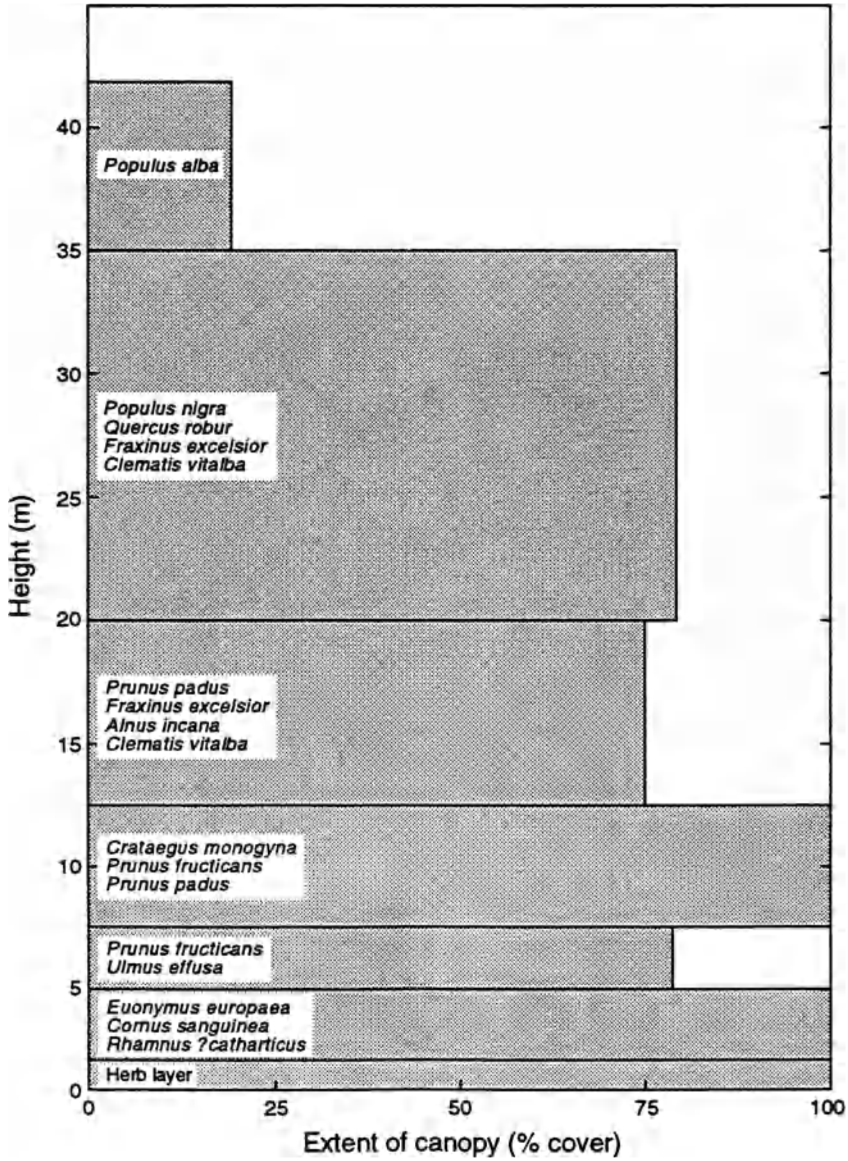

Figure 10.4 Structural complexity of an alluvial forest on the Rhine at the oak–elm stage (adapted from Walter, 1979).

(vi) Increase in overall biomass

The great productivity of riparian ecosystems, with their aerated soils which are well provided with nutrients and water (Chapter 9), is reflected in a great increase in the overall biomass during succession. For example, on the Upper Rhône in France plant biomass in the pioneering stages dominated by *Phalaris arundinacea* lie between 7 and 10 t ha^{-1} of dry matter, those of the intermediate stages dominated by *Salix* vary from 30 to 50 t ha^{-1} and those of the last *Quercus* and *Fraxinus* stages reach 350 to400 t ha^{-1} (Pautou and Décamps, 1985).

(c) Differences between ecological successions in fluvial hydrosystems

(i) The biogeography of vicarious species

The major cause of the differences which appear on the intracontinental and intercontinental scales are associated with the areas of geographical distribution of the species concerned. Some of the different vicarious species of three genera found in Europe and North America are shown in Table 10.1.

Table 10.1 Examples of vicarious species (modified after Pautou and Décamps , 1985)

North America (North East)	Europe
Alnus rugosa	*A. glutinosa*
Ulmus americana	*U. minor* (*U. laevis* in Central Europe, *U. procera* in Great Britain)
Acer saccharinum	*A. pseudoplatanus*
Fraxinus pennysylvanica (Central and East USA) *F. nigra* (North East USA and Canada)	*F. excelsior* (*F. pannonica* in Central Europe, *F. oxyphylla* in Southern Europe)

(ii) Nature and texture of the soils

Within one biogeographical zone local conditions such as chemical composition (calcium content, pH) or particle size of the alluvium can give rise to the differences in species composition during similar stages of the succession. Thus in western Europe, depending on the watercourses, the following may be found among the woody plants of the first stages: *Salix elaeagnos* on gravelly soils, *S. purpurea* on sandy soils, *S. alba* and *S. viminalis* on sandy–silty soils, and *S. triandra* on silty soils (Pautou and Décamps, 1985).

Differences between the upstream and downstream reaches may appear within a single watercourse related to the increasing fineness of sediments in the downstream direction (Table 10.2). The decrease in particle size is reflected by a reduction in the porosity of the soil which gives rise to an increase in waterlogging.

Similar changes may be found within one watercourse not only along a longitudinal gradient but also along a transverse gradient from the bank levees to the immediate proximity of the active channel, including marginal depressions where alluvial deposits are finer and soils are more waterlogged (Chapter 5). The conditions in these depressions are very frequently accompanied by enrichment in organic matter, although it can be very difficult to distinguish the intermediate and final stages of terrestrial successions originating in these depressions from the final stages of some successions which originate in old channels.

Table 10.2 Differences in the species composition of communities in the succession on raised alluvial ground on the Rhine (after Carbiener and Schnitzler, 1990).

Upstream	Downstream
Alnus incana	*Alnus glutinosa*
Poplus alba	*Poplus tremula*, *Poplus x rubens*
Salix alba	*Salix fragilis*, *Salix x rubens*
Carex acutiformis	*Carex gracilis*
High species richness	Low species richness
(60 woody species)	(30 woody species)
Complex structure (5–6 layers)	Simple structure (3–4 layers)
Creepers very abundant	Creepers rare

10.2.2 SUCCESSIONS IN OLD CHANNELS

(a) Two types of successional sequences

There are two types of sequences which correspond to the two extreme types of channels, meandering channels and braided channels (Chapter 5). However, as we will see from an analysis of the mechanisms involved in their succession, there are also intermediate forms.

(i) Successions in cut off meandering channels

This type of succession takes place not only in old meanders *sensu stricto* but also in old anastomosing channels which have similar morphometric characteristics. These are large deep water bodies, formed in relatively flat areas, which after abandonment are located away from the axis of main flow. They are locally described as lakes, pools or backwaters (oxbow lakes in English, *Altwasser* in German). These open and well-insolated environments tend to be well provided with nutrients encouraging relatively rapid and substantial plant growth.

Closure of their upstream ends by a deposit of alluvium allows planktonic communities to develop. This is the open water stage during which submerged macrophytes (for example, Stoneworts (Characeans), various species of narrow leaved *Potamogeton* and *Myriophyllum*) appear in the shallower areas. Helophytes begin to gain a hold on the edges, more particularly on convex banks of shallow slope.

The next stage is marked by a proliferation of hydrophytes which invade the entire water body. In addition to the submerged macrophytes mentioned above, several floating leaved species become rooted in the fine sediments (for example, *Nuphar lutea, Nymphaea alba, Potamogeton natans* and *Trapa natans*) or float freely on the surface (for example, *Hydrocharis* and duckweed). Submerged plants without roots are also found at this stage (for example *Ceratophyllum* and *Utricularia*). Starting from the edges, the floating-leaved vegetation progressively covers the entire water surface whereas the zone of helophytes around the edges becomes broader.

After a century or more the helophyte communities have completely invaded the old meander, transforming it into a marsh. Eutrophication and the subsequent accumulation of organic matter in the sediments is reflected in the development of plant groupings belonging to *Caricetum elatae* and/or *Scirpeto–Phragmitetum*. Peaty soils are colonized by groupings containing *Cladium*.

These marshes are in turn invaded by shrubby formations which in Central European hydrosystems are dominated by *Salix cinerea*, whereas Van der Valk and Bliss (1971) mention *S. bebbiana, S. lutea* and *Betula pumila* in Alberta. These shrubby formations are succeeded by communities of trees on waterlogged soils which are flooded for the greater part of the year, dominated by *Alnus glutinosa* in Europe, *Populus balsamifera* in Western Canada (Van der Valk and Bliss, 1971) and *Alnus rugosa* in Eastern Canada (Tessier *et al.*, 1981). As conversion to dry land proceeds over a number of centuries hardwood species like ash (*Fraxinus excelsior*) become predominant in Central European hydrosystems.

(ii) Successions in cut off braided channels

These are environments through which water continues to flow at a low rate even after alluvial plug has been formed at the upstream end of the former channel, because of their slope (Chapter 5). The rate of flow depends on the effectiveness of the alluvial plug and the amount of groundwater input.

The succession begins with typically a very short open water phase during which the plankton never achieve the abundance observed in old meander channels. The main reasons for this are the relative narrowness of the braided arms, and therefore the reduction of phytoplankton productivity due to shading by adjacent woodland (Chapter 6), as well as the semilotic nature of these environments (weak currents and frequent incursions of river water due to overflow over the alluvial plug).

Submerged macrophytes, among which the Characeans dominate, appear very rapidly. A community which incorporates *Potamogeton coloratus* is established in the cut off braided arms of pre-Alpine watercourses which are fed essentially by oligotrophic calcium bicarbonate-rich groundwater (Kohler and Schiele, 1985; Carbiener *et al.*, 1990, Bornette and Amoros, 1991). The constancy of the flow and its origin explain the fact that these old arms are described as phreatic rivers (*Brunnenwasser* in German-speaking countries).

The degree of eutrophication in these old channels is reflected in the communities of submerged macrophytes. The joint presence of the submerged forms of *Berula erecta* and *Mentha aquatica* indicates the mesotrophic stage, with a community containing *Callitriche* appearing during the meso-eutrophic stage. The eutrophic stage is characterized by *Zanichellia palustris, Potamogeton densus* and *Ranunculus trichophyllus*. Finally, when the succession proceeds to a highly eutrophic stage the lotic stretches of these channels are colonized by *Ranunculus fluitans* and the lentic stretches by *Potamogeton pectinatus* and *Oenanthe fluviatilis*.

Conversion to dry land by groups of helophytes dominated by *Phalaris arundinacea, Myosotis scorpioides, Rorippa amphibia* and various species of *Rumex* starts from the banks upstream, followed by downstream alluvial plugs, and bars deposited during floods. The helophyte groupings are in turn replaced by shrubby formations dominated by either *Salix cinerea* accompanied by the moss *Acrocladium cuspidatum* where the soil is sufficiently rich in organic matter, or by *Salix alba* if the inputs of sand and silt remain considerable. The terrestrial wooded community which then becomes established is dominated by *Ulmus minor* accompanied by *Crataegus monogyna* and other mesophyllic species.

The time required for these successions is highly variable (from several decades to more than a century), because it depends not only on the initial conditions (for example, depth and width), but also on the magnitude of the various allogenic processes which may be involved. The successions in old braided arms differ from those in old meander channels not only in their associations of flora (Table 10.3) and fauna (Chapters 7 and 8), but also in the nature and magnitude of the processes involved.

(b) The processes

Comparison of the two types of successions, i.e. in cut off meandering and braided channels, indicates the mechanisms which are involved in the transformation of biotopes and ecosystems.

Table 10.3 Successions in cut off meandering and braided channels

Old meandering channels	Old braided channels
• Open water • Very abundant plankton • Submerged macrophytes: *Characea*, *Potamogeton*, *Myriophyllum* • Floating-leaved macrophytes: extensive cover of *Nuphar*, *Potamogeton natans*, *Trapa natans*, *Hydrocharis* • Emergent macrophytes: *Typha*, *Phragmites*, *Scirpus*, *Carex* • Shrubby formation: *Salix cinerea*[a] • Wood formation: *Alnus glutinosa*[a]	• Open water • Low abundance of plankton • Submerged macrophytes: *Characea*, *Potamogeton coloratus*[a] • *Berula erecta*,[a] *Mentha aquatica*[a] • *Callitriche*, *Ranunculus*, *Elodea*, *Potamogeton lucens* • Floating-leaved macrophytes: sparse cover of *Callitriche*, *Ranunculus* • Emergent macrophytes: *Phalaris arundinacea*, *Myosotis*, *Rumex* • Shrubby formation: *Salix alba*[a] or *S. cinerea*[a] • Wood formation: *Ulmus minor*,[a] *Crataegus monogyna*[a]

[a] In central European hydrosystems.

(i) Abandonment by the active course

The transformation from a lotic environment (flowing water) to a lentic environment (calm or stagnant water) is the result of natural hydrogeomorphological processes such as lateral wandering of the active course (Chapter 5), or the effects of human intervention such as embanking or course straightening (Chapter 11). Given the differences in sinuosity and gradient, change occurs quickly when a meander is cut off, while the transition is very much more progressive in the case of the upstream isolation of a braided arm through the formation of an alluvial plug. In the latter case the functioning of the first stages in the succession is marked by an alternation of periods of still water and running water. The latter occurs whenever the level of the river rises above the alluvial plug.

(ii) Colonization

In addition to the methods of dispersal which are common to all ecological systems, transport of plant fragments by water and their subsequent natural propagation represents a particularly frequent form of colonization in fluvial hydrosystems, for both aquatic plants and the terrestrial plants of the first stages of successions on new deposits of sediments. As the effects of connectivity on the processes of dissemination and colonization have been described in Chapter 9, we will restrict ourselves here to an examination of other factors which encourage or limit the establishment of plant species in old channels.

The growth of planktonic algae is encouraged by the absence of current. These conditions are at an optimum in old meanders at the start of a succession, whereas in old braided arms they are restricted to episodes of low water levels during which the alluvial plug completely obstructs the upstream end.

Given the amount of light which is required for germination and then for development of the young plants, colonization by aquatic macrophytes is limited by water depth and turbidity. This limit of colonization has been observed to range from 2 m on the Pembina River in Alberta (Van der Valk and Bliss, 1971), through 2.50 m on the old beds of the Rhine (Donselaar *et al.*, 1961; Philippi, 1978) to 3 m on the Hungarian Danube (Rath, 1979). In the old channel beds of the Rhône it varies between 1.5 and 3 m (Balocco-Castella, 1988). Turbidity is proportional to the abundance of phytoplankton and the concentration of suspended matter. The abundance of phytoplankton depends, in turn, on the concentrations of nutrients and insolation, in addition to the current speed. As for the suspended materials, these essentially have their origin in incursion of river water. In some cases episodic lateral inputs due to run off from adjacent land or resuspension by the action of winds over very large meanders such as those of the Mississippi (Dorris, 1958), can contribute to increasing turbidity. A combination of these various factors results in slower colonization by macrophytes in old meanders having a greater initial depth than in the old braided arms of the same river, which are shallower and not shaded by adjacent woodland. Conversely, once the macrophytes have become established, productivity is generally lower in old braided arms as a result of shading, disturbances by floods, and the input of oligotrophic or mesotrophic groundwater (Chapter 6).

(iii) Competition

In cut off channels, as on the alluvial plain, competition between plant species is generally concerned with the occupation of space in both its horizontal and vertical dimensions. Occupation of the vertical space and the resulting shading governs competition for light energy. Thus when microscopic phytoplankton are not very abundant submerged hydrophytes can receive sufficient light for growth. As soon as the reduction in depth permits floating-leaved plants to become established and proliferate, the latter form a surface layer which considerably reduces the amount of light energy which can penetrate into the water, and which results in a rarefaction of the phytoplankton and disappearance of submerged hydrophytes, with the exception of a few species which do not have exacting light energy requirements such as *Ceratophyllum demersum*.

A similar process leads to the elimination of floating-leaved hydrophytes through the growth of helophytes (e.g. *Phragmites* and *Typha*) which are in turn eliminated by shading from shrubby willows (*Salix cinerea*), which themselves give way to trees (*Alnus glutinosa*). This vertical extension of the plant communities is accompanied, at least in the aquatic phase, by rapid horizontal extension due to the vegetative reproduction of hydrophytes and helophytes (e.g. growth of rhizomes and stolons). The effectiveness of these competitive capacities is sometimes revealed by the establishment of virtually monospecific communities (e.g. *Nuphar lutea, Phragmites australis* or *Cladium mariscus*).

A variant on the two types of succession described above may result from successful competition for light by algae in the initial stages. High concentrations of nutrients can cause a great proliferation of filamentous and planktonic algae which because of their very short generation times, typically, in the order of a few hours can considerably reduce the transparency of the water before hydrophytes, and in particular plants with floating leaves, have the time to develop. In shallow environments filamentous algae can grow abundantly on the helophytes as they grow up through the water and obstruct their development. This absence of macrophytes due to hypereutrophication, which is well-known in lakes (Phillips *et al.*, 1978; Lachavanne, 1985; Pieczynska, 1990) has been seen in the old fluvial channels of the Rhine (Van der Brink *et al.*, 1991) and the Danube (Vranovsky, 1991).

Allogenic processes, such as medium level disturbances caused by floods can interact with the autogenic process of competition. When floods reduce population densities, by breaking down or tearing up plants they greatly decrease the intensity of competition and thus prevent the least competitive species from being eliminated. In extreme cases, floods can clear some parts of the bottom of former channels, creating empty spaces which can be colonized by new species whose propagules are transported by the flood waters. This explains the greater floral and faunal variety and diversity in old braided arms, which are frequently disturbed, than in old meanders. The increase in diversity as a result of medium levels of disturbance (Connell, 1978; Ward and Stanford, 1983) has recently been incorporated in the general ecological theory of patch dynamics (the patch dynamic concept: Pickett and White, 1985; Townsend, 1989). The effect of major disturbance, and in particular the initiation of regressive successions, will be described later on.

(iv) Evapotranspiration

In addition to competition for light, the development of floating-leaved communities, and then helophytes, shrubs and finally trees, is accompanied by an exponential increase in evapotranspiration, which is proportional to the increase in leaf volume exposed to the air. This evapotranspiration is greater when the plants in question have at least their roots in a waterlogged soil and are thus without stomatic regulation. In experimental tanks evapotranspiration by helophytes in summer is 2–3 times greater during the day than the evaporation from an identical surface of open water (Hutchinson, 1975). Hutchinson also reports that in reed beds in Germany, the intensity of transpiration by *Phragmites australis* in late summer is seven times greater than evaporation.

The consequence of this increase in evapotranspiration is reflected in a marked lowering of the water level during the growing season, which encourages the spread of littoral species, and therefore later successional stages, to the deeper parts occupied by species belonging to the earlier stages. Given the competitive advantages with respect to light of the vicarious species in a given stage with respect to the species of the previous stage, all these phenomena create a positive feedback loop which results in acceleration of the succession towards dry land.

(v) Nutrient inputs

Inputs of nutrients from the main channel which can be important in maintaining the productivity of a given stage in the succession process, depend on connections between the cut off channels and the main course (Chapter 9). There seems to be no net difference in relation to the geomorphological type of the old channels, except for the frequency of connections, which is often greater in the case of cut off braided arms.

It should not be forgotten that very high inputs of nutrient salts can alter the progression of successions through the rapid growth of filamentous and planktonic algae, which out-compete the aquatic macrophytes.

(vi) Eutrophication

Eutrophication occurs due to the accumulation of biomass by perennial species and detritus in old channels. The accumulation of nutrients in the large deep water bodies of meanders away from the main axis of flows (Chapter 6) enables a substantial breeding to occur over time. Conversely, in old braided arms, scouring during floods removes a large part of the biomass produced, and limits plant production by breaking or tearing up macrophytes. Also, in old braided arms, alluvial deposition accelerates conversion to dry land, which may be completed before eutrophication occurs.

(vii) Alluvial sedimentation

We have seen previously (Chapter 5) that the amount of alluvial deposition depends on the functional sector, the morphology of the former channel, its location with respect to the main course (distance and angle), and any obstacles to flow such as the existence of log jams or wooded stretches (Chapter 9). As a general rule old braided arms with low sinuosity receive more fluvial sediments than cut-off meanders, even though the latter are located close to the main course. In fact the flows which enter old meanders usually travel along a trajectory which forms an acute angle with respect to the axis of the active course. By thus suddenly changing direction the flows lose a great deal of their speed and thus their alluvial load as soon as they leave the normal active bed, giving rise to the formation of alluvial plugs at the ends of these old meanders. In some cases old braided arms may also receive small amounts of alluvium if they are far from the main course following a major change in the latter, or if obstacles such as a wooded bank or an embankment prevent direct inflows from upstream. Apart from the latter, by receiving more alluvium than old meanders, cut off braided arms become dry land faster. The presence of vegetation in an old channel increases alluvial deposition by slowing down the current, and thus accelerates the process of raising the bed which in turn encourages further colonization by plants. This is a positive feedback load associated with both an autogenous process, vegetation growth, and an allogenous process, the deposition of alluvium.

Dams which are located upstream hold back sediments and as a consequence bring about a general reduction in the amount of alluvial deposition in old channels (Chapter 11). Conversely, an increase in erosion in the catchment area increases the alluvial load of watercourses and thus the amount of alluvial deposition.

(Viii) Groundwater inputs

Inputs of groundwater containing low concentrations of nutrients and of relatively low temperature during the summer season restrict the productivity of cut off channels. If the inputs exceed water losses due to seepage or evapotranspiration, a drainage channel is maintained downstream, with a consequent export of some nutrients from the old channel. Thus the ecological succession in an old channel may be slowed down in relation to the amount of groundwater which it receives and/or its quality (temperature and nutrient concentrations). A lowering of the main bed and a corresponding fall in the water table conversely result in an accelerated conversion to dry land. A similar effect occurs when levels are lowered by pumping (Chapter 11).

The accumulation of organic matter which occurs in the bottom of old channels during succession progressively reduces outward seepage of groundwater. This again is a positive feedback loop because this reduction in nutrient loss supports plant productivity and stagnation of the water, and thus the further accumulation of organic matter.

(ix) Scouring by floods

The location of braided arms close to the main course and their relatively straight nature makes them subject to more frequent and more intensive scouring by flood water than old meanders. Depending on its intensity, this scouring may carry off some or all of the plants and animals in the old channel. It may even strip the bed and remove accumulated organic matter. Depopulation of the old channel, together with stripping, 'rejuvenates' the old channel by causing a regressive succession which can return it right back to the open water stage. Scouring by floods may also destroy the alluvial plug upstream of a braided arm, and thus wholly reconnect it to the main course. In this case the old inactive arm again becomes a secondary arm of flowing water.

The recurrence of these disturbances and the resulting alternation of progressive and regressive successions in old braided channels is known as 'oscillating successions'. In this case conversion to dry land depends essentially on the deposition of river alluvium and changes in habitat conditions caused by the river dynamics.

(x) Interactions between processes

Mechanisms do not act in isolation, but interact, sometimes forming feedback loops. A summary diagram (Figure 10.5), even a simplified one, reveals the complexity of the reactions which govern the direction and the rate of successions. The strength of the parameters, the relative intensities of the different processes and the nature of the populations which succeed each other (Table 10.3) have made it possible to put forward two models of successions (Bravard *et al.*, 1987b).

(c) Two models and their variations

Ecological successions in braided arms are essentially determined by allogenic processes, even though the latter are sometimes modulated by autogenous processes. The intensity of these allogenic processes depends above all on the active dynamics of the river (the amount of alluvial deposition or erosion, the frequency and vigour of scouring by floods) or its inheritance (porosity of the alluvia governing the input of groundwater). The magnitude of these processes, combined with the

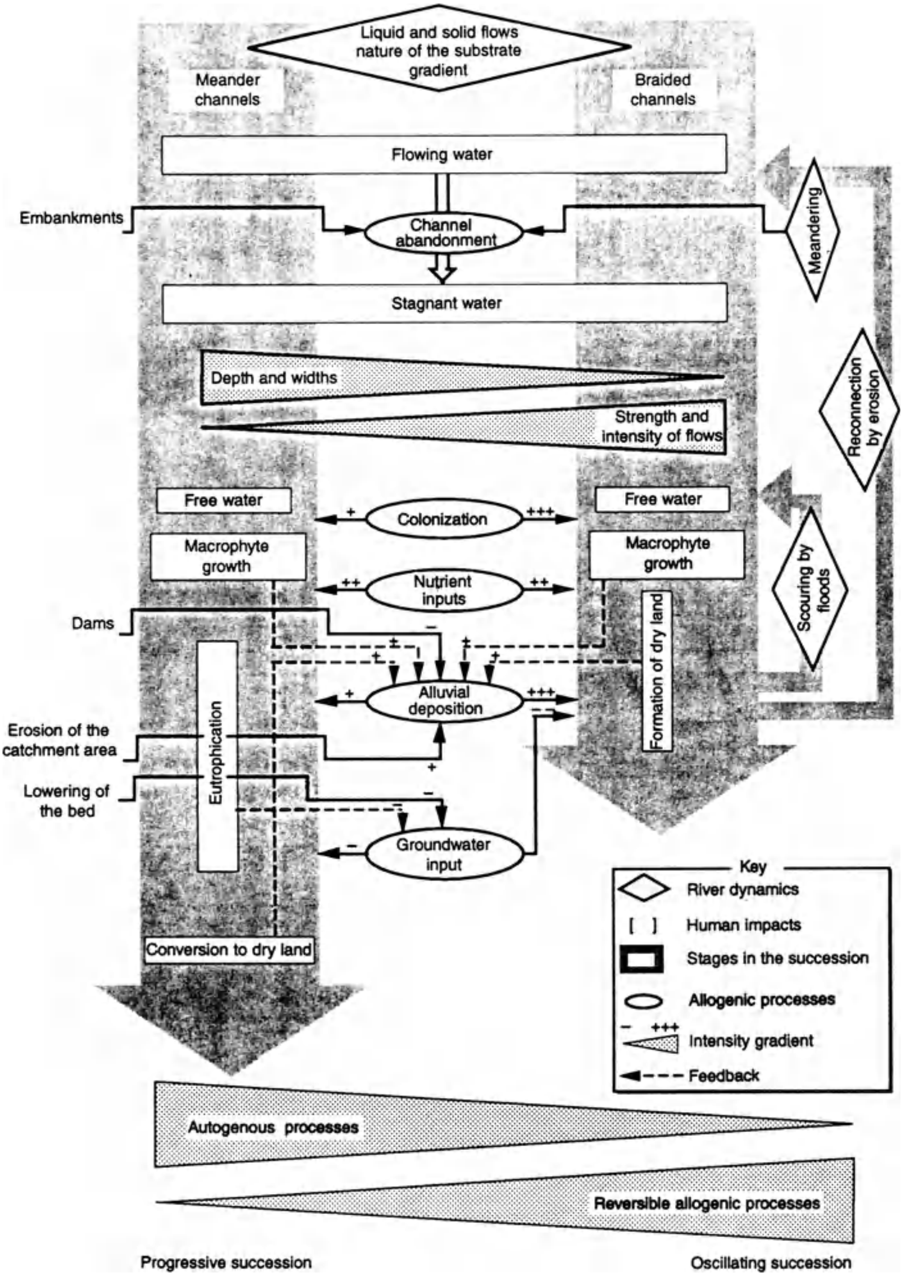

Figure 10.5 Simplified model of succession in old meanders versus braided channels (the processes of river dynamics are explained in Chapter 5); actual cases lie between these two extremes depending on the relative activity of autogenous versus allogenic processes.

generally shallower depth in braided arms, results in ecological successions taking place relatively faster in these arms than in old meander channels. Thus on the Upper Rhône, for example, old braided arms isolated from the active course at the end of the 19th century or early in the 20th century had, by 1980, been converted into helophyte marshes (*Phalaris arundinacea*) or even wooded terrestrial environments (*Ulmus minor, Crataegus monogyna*) (Bravard *et al.*, 1986). These allogenic processes have, however, proved to be reversible, because the kinetic energy of the river, which is the origin of the alluvial deposits, is equally able to remove them and cause regressive successions. The alternation of progressive and regressive phases results in an oscillating succession.

Conversely, in old meanders, which are more sinuous and further from the main course, floods cause less disturbance (Carrel and Juget, 1987) and succession generally take place progressively. The deposition of alluvium of fluvial origin is generally small. The succession towards the formation of dry land is essentially determined by autogenic processes and succession through to a terrestrial state requires a very much longer time than in the case of old braided arms. On the Upper Rhône, for example, downstream from the braided arms mentioned above, meanders abandoned in the 18th century still include water bodies occupied by submerged and floating-leaved hydrophytes (*Myriophyllo–Nupharetum*), with a maximum depth of 1–2 m (Balocco-Castella, 1988).

These two models of succession correspond to two highly characteristic and extreme situations. However, given that autogenic processes always coexist with allogenic processes, and frequently interact with them, intermediate situations can be seen resulting from either the spatial position of the biotypes in question, changes in river dynamics, or human intervention.

Transitional zones can appear at the hydrosystems scale between braided sections and meandering sections (e.g. the Rhine downstream from Rastatt), in which the morphology of the old channels and the hydrogeomorphological functioning of the section show intermediate characteristics. Within a given section, old meanders may be at a variety of distances from the active course and may thus be subjected to allogenic processes to a greater or lesser extent. It is worthwhile remembering the distinction, among old meanders, between those which have been formed by neck cut off, and those which have been cut off by overflow (Chapter 5). In the latter case the angle between the axis of the old bed and the axis of the active course is relatively small (Figure 5.7), which encourages penetration by flows of fluvial origin and as a consequence increases the importance of allogenic processes. Successions of this type have been described for old meanders in the lower course of the Ain, in France (Castella and Amoros, 1986).

The balance between autogenic and allogenic processes can also change as a result of changes in the hydrogeomorphological functioning of the hydrosystem which are caused by changes in the river (Chapter 5).

The effects of human activities (Chapter 11) can also alter the relationship between the two categories of process. Thus flood protection dykes completely isolate old braided arms and considerably reduce the role of the allogenic processes. Some examples of old isolated braided arms which are developing essentially under the effect of autogenic processes can be observed on the right bank of the Rhine in the Taubergiessen area. The retention of sediments by upstream dams reduces sediment flows and thus alluvial deposition in old channels. Conversely, this process could be increased by a resurgence of erosion in the catchment basin as the result of, for example, ground clearance. Finally, the effects of dredging watercourses and the consequent lowering of the water table on ecological successions will be described in greater detail in Chapter 11.

10.2.3 SUCCESSIONS IN GROUND WATER ENVIRONMENTS

This topic has received very little attention up to now. Nevertheless, preliminary results suggest that in parallel with the changes which affect the surface ecosystems of old channels after their abandonment by the active course, hypogeal ecosystems also undergo changes.

(a) Synchronous comparisons

In an alluvial plain of the Upper Rhône in France, which is subject to flooding, a comparison was made of samples taken from a depth of 0.5 and 1 m in the gravel banks of an active channel with those from beneath the old water-filled beds of braided arms isolated at the upstream end between 1800 and 1940 (Dole, 1983; Marmonier *et al.*, 1992). It was found that the percentage of stygobiont taxa increases in relation to the length of the isolation period, whereas the total number of taxa remains relatively constant. The proportion of subterranean species increases further still with increase in distance from the active course and increase in the age of the channels studied so long as they are rarely disturbed by floods. It will be noted that strict phreatobionts appear under these circumstances. This replacement of epigeal and stygophilic species by stygobionts which are increasingly dependent on a deep aquifer appears to be due to:

1. The reduced seepage of surface water due to the progressive clogging of the bottom of old beds through the accumulation of organic matter, which increases the thermal and chemical stability of interstitial waters.
2. The increase in the physical stability of the sediments which as a

result of the growth of aquatic vegetation and woodland on the banks, become increasingly protected from reworking by floods.

(b) Diachronous changes

(i) Eutrophication successions

Changes in underground communities have also been demonstrated by following the populations at a given station for a number of years (Richoux and Reygrobellet, 1985; Marmonier, 1988). The samples were obtained over a seven-year period from beneath an old gravel pit located in an alluvial plain of the Upper Rhône which was relatively well-protected from floods. As the old gravel pit became invaded by vegetation and a layer of several centimetres of organic matter covered the bottom, it was found that, as far as populations of ostracods living in the interstitial environment were concerned, certain species persisted, for example, *Pseudocandona triquetra* whereas *Pseudocandona albicans*, a species frequent in oligotrophic springs, was progressively replaced by *Cypridopsis vidua* a species abundant in the interstitial waters underlying inactive arms heavily colonized by aquatic vegetation, reflecting the eutrophication of the site investigated.

(ii) Regeneration successions

Dole-Olivier and Marmonier (1992) monitored the re-establishment of underground aquatic communities over several months in gravel banks in an active channel on the Upper Rhône down to a depth of 2 m, after their disturbance by floods. The vertical distribution of organisms living in the first metre of alluvium are strongly altered by flooding. Beyond that the populations appeared to be more or less stable. Immediately after the disturbance the interstitial environments were colonized by epigeal organisms (*Gammarus, Chironomidae* larvae), whereas hypogeal animals, driven out by the flood, were only represented very infrequently by rare individuals. During subsequent weeks the abundance of the epigeal organisms decreased, and some then regained the surface of the fluvial sediments. At the same time the stygobiont fauna recolonized the interstitial environments. The most ubiquitous species (e.g. *Niphargus rhenorhodanensis*) were the first to reappear, the more exacting ones (e.g. *Salentinella*) regained their maximum abundance more than a month after the flood.

The changes in the interstitial environment induced by the flood, such as increased circulation of water in the interstices of the alluvium, inputs of fine sediments, organic matter and well-oxygenated water, made the environment susceptible to colonization by the epigeal fauna. Progressive return to the conditions which preceded the disturbance explains the sequence of the regeneration succession.

Dole-Olivier and Marmonier (1992) also demonstrated a variation in response which depends on the magnitude of the disturbance, the season during which it occurs and the length of time separating it from the previous disturbance. This variability is comparable to that of regeneration successions of lotic ecosystems.

10.2.4 SUCCESSIONS IN A LOTIC ENVIRONMENT

In order to attempt to clarify a debate which is still current, a distinction must be made for the changes which occur over the course of time at a given site, and what Margalef (1960) called the 'longitudinal succession', that is the upstream–downstream zonation of a watercourse as a whole.

(a) Successions at a given site

Most of the data available relate to investigations of the regeneration of communities after natural or artificial disturbance of a watercourse, for example, a very large flood, drying out, dredging or the spread of toxic substances. A more or less rapid return to the initial condition is observed, reflecting a dynamic equilibrium with environmental factors which appear to exert fairly strong constraints on any further development of any succession. Return to this initial condition of dynamic equilibrium is revealed by the clearly asymptotic shape of graphs measuring the re-establishment of communities (Fisher, 1983). The re-establishment time varies from a few weeks to a few years, depending on the magnitude of the disturbance, the generation times for the taxa affected, and their potential for recolonization. For example, an algal population of diatomaceans can be restored in a few weeks. A fish population will require several years if it is relatively isolated, or only a few weeks if it is closely connected to other ecosystems of the same type. However, all the species which follow each other during the course of the re-establishment stage remain characteristic of frequently disturbed ecosystems.

Less severe disturbances may interfere with biotic interactions and give rise to alternations of dominant species. Thus Dawson *et al.* (1978) have observed cyclical oscillations between two dominant plant species in an English river, the Bere Stream. *Ranunculus calcareus* is a submerged species which is dominant in winter and spring, but whose growth makes it possible for *Nasturtium officinalis* to become established. The latter, an emergent species, proliferates, becomes dominant during the summer and eliminates *R. calcareus* by shading it out. The autumn floods sweep away *N. officinalis*, which permits recolonization by *R. calcareus*

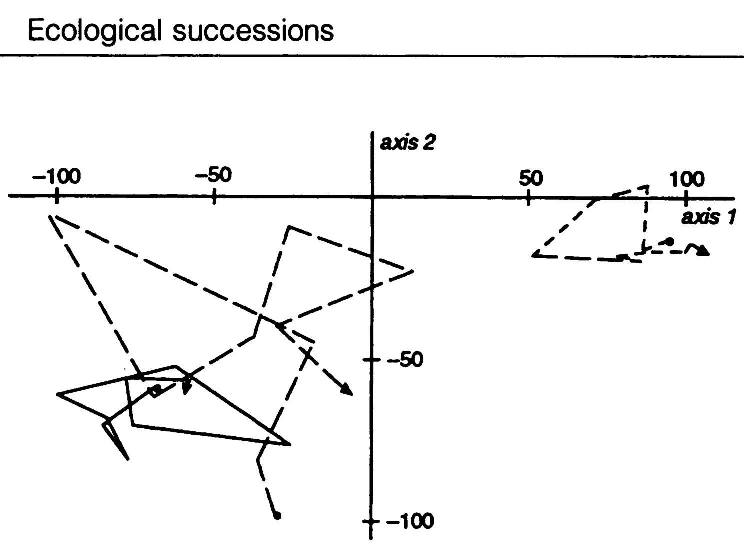

Figure 10.6 Example of dynamic equilibrium in a lotic environment. Factor chart of data for aquatic vegetation assessed annually for the years between 1978 and 1988 at three different sites along the Delme River (Northern Germany). The first axis of the canonical analysis of correspondences expresses the position of the sites along the river, the second axis expresses the variation in disturbance (after Wiegleb *et al.*, 1989).

from the root stocks which persisted in the river bed where current speeds remained higher than average.

In more slowly flowing rivers, in the plains of Northern Germany, Wiegleb *et al.* (1989) describe a more diverse vegetation, but one which remains on the whole stable over a 10-year period despite major fluctuations from one year to the next in the abundance of individual species. No preferred direction appears in the changes in species dominance over this period, despite the constant input of propagules from upstream or tributaries, and the presence of empty spaces. This could be due to the fact that the total vegetation cover rarely exceeds 70% (Figure 10.6).

In mountain torrents where floods do not cause any change in an ecosystem adapted to violent currents and very strong shear forces, the ecosystem must be regarded as constituting the climax because the communities in place are not susceptible to replacement by other communities (Fisher, 1983). Nevertheless, the same ecosystem in a less stressful environment would be regarded as a pioneer ecosystem. Dawson *et al.* (1978) propose to apply the concept of cycloclimax to the alternation of *Ranunclus calcareus* and *Nasturtium officinalis*, which appears to be relatively stable. In both cases the perception applies to a restricted spatial and temporal frame. If this frame is extended to the hydrosystem the successions in lotic environments can be regarded as truncated successions, maintained at relatively juvenile stages by a constant flow of kinetic energy, that is running water. The greater the flow of kinetic

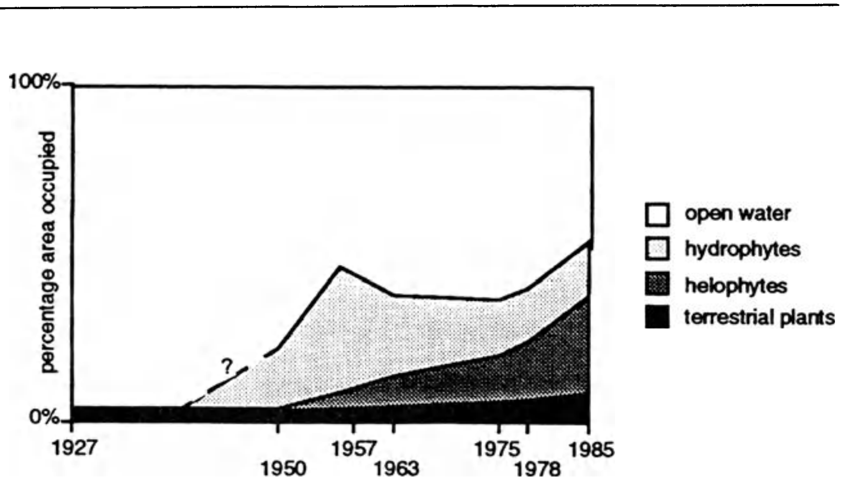

Figure 10.7 Example of an essentially allogenic succession over 296 ha of the left bank of reserve 19 on the Upper Mississippi after the construction of the Keokuk dam in 1913. The average annual sedimentation rate has been 50 mm year^{-1} since 1946 (after data by Bhowmick and Adams, 1989).

energy passing through the ecosystem, the more it will be held at a juvenile stage, marked by pioneering communities and weak biotic interactions. The extreme situation is represented by algal communities which are limited to diatomaceans attached to rocks, the only stable substratum in torrents. Increasing the energy flow during a flood causes 'rejuvenation' of the ecosystem. A decrease in this flow of energy, or its stoppage, by cutting off and abandoning the loop of a meander for example, allows the succession to continue, that is old channel succession. Human activities can also alter these energy flows bringing about ecological successions in a lotic environment (Figure 10.7 and Chapter 11).

(b) Ecological succession in the water mass and longitudinal zonation

The concept of ecological succession can be applied to a water mass moving down a river system. The organic matter produced in the headwaters of a river changes over time as it flows downstream, invertebrate shredders reducing the coarse particulate matter into smaller-sized particles which can be used downsteam by scavenging invertebrates. Aquatic macro- and microphytes take up nutrients from the water mass and there are also small organisms (fungi, algae and macroinvertebrates of the potamoplankton) which complete their entire life cycle within the moving mass of water. Although this river continuum is generally considered as a spatial zonation (Vannote *et al.*, 1980) given that most of the biota are fixed, e.g. epilithic algal communities, rooted macrophytes and benthic invertebrates, its interpretation as a succession may stimulate the development and direction of novel research and promote discussion Margalef, 1960; Odum 1969; Naiman and Sedell 1980; Fisher, 1983.

10.3 STABILITY AND DIFFERENT SPATIAL AND TEMPORAL SCALES

So far we have concentrated on the functional unit within ecological succession. What actually happens in the hydrosystem to the components of different hierarchical levels over the course of time? In order to examine these hierarchical levels of the hydrosystem the succession process needs to be viewed at different spatial and temporal scales.

10.3.1 CHANGING THE SCALES

At the scale of the individual organism, during a decade instability at the species level may be observed with every living organism dying through senescence, disease, predation, or by destruction following a disturbance. Moving to a higher level of organization, that of the functional unit during the same period of time, e.g. a fenland community dominated by helophytes (*Phragmites*, *Carex*) it can be said that there is some stability. Certainly some parameters of the environment, such as the water level, will undergo fluctuations during this period of time, but it is precisely these fluctuations which provide the constraints and select the species present, thus ensuring the stability observed.

Conversely, if the period of observation is increased up to the scale of, for example, a century while retaining the same spatial scale (Table 10.4), colonization of the fenland by bushes and sometimes even its conversion into a forest unit will be observed. At this time-scale the functional unit appears to be unstable because of the progress of ecological succession.

If the spatial scale is widened to consider the functional sector but keeping to the same time-scale, i.e. a century, we will observe an overall stability. Whereas the units of the old channels become converted into

Table 10.4 The degree of stability in relation to the scale of spatial and temporal changes

Spatial	Dynamics	Time-scale
Individual	Unstable	Decade
Functional unit	Stable	
	Unstable	Century
Sector	Stable	

land and those units which are being raised by alluvium become more mesophilic, the process of fluvial dynamics (erosion, lateral wandering by channels, sedimentation) excavates new beds, cuts off and abandons old beds, deposits alluvium and builds new bars or islands, and thus begins new sequences of ecological successions at other points in that sector of the hydrosystem. In other words, to use anthropomorphic language, the fluvial dynamics compensate for the 'ageing' of units, 'giving birth' to new ones. At any one time different stages of succession (pioneer, intermediate, mature) can be found within a given sector. This remains true as long as the hydrogeomorphological functioning of the hydrosystem remains stable. Changes in fluvial dynamics or fluvial metamorphosis (Chapter 5) giving rise to new types of successions or, on the contrary, failing to renew others by causing certain types of habitats to appear or disappear can be observed on the scale of millennia and for the hydosystem as a whole.

10.3.2. THE ROLE OF DISTURBANCE AND THE REVERSIBILITY OF PROCESSES

At the spatial scale of functional units, autogenic successional processes (e.g. competition for light and the build-up of organic material) prove to be irreversible because the successions generated by such processes can only regress under the action of different processes initiated by the injection of a large quantity of external energy in the form of a disturbance (e.g. destruction of the tree layer, complete stripping of soil horizons or accumulated organic matter in the bottom of an old channel). Conversely, allogenic successional processes (e.g. the deposition of alluvium) prove to be reversible. The kinetic energy of a watercourse which gives rise to sedimentation can also give rise to erosion. As a consequence, successions which are controlled by allogenic processes can have a pattern of the oscillating type, as long as the interactions with autogenic processes remain weak. This ensures relative stability at the scale of the functional unit solely through the interplay of reversible processes.

At the sector scale, the reversibility of processes and therefore the renewal of successions depends on changes in the fluvial dynamics at the scale of centuries or millennia (Chapter 5). Constant active dynamics ensure maximum reversibility. A trend to raise the alluvial floor seems to retain relative reversibility, whereas a tendency for the bed to cut down appears in our present state of knowledge to be irreversible. Human activities can interfere with fluvial dynamics and reduce the reversibility of processes (Chapter 11).

10.3.3 IMPLICATIONS OF PHASE DIFFERENCES IN SUCCESSIONS

(a) Perpetuation of communities

One of the consequences of this spatial–temporal dynamic within a given sector of the hydrosystem is the simultaneous presence of communities corresponding to all stages in different ecological successions within that sector. This means that a species from one patch of habitat can always find similar habitat conditions which are suitable for it in some other part of the sector and can therefore perpetuate itself despite continuing changes in ecosystems. The result of this is maximum floral and faunal diversity which is greater than the diversity of the succession climax stages alone. Here again there is a relationship between disturbance and diversity, incorporated in the concept of patch dynamics, which was introduced when investigating competition at the level of functional units in old channels. All these successional subsystems which are out of phase with each other but are all necessary for the functioning of the system at a regional scale and for perpetuating species and communities are known as a metaclimax (Blondel, 1986).

In the context of research applied to the ecological management of hydrosystems, Bravard *et al.* (1986) placed emphasis on the spatial nature of the concept in a heterogeneous space, and its applications. They describe the organization in space of a functional sector and all its functional units at various stages of succession as a 'spaciosequence'. This spatial organization might simply depend on the topography, in which case it would be described as a toposequence (zonation of units as a function of the elevation of the ground or the depth of water). In general, at the scale of a functional sector the configuration is more complex and reflects the juxtaposition or even the overlapping of several fluvial forms. It is here that the practical advantage of the concept lies. Identification of the units of a spatial sequence on the ground or on an ecological map makes it possible to set boundaries to the space in which the hydrogeomorphological processes have functioned or are still functioning. For example, in a braided–anastomosing sector of the Upper Rhône in France, before engaging in hydroelectric works the territory occupied by units of the succession in old anastomosing channels can be used to identify and set boundaries to a space of relative stability where ecosystems have greater homeostasis, develop more slowly and will better resist disturbances than ecosystems in the spatial sequences of the braided belt.

(b) Maintenance of functional heterogeneity

The coexistence and juxtaposition of various stages of different successions maintains a diversity of communities and habitats, which are marked by special forms of functioning (Chapters 6, 7 and 8). This makes it possible to maintain the functional complementarity of the pieces in the hydrosystem patchwork (Chapter 9).

(c) Maintenance of connectivity

The progress of each succession causes a reduction in local connectivity (Chapter 9). For example the formation and overgrowing of alluvial plugs reduces the connectivity between old channels and the active course. The clogging of old beds by accumulated organic matter reduces the connectivity between surface water and groundwater. The raising of islands and banks and the resulting increases in the distance between the ground surface and the water table reduces connectivity between bank woodland and groundwater. It is therefore pioneering and juvenile stages which have maximum connectivity, and it is these stages which generally are the shortest lived. Rejuvenation and renewal of successions is therefore essential in order to maintain connectivity between the various parts of the patchwork on the scale of functional sectors.

By changing the composition of populations and some habitat characteristics the progress of successions contributes to the generation of the hydrosystem patchwork and its dynamics, amplifying the diversity brought about by the hydrogeomorphological processes of the fluvial dynamics. However, if there were no renewal of sequences, in the long term there would be a fall in biodiversity as all sequences reached their final stages. The disturbances experienced by functional units following floods or as a result of river dynamics are therefore necessary in order to maintain the dynamics of the pieces of the patchwork. Although the direct impacts of human activities are relatively visible, their indirect impacts are often neglected. These include modification or stopping fluvial dynamics and threatening the renewal of successions and therefore diversity, the functional complementarity of its units and their connectivity. These would occur over the medium to long term, and in places which are sometimes far from the intervention.

Human impacts on fluvial hydrosystems

11

J.-P. Bravard and G. E. Petts

For thousands of years rivers have been altered by many forms of human activity. Deliberate changes of fluvial hydrosystems have resulted from the power of technology to satisfy the many demands upon water resources. River regulation by dams for domestic and industrial water supply and for irrigation, which today often include intercatchment transfers, and for flood control has markedly altered the flows, sediment loads and water quality characteristics of many rivers (Petts, 1984). Channelization for navigation and land reclamation has further altered the ecological character of fluvial hydrosystems by isolating the channel from its floodplain (Brookes, 1988). These direct impacts have been compounded by indirect impacts associated with the range of land-use changes that have altered the catchment areas over the period of human occupation – several thousand years in some cases.

11.1 CATCHMENT SCALE IMPACTS

11.1.1 CATCHMENT LAND-USE CHANGES

Deforestation for pastoral and then agricultural purposes significantly affected catchments throughout Europe during the Neolithic, about 3000 years ago. The accelerated erosion which followed led to increased sediment yields and induced a sequence of river channel changes (Gregory, 1987; Gregory *et al.*, 1987; Starkel *et al.*, 1991). The case of Northern Greece may be used to illustrate the difficulty of investigating these changes in the Mediterranean environment. Pollen research has detected

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increased human pressure between 4500 and 3100 BP, perhaps associated with invasion by Eurasian pastoralists and the Dorians. The oak forest, which was established in the early Holocene, retreated giving way to open forms of vegetation. In theory such a change in the landscape causes an increase in the amount of run-off, accelerated slope erosion and thus massive inputs of sediments into rivers. In fact, lagoon shore environments record a significant increase in deposition from 3200 BP in Macedonia and 2900 BP in Thessaly. Although we know little about the climate history, the ash (*Fraxinus excelsior*), which grows on deep alluvial soils, retreated giving way to the plain tree (*Platanus orientalis*) which, today, characterizes the beds of Balkan torrents with pebbly bedloads. One possible explanation lies in the combination of increased anthropogenic erosion but a change in the seasonal distribution of rainfall with drier summer months (Bottema, 1982) may also have been influential.

The alluvial plains of major rivers in Northern Europe have preserved in the sedimentary record more evidence of geomorphological adjustments associated with catchment changes. For example, there is evidence of channel changes during the Iron Age (8th–5th centuries BC) and the Little Ice Age (15th century–19th century). Human activities in catchment areas, usually associated with increased sediment yields together with climatic deterioration caused major channel changes: typically, channels with a single incised bed changing to a braided style. Climatic variations may have been particularly important in triggering change in an environment in which human activity had lowered resistance thresholds (Neboit, 1983). Certainly, human activity is likely to have accelerated the geomorpholoical response. Major progress has been made in reconstructing changes in fluvial hydrosystems over historic time-scales (Petts *et al.*, 1989b) but isolation of human impacts from climate-induced changes, remains problematic. One of the classic scientific debates in Europe has focused on the role of land clearance by peasant farmers in the catastrophic floods of the 19th century, particularly those of 1840 and 1856 in alpine France. Many consider the impact of ground clearance may have been overestimated.

The links between cause and effect are very much clearer when recent events benefit from quantitative observations. Thus, in the wooded mountain catchments of the Pacific Northwest in the United States which are intensively worked by clear-cut logging served by specially constructed road systems (Maser and Sedell, 1994). Landslips can provide up to 85% of the total sediment yields to streams in some basins. These are carried downstream by debris flows. Masses of blocks and coarse woody debris accumulate in the channels where they may be stored for long periods. These processes are present under natural conditions, but are exacerbated by human activity including some forms of forest management. One measure to mitigate such impacts, the maintenance of narrow wooded corridors or buffer strips along channels during felling, is gaining popularity.

Despite global concern for deforestation at the present time, in many areas major impacts on rivers are not apparent. For example, deforestation has affected less than 5% of the territory of the Peruvian Amazonia and Rondonia, and at present there is no evidence that the hydrology has been disturbed (Sternberg, 1987). Furthermore, with only local exceptions, accelerated erosion is no longer a feature of European mountain chains. In the French Alps, the policy of restoring mountain environments was begun as early as 1860. Torrent correction works, supplementing reafforestation, had the effect of holding back an increasing proportion of coarse materials, thus making a contribution to the fluvial readjustment which is a feature of the 20th century, namely the progressive disappearance of braiding in Alpine valleys and the subsequent simplification of the river patchwork.

11.1.2 THE IMPACTS OF LARGE-SCALE URBANIZATION

In many countries, this century has been marked by the spontaneous or planned development and the growth of new towns in rural environments. The first impacts of urban development involve road construction and earthworks which increase the intensity and frequency of floods, causing channel erosion and enlargement. The creation of impermeable surfaces might affect channels when it exceeds 5% of the catchment area and can cause substantial changes when it exceeds 30% (Morisawa and Laflure, 1979). However, the mobilization of sediments on slopes and erosion of the channel bed and banks increases the volume of the load being transported downstream where problems of sedimentation may be encountered.

11.1.3 WATER POLLUTION

Pollution problems attract a great deal of attention. In a river like the Rhine, which is regarded as a typical watercourse in an industrialized catchment, the CO_2 pressure in the water is 20 times higher than in the atmosphere, reflecting the very high activity of the processes decomposing organic matter of domestic and industrial origin (Kempe *et al.*, 1991).

Diffuse pollution sources create major problems by contaminating both surface water and groundwater. Surplus fertilizer and toxic substances (herbicides, pesticides) originate from agricultural areas, whereas urban or industrialized areas provide heavy metals and hydrocarbons (Chapter 3). In addition to this, all forms of disturbance in the catchment, such as deforestation, cultivation, grazing and construction, when not correctly managed can increase runoff and thus increase pollution. A characteristic feature of developing societies – and many developed ones before the implementation of controls – is high phosphate loads in rivers. For example, the annual phosphate load in the Rhine at Lobith in 1978 was 25 000 t year^{-1} (P-PO_4) (Kempe *et al.*, 1991).

Major accidental pollution incidents can have catastrophic effects on watercourses. In November 1986 a wave of very heavy pollution swept down the Rhine following firefighting operations at the Sandoz works in Basle, which resulted in the spillage of insecticides and fungicides. The ecological impact of this accident was observed right down to the delta of the river, 800 km from the source of pollution. The dramatic consequences of exceptional events should not, however, obscure less serious but much more frequent accidents which can produce more serious effects in the medium and long term. In the catchments of the Severn and Trent (UK), 4200 incidents of accidental pollution were recorded in 1986 and 1987 (Brewin and Martin, 1988). Accidents of this kind are due to failures in monitoring systems at discharge points, leaks, spills, or even the deliberate disposal of industrial, domestic or agricultural waste.

It is tempting to attribute the pollution of watercourses in the temperate zone to the growth of human activities in the second half of the 20th century. In fact, the effects of recent changes are superimposed on a long history of progressive deterioration brought about by changes in catchment areas, civil engineering works and the increasing use of water resources. In general, major water quality deterioration problems have occurred in the following order, faecal pollution, organic pollution, dissolved salts, metals, eutrophication, organic micropollutants and finally acidification (Meybeck and Helmer, 1989). The historical heritage of pollution is found in the high heavy metal concentrations in sediments in the beds of some watercourses (Thomas, 1987) and flood plains (Macklin and Klimek, 1992). Although pollution of small watercourses had been mentioned from the middle of the 17th century, severe pollution problems in European rivers, which reached their height in the years 1960–1970, began around 1850.

11.2 DIRECT IMPACTS ON RIVER BEDS

11.2.1 THE REMOVAL OF DEAD WOOD

At the present time watercourses in Europe are almost devoid of large woody debris, and river management, whether for hydraulic or fishing purposes, requires bed cleaning as an absolutely necessary form of maintenance. This view has been inherited from centuries of intensive use of flowing waters and their floodplains: the free passage of floods, the operation of mills, shortages of fuel, the floating of lumber and navigation have provided reasons for the regular removal of trunks and branches.

Historical ecological studies in recently developed countries have the advantage that they can reconstruct, if not the natural environmental conditions, at least the early conditions. American investigations emphasize the abundance and ecological importance of dead wood in rivers in the 19th century (Sedell and Froggatt, 1984; Triska, 1984). In low order streams, trunks form organic ladders or bars which may be stable for decades. These successive log jams create a rich diversity of biotopes: refuge pools, gravel deposits favourable for spawning, beaches of fine sediment colonized by aquatic plants, etc. The decomposition of organic matter, which takes place over several decades, progressively releases organic compounds which are used in the biological cycle downstream. This type of functioning is now a relict type in North America, given that the method of exploiting forests has reduced the possibilities for reinjecting wood into channels and that rivers have been used for the transport of tree trunks in imitation of European practices. By the end of the 19th century, the morphology of major rivers had been affected to such an extent that the principles of quantitative fluvial morphodynamics were no more pertinent than they are to the rivers of the intertropical zone today. The Red River, a tributary of the Mississippi, with a mean flow of around 700 $m^3 s^{-1}$, was obstructed by the 'Great Raft' for 400 to 480 km of its 1200 km length. Raising the channel by 7 m increased the number of impounded reaches along the main river. It was the rise of steam navigation which prompted the 'cleanup' of the Red and Mississippi rivers.

11.2.2 EXTRACTION OF MINERAL RESOURCES

For centuries, rocks and blocks have been removed from the torrential rivers of Europe to assist the descent of boats and rafts of tree trunks. This was the situation in the rivers of the Pyrenees and the Massif Central, as well as the Dordogne and Allier. This policy became an organized activity under the reign of Louis XIV, because, on the initiative of Colbert, who issued the edict of 1669, supply to the arsenals became a strategic objective. This contributed to the early canalization of streams in France which were suitable for rafting. In the same spirit the Highways and Bridges Authority attempted to correct rivers with pebbly beds from the end of the 18th century onwards, particularly in order to eliminate bars with an insufficient depth of water. Thus, in the middle Garonne, specially designed boats dredged artificial channels after each flood. This work, which was not very effective, was reinforced by major civil engineering structures such as the embankments of the 19th century.

The second half of the 20th century marks a break in the sense that rivers with a mobile bed were subsequently viewed as unlimited sources of sand and aggregates. Since the 1950s growth in construction has been responsible for excessive removal of material from active channels, without any regard to morphological and ecological diversity. This has had many consequences. Removal of material destabilizes the substrate and can cause banks to collapse, thus endangering microhabitats and spawning grounds. Bed overdeepening sometimes creates what are really trenches, at the bottom of which the water, which may become deoxygenated when flows are low, offers a hostile environment to fauna. To this is added a loss in water transparency resulting from the suspension of fine sediments which locally give rise to reduced photosynthesis and may clog gravel beds. One major phenomenon, deepening, may reach several metres in Alpine valleys and piedmonts. In the exceptional cases of the River Arve in the French Alps (Peiry, 1987), the channel was deepened by 12 m, and along the River Fier, the channel incised by 14 m. As a general rule there has been deepening of between 1 and 3 m over hundreds of kilometres of streams on the periphery of the Alps.

Changes experienced by functional units in the main channel may be reversible, in particular when the disturbance ceases allowing sediment transport to re-establish, deepening of the main channel has an irreversible effect on the alluvial plain. It is responsible for lowering the water table, and consequently drying out the aquatic environments abandoned by the river. For example, in the lower valley of the Drome, the channel has deepened by between 2 and 4 m since the late 1950s, and this has reduced water resources for irrigation provided by groundwater, and endangering the survival of riverbank woodland, which is considered to be of great ecological interest. Again, this impact is fairly common along the edge of European mountains like the Alps and the Apennines. However, in many cases aggregate extraction has affected river systems already in a state of change due to land use change or dam construction, and the cumulative impacts have rarely been considered.

11.2.3 THE IMPACT OF EMBANKING AND STRAIGHTENING

Embanking has been undertaken to correct channels so as to provide protection against erosion damage or flooding, and to 'improve' channels for transport. Since the end of the 18th century, technical progress has enabled industrial societies to 'train' channels in a systematic way.

(a) Embanking of braided sections

Historically, the first valleys which were subjected to corrective works were those in which the watercourse had a braided style. The upper valleys of the Rhine and Rhône had a major bed in which the active braided strip occupied a width of several kilometres. Begun in the 18th century, major longitudinal embankments were built from 1820 until the 1900s. In the case of mountain streams it was above all a question of protecting agricultural land, even though it prevented the deposition of fertile silts behind the embankments. This was the situation in the valley of the Isère upstream from Grenoble. On major rivers like the Rhine downstream from Basle, the Danube downstream from Vienna and the Rhône downstream from Lyon, river correction consisted of constraining the flows between embankments to increase low water levels and permit stream navigation throughout the year (Figure 11.1).

Work began on the Rhône about 1840, at a time when technical decisions were still based on empiricism. Successive attempts resulted in the superimposition of several generations of structures (longitudinal dykes, transverse groynes and grid structures, low submersible embankments), with the result that the engineers' success resulted in the complete isolation of the river from its flood plain. Initially, channel stabilization allowed ecological successions to proceed. However, approximately a century after embanking, the diverse patchwork of habitats had been reduced by the progress of ecological succession. Embanking prevents the rejuvenation of geomorphological units by erosion and, thus, in the long term results in the disappearance of communities which are characteristic of the pioneering and intermediate stages in ecological successions (Chapter 10). The fall in the water table resulted in change of the alluvial forest. On the silty sediments, the softwood forest developed into a hardwood forest, or, most frequently, into rich valley-bottom agriculture.

Embankments along the Rhine, constructed for the same purpose, have had even more dramatic effects in the long term. The plans of the engineer Von Tulla, of Baden, which were conceived in 1809, were implemented between 1884 and 1870. These comprised a submersible embankment within the main channel and, further back, a flood way contained between two embankments. Between Basle and Strasbourg the new course of the Rhine was selected from many braided channels so as to shorten the channel length by 14%. The desired result was achieved: deepening of the bed to reduce flooding and better protection of the floodplain from inundation. Since that period this stretch of the Rhine valley has been regarded as a classic example of downcutting, amounting to about 8 m upstream of the Istein bar, as a result of the channelization (Tricart and Bravard, 1991).

(b) Straightening of meandering sections

Large meandering rivers have also been subjected to major civil engineering works. As the floodwaters brought about the deposition of very

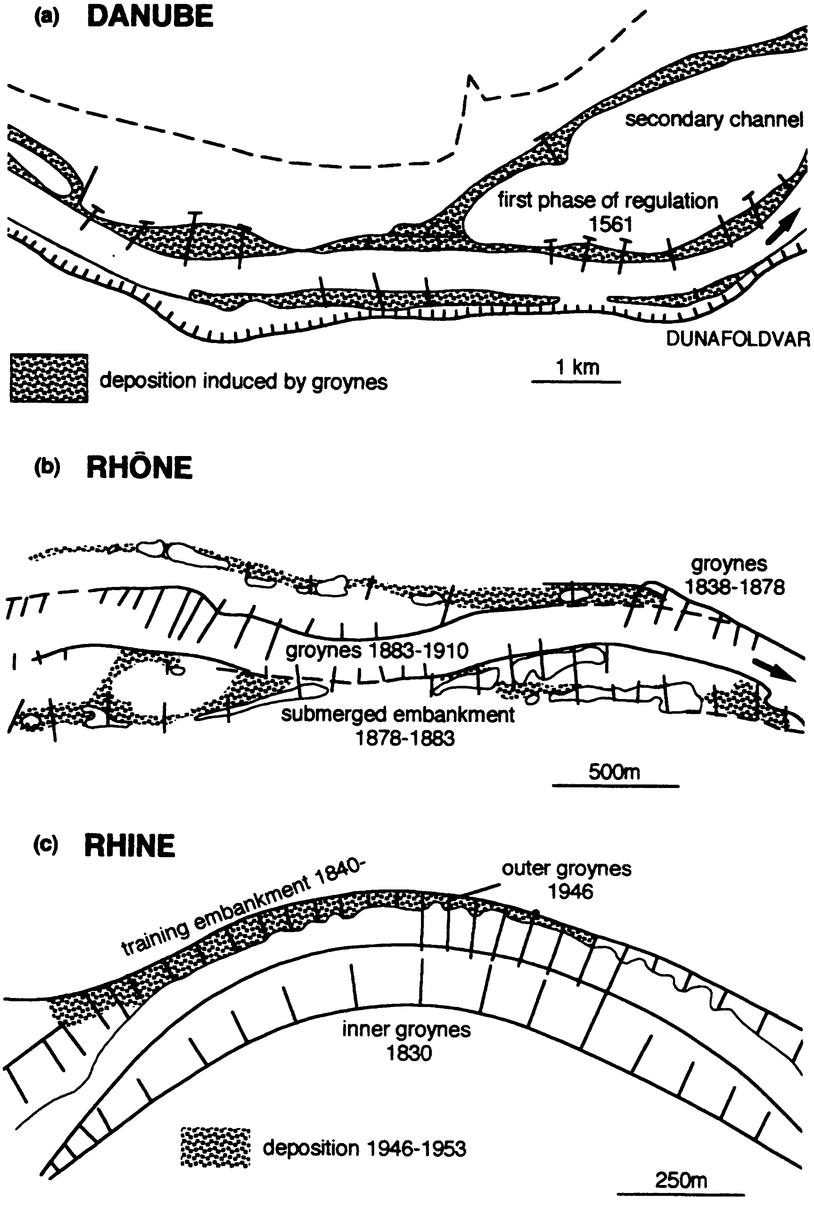

Figure 11.1 Embankment of the braided sections of large central European Rivers in the 19th century: (a) the Danube downstream from Vienna; (b) the Rhône downstream from Lyon; (c) the Rhine downstream from Basle (Tricart and Bravard, 1991).

fertile silty sediments, the conventional solutions adopted were earth banks designed to protect the floodplain from inundation. Thus, the Danube downstream from Budapest and its tributary the Tisza, the lower valley of the Rhine and the downstream plains of the Rhône, were embanked from the end of the 18th century. However, meandering rivers were also the object of work designed to improve conditions for navigation and to allow the faster evacuation of floodwaters. In 1781, the Hungarian engineer Vasarhelyi conceived a project to use the increased stream power produced by straightening (caused by the increased gradient) to deepen the bed of the Tisza. The river was thus shortened from 1214 to 761 km. Likewise 23 meanders were cut off on the Danube downstream from Budapest in the years 1820–25, so that the length of the river in this stretch was shortened from 494 to 417 km. The Mississippi suffered the same fate because 16 cuts between 1929 and 1942 reduced the length of the river by 240 km, or 35%. Erosion not only affects the river bed, but also the banks, because rivers seek to return to their natural gradient. Thus, after channelization, the course of the Tizsa extended by 5 km between 1870 and 1952. The banks of the Mississippi also have to be protected because erosion was removing 900 000 m^3 every year.

Deepening the channel bed has certainly had favourable short-term effects through the controlled sections, but it also had the effect of transferring flood peaks downstream more quickly, thus making flooding worse in some locations. This was the situation regularly experienced by the town of Szeged on the Tisza, and towns on the Rhine between Lauterburg and Mannheim. Deepening of the bed also caused a lowering of floodplain water tables. The Hungarian example is again significant. Drying out of the alluvial soil brought about an increase in agriculture during the 1890s, but because of the climatic peculiarities of the Great Plain, salinization of the soils occurred. In 1960 it became necessary to drain and irrigate 27 000 ha by pumping river water from which the 19th century works had protected the plain.

The elimination of lakes and wetland areas from the floodplain through the effect of embankments and lowered water tables has had serious indirect ecological effects. The reclamation of 2.1 Mha, or 88% of the floodplain of the Tisza, caused a 99% fall in fish yields. The reduced extent and duration of floodplain inundation caused the loss of spawning areas and a reduction of floodwater temperatures during periods which were critical for the fish.

In some parts of the alluvial plains of the Rhine and the Danube, the embankments are located away from the main channel and divide the floodplain longitudinally, placing a boundary between an active portion in which the ecosystems present remain dependent on the river and (the fossil alluvial plain) on the other side (Foeckler, 1990) protected from inundation by the river. Thus, the relative importance of main river floodwaters, tributary floodwaters and groundwaters may vary markedly across the valley floor. Ecological conditions become different on either side of the embankment, even in ecosystems of the same type. In the Danube plain, for example, an old meander located beyond the embankment, is characterized by stagnant water mollusc species, whereas in meanders with faster flow located on the river side of the embankment species more typical of running water dominate (Foeckler, 1990).

Such situations can be complicated even further by inputs of polluted water either from tributaries or local agricultural sources. Eutrophication of the aquatic environments isolated from the main river may be accelerated, sometimes causing the development of extensive algal mats or dense macrophyte growth. The fauna then loses some of its diversity.

The construction of embankments sometimes gives rise to new environments in the fossil alluvial plain. Where large floods break through an embankment, the water surges through the breach and excavates deep funnel-shaped pits, which in the plain of the Rhine can reach a diameter of 200 m and a depth of 17 or 18 m. These become stagnant ponds which are rapidly colonized by algae and macrophytes around the perimeter, and the fauna is sometimes highly diverse. Thus, 26 species of molluscs were recovered from the banks of one of these pits in the alluvial plain of the Rhine (Schmid, 1978).

11.3 THE IMPACT OF DAMS ON FLUVIAL HYDROSYSTEMS

Dams have been constructed for more than 5000 years and today the proportion of river flow stabilized by dams exceeds 20% in Africa and North America, 15% in Europe and Asia and 5% in South America. In France there are 420 dams more than 15 m high or impounding more than 10 million m^3 and 1200 mini power stations, in all creating 230 000 ha of artificial water surface. The impact of dams depends on several factors. These are the depth and dimensions of the impoundment (the African structures of Lake Nasser and Lake Kariba control 157 and 160 thousand million m^3, respectively), and the management of the reservoir, which depends on its functions (hydroelectricity generation, irrigation, flood control, leisure, etc.). Impacts can be classified into two major categories, depending on whether they affect the reservoir itself or the river downstream from the dam.

11.3.1 IMPACTS IN RESERVOIRS

(a) Loss of water by evaporation

Reservoirs lose some of their water by evaporation. For example, in 1976 the water balance for Lake Nasser showed a deficit of 12.4 km^3 for inputs amounting to 68.9 km^3. This was due not only to evaporation but also to seepage. In the long term, deficit balances will have a possible effect on water quality by concentrating dissolved substances.

(b) Loss of sediment

Reservoirs are sediment stores. For example, the Sautet dam on the River Drac, which was built in 1935 downstream of a catchment area where specific erosion amounted to 700 t km^{-2} year^{-1}, silted up at the rate of 370 000 m^{-3} year^{-1}, 0.3% of the useful reservoir of 100 million m^3. In some regions such as China, some reservoirs have lost 40–60% of their capacity in 15–20 years.

Attempts have been made to extend the service life of reservoirs and ensure conservation of the resource (Bruk, 1986). Some are intended to minimize silting by a policy of soil conservation in the upstream catchment areas, or through the construction of supplementary retention structures located upstream from the reservoir. The Guanting reservoir in China was supplemented with 300 upstream dams which reduced the rate of silting from 70 to 7 million m^3 year^{-1}. In other cases accelerated sedimentation is induced on the floodplain of the river upstream of the reservoir. Thus, alluvial Tamarisk forests extend over more than 10 km^2 of the Rio Grande plain upstream from the Elephant Butte reservoir and these have had the effect of reducing rates of flow during floods, causing the floodplain to rise through the siltation. However, a negative impact is that these forests consume a volume of water amounting to 10% of the natural resources through evapotranspiration. In any case, there is a marked reduction of the sediment load reaching the river downstream of the dam.

Some methods can be used to move material through the impounded stretches. In China the summer floods, which provide 80–90% of the annual solid inputs in loess country, in 25–50% of the total annual flow, are used to flush out sediments from reservoirs. This has been applied successfully, for example, in the Sanmexia dam on the Yellow River, but sediment concentrations downstream from the dam can exceed 900 kg m^{-3}. On the Rhône, materials have been flushed through reservoirs by operational management. Every three years, in the month of June, 650 m^{3}s^{-1} of clear water are drawn off from Lake Geneva to remove suspended matter brought in by the Arve at the rate of 500 000 t year^{-1} and deposited in the Swiss and French reservoirs of Verbois, Chancy-Pougny and Genissiat. The difficulty is then to prevent the redeposition of these materials in hydroelectric diversion works downstream.

(c) Impacts of impoundment on water quality and aquatic biology

Under certain conditions of depth (7–15 m at least) and retention time (the retention time is the ratio of the volume of inflow to the total volume of the reservoir), processes of thermal and chemical stratification of the type occurring in lakes may occur (in summer, warmer water at the surface and colder water at the bottom; highly oxygenated water at the surface and water which is very poor in oxygen, or even anoxic at the bottom). As a general rule, this change in the trophic systems is marked by an increase in plankton production and the development of a limnophilic benthic fauna dominated by molluscs, oligochaetes and chironomids. Fish populations are abundant during the first few years in the life of a reservoir frequently productivity declines after a few years of operation. This was the case with Lake Kariba, which reverted to oligotrophic characteristics a few years after the filling stage following the leaching of nutrients from 500 000 ha of drowned land.

In any case, salmonid populations are replaced by cyprinid populations which have a lower market value (Chapter 8). Thus, managed mountain rivers lose their rhithronic characteristics and become potamic and lacustrine. However, fish production may remain higher than under the pre-reservoir conditions. On the reservoirs of the Volga, like Kyubishev, Rybinsk and Volgograd, the fish catches have increased, because of an increase in benthic production associated with the silted substrate. Bream and their predators, saugers and pike, proliferate, despite the adverse effect of seasonal drying out and the dredging of the navigable channel. However, fish productivity remains 6–7 times less than in lakes in temperate latitudes.

11.3.2 IMPACTS ON FLOWING WATERS DOWNSTREAM FROM DAMS

(a) Breakdown of longitudinal connectivity

Dams block the migration of catadromous fish like eels, but most of the problems relate to anadromous fish which leave the sea to return to the streams in which they were born. These include, for example, Pacific salmon and sea trout on the northwestern coast of North America, the Atlantic salmon and shad in Western Europe and the sturgeons of the Black Sea and Caspian Sea. However, dams not only introduce a physical barrier to migration, river impoundment influences migrating behaviour by changing the flow and water quality regimes.

On the Volga, catches of sturgeon fell from 27 000 tons at the turn of the century to 10 000 tons. Since 1958 the Volgograd dam has stood in the path of the return of the large sturgeon called the Beluga. Likewise the construction of the Iron Gates Dam in 1973 blocked migrations along the Danube. In France salmon, lamprey and shad used to travel up the Loire. At the beginning of this century this migration was reduced by construction of the small Decizes dam, and then stopped in the gorges upstream from Roanne by the La Vourdriat dam in 1909. Restored in 1927, through the provision of a fish pass, the migrations were stopped again by the construction of the Grangent dam in 1957. The same problems occur in the tributaries of the Loire. Around 1920 the Vienne was equipped with 100 dams for mills over a length of 140 km. Their height of between 0.80 m and 3 m inhibited the migration of salmon, which have difficulty in clearing obstacles of more than 1.20 m.

(b) Change in hydrological regimes

Dams affect the hydrological regimes of watercourses and their impacts depend on the method of management adopted (Petts, 1984). The biological components of running water systems are adapted to the complex fluctuations in natural flows. Floods clean the sediments of spawning grounds, facilitate upstream migration, provide a periodic connection between water bodies in the floodplain, and replenish alluvial aquifers; they constitute a driving force for the pulsed functioning of the hydrosystem (Chapter 9). Hydroelectric dams operate to meet variable energy demands which in general vary on weekly and daily time-scales. Thus, on the Flathead river (Montana) the Hungry Horse dam creates a daily variation of between 7.5 and 260 $m^3 s^{-1}$. On other rivers, flow management reflects multipurpose uses. On the Rhône, the Genissiat dam controls the operation of a chain of locks downstream, and a compensation structure, had to be built at Seyssel, in order to attenuate the magnitude of the fluctuations. Early this century on the Rhône, the need for a sufficient draught to ensure navigation during the low water period required a flow of at least 90 $m^3 s^{-1}$ at the outlet from Lake Geneva, whereas the cooling of nuclear power stations now requires a minimum of 150 $m^3 s^{-1}$.

On another scale, major reservoirs are likely to impose seasonal types of flow which are very different from natural types. Winter energy output in Switzerland is obtained by constructing high altitude reservoirs like the Grande Dixence and by improving control of the levels in Lake Geneva. This has resulted in the retention of summer high flows and has destroyed the snow and ice-melt characteristics of the regime of the Rhône downstream from the lake. Another example is on the Murray, in Australia, where hydrological regime has been reversed (Baker and Wright, 1978); the storage of spring floods providing for irrigation needs by releases in summer and autumn. This type of impact undoubtedly has consequences for fluvial ecosystems. For example, the spring floods enable some species of fish to reach the calm waters of the floodplain, where they reproduce. The elimination of these floods prevents them from using these spawning grounds at the appropriate time. The most significant impact, however, comes from the reduction in flood peaks which results in a series of geomorphological adjustments, usually characterized by a reduction in channel capacity and the spread of the riparian woodland onto the new floodplain. Some reservoirs supply consumptive uses, including irrigation and interbasin transfers for drinking water supplies. In such cases, the water cycle is completely disturbed because the river loses most of its flow downstream from the reservoirs. Impacts can extend to the marine environment at the mouths of major rivers. Thus, before 1964 the Nile carried 34 000 000 m^3 $year^{-1}$ into the Mediterranean and the flood from August to November influenced the saline environment up to 80 km from the coast to a depth of 150 m. Subsequently, 60% reduction in inputs has changed the pattern of water circulation in the sea and increased the salinity, which has risen from 30 to 39% near the coast (Din, 1977).

Finally, there are diversion structures in which reaches of a river are short-circuited by an artificial canal equipped with a hydroelectric power plant (Figure 8.6). Parts of the course of the Rhine, Danube and Rhône have been changed in this way. The short-circuited sections are sustained by a 'compensation' flow, which is only a fraction of the natural flow (for the Rhône downstream of Lyon around 10–20 m^3 s^{-1}, whereas the mean is over 100 m^3s^{-1}). However, during floods these sections receive all or a major part of the natural flows, maintaining the original geomorphological features. However, the flow regime is artificial, being bi-modal and characterized by high floods superimposed on a constant baseflow or one of low variability.

When the compensation flow only corresponds to a small percentage of the incoming flow the short-circuited reach of river develops new ecological conditions. The Ephemeroptera and Trichoptera which are typical of the fluvial course (*Heptagenia* and *Hydropsyche*) diminish in density, except on rafts (Fruget, 1989). Other species, which are sensitive to sudden changes in level due to the operation of dams are eliminated (*Baetis fuscatus*) (Bournard *et al.*, 1987). The shallow depth of the flow encourages the development of an algal cover, and grazers and scrapers become established. This situation is somewhat similar to the secondary arms of natural rivers.

The fauna of the artificial canals, whose uniform concrete banks offer little or no refuge microhabitats, proves to be very poor. The constraints of power generation also result in major changes in the speed of the current which prevents colonization by sensitive species. In the Upper Rhône in France, the number of species on such artificial banks has been reduced by half and the diversity by approximately three quarters in comparison with the populations of the natural banks of the river

(Cogerino, 1989). Only the most resistant species remain (oligochaetes, chironomids), whereas the new conditions favour the proliferation of zebra mussels, whose colonies become attached below the lower limit of the water level range.

(c) Changes in thermal regime and water quality

Reservoirs also have effects on the thermal regime and water quality in their outlet channels. The thermal regime of waters is determined by the depth at which the gates are located, by the existence or lack of thermal stratification and finally by the released flow. If the reservoir is not thermally stratified, warmer water is released. In general there is a regulating and retarding effect on seasonal rhythms. If the reservoir is thermally stratified, summer water temperatures are reduced and winter temperatures are increased. When management of the dam uses a bottom gate, hypolimnial water is drawn off and this reduces the amplitude of daily and seasonal changes. Thus during cold snaps which freeze the waters of the River Saône, the waters of the Rhône upstream are affected by releases from Lake Geneva and the Genissiat reservoir, whose temperature remains around 4 °C.

Temperature changes experienced by regulated rivers can give rise to thermal shocks. This occurs during summer low-flow periods when locks release cold water and in 1976 the locks on the dams of the River Ain, France, caused temperatures to vary between 18 and 26 °C. Fish mortality has also been recorded when artificial reductions in flow have caused elevated temperatures. As far as other physical and chemical parameters are concerned, waters drawn from the hypolimnion of deep reservoirs suffer from an oxygen deficit. They contain iron and manganese as well as reduced compounds, and have a low pH. Their effect downstream is unfavourable when the flow is small and a river may require several kilometres to become reoxygenated. Conversely, water passing through turbines and laden with oxygen can create episodes of supersaturation and fish mortality downstream from dams. Techniques of selective withdrawal have been used to mix waters from different layers in the reservoir to overcome these problems (Petts, 1984).

Finally, the negative impact of flushing operations to clean out reservoirs should be mentioned. The transport and redeposition of fine sediments on the channel bed can asphyxiate fry and fish as well as benthic organisms. In some cases the flushing out of sediments rich in reduced substances and only partially decomposed organic matter can reduce oxygen levels by consumption, and may even be toxic if the sediments contain ammonia.

(d) Geomorphological readjustments and the transformation of habitats

The geometry of the bed of a river is adjusted to the set of variables comprising the flow and the sediment load (Chapter 5). Dams, however, can suppress or greatly reduce the load and alter the transport capacity of rivers, particularly by reducing flood peaks. Very frequently there is an increase in the relative downstream transport capacity of rivers, i.e. an increase in the energy available. They may degrade their beds downstream from dams, thus reducing their gradient and therefore the velocity of the flow. On the Colorado, degradation by 7 m in 10 years has been recorded downstream from the Glen Canyon and Hoover Dams. Maximum degradation usually occurs immediately downstream from the dam and is progressively attenuated further downstream. The extent of degradation changes over time. One year after completion the affected section downstream from the Hoover dam was 28 km long. After 5 years in operation the length had increased to 120 km. Eventually, a new stable or quasi-'equilibrium' channel morphology will be established; one which is adjusted to the regulated flow and sediment load regimes. However, in 91% of cases the time-scale of channel changes has been estimated as between 7 and 500 years (Williams and Wolman, 1983).

Down-cutting is a cause for concern in so far as it affects many units in the hydrosystem and in the long term can threaten the stability of dams. Degradation may be inhibited by coarse sediment on the channel bed when the regulated flow is no longer able to mobilize it during floods. In this sense erodibility is at a maximum on sandy beds, but may be significant in cobble and boulder bed rivers. In the case of beds of mobile gravels, sorting processes increase the size of the surface layer producing a stable 'armoured' bed (Petts, 1984).

Rivers can also dissipate their energy by channel enlargement through lateral erosion of the banks, in particular if the bed is armoured. Lateral erosion often results in increased sinuosity, i.e. a lengthening of the course, and thus a reduction in the gradient and stream power. However, by reducing the flow downstream, dams also give rise to a reduction in the width of the channel. The Platte (Nebraska, USA) currently has a width of 10–20% of what it was in 1865 before some of the water was diverted (Williams and Wolman, 1983).

At the scale of functional units, flow regulation alters the spatial and temporal patterns of water depth and velocity distributions not only of lotic units, but also terrestrial or aquatic units on the floodplain. In extreme cases, floodplain lakes, secondary channels and even the main channel under dry-weather conditions abstractions can reduce aquatic habitats to a series of stagnant pools. Compensatory measures (Petts and Maddock, 1994) can establish a minimum flow and flood flows at the optimum time for ecosystems, and provide artificial spates from dams to flush unwanted deposits of fine sediment on the river bed and to stimulate fish migration.

(e) Impacts on aquatic fauna

In detail, impacts of habitat change are complex but in general river works reduce species diversity and increase the abundance of benthos. This occurs in particular when the flow is stabilized, winter temperatures are increased, and depths are shallow; warming of the water and stability of the substrate favour algal growth. Conversely, macroinvertebrates can suffer from releases of hypolimnal water which is low in oxygen and cold in summer, or frequent and rapid fluctuations in flow.

Fish populations are affected by changes in the thermal and hydrological regimes. The former is responsible for inhibiting reproduction if the water is too cold, and this has severely affected the indigenous species of the Colorado river, for example (Mullan *et al.*, 1976). Conversely, some species may be favoured. White fish gave way to trout in the River Lot, France. As well as influencing species composition, a fall in temperature may also reduce the rate of fish growth, or even cause changes in species. Furthermore, thermal shocks can be lethal. In July 1976 mortality occurred among grayling in the River Ain, a tributary of the Rhône, because of the twice-daily thermal shock of releases of cold hypolimnic water from upstream reservoirs.

A reduction in floods reduces or eliminates floodplain inundation. On the Volga, inundation of floodplain backwaters to the river has decreased from 50–70 days/year to 10–15 days/year since regulation began. The impact on the fish population has been dramatic because at least 40 days are necessary for a good growth of juveniles before they descend towards the Caspian Sea (Marchant, 1991).

(f) Impacts on vegetation

Downstream from dams, the regulation of flow and the reduction in the frequency of flooding causes a general growth of vegetation in the main channel. Plant spread is sometimes confined to a single strip on either bank, as on the sandy shores of the canyon of the Colorado, which have become thinned by desiccation (Dolan *et al.*, 1974). In braided rivers invasion by plants occurs through the colonization of pebble bars. The reduction in floods allows seeds to germinate and young plants to survive, reduces submersion times and the constraints experienced by woody plants (uprooting, breakage). The disadvantage of this type of impact is that it reduces the ability of the channel to convey flood flows, by increasing flow resistance. In the valley of the Rhône, short-circuited sections have been subjected to this type of impact because flood flows are lower and especially because the disappearance of high water during summer favours colonization. The Companie National du Rhône carries out regular mechanical ground clearance to control the pioneering stages of willow and poplar growth.

The change in soil moisture regime within the floodplain is the main determining factor for plant populations. For example, the root system of softwood species, like white willows, can lose contact with the water table and cannot then adapt to the new conditions where the substrate is permeable. The theoretical succession shows hardwood species to succeed softwood species. The construction of artificial sills to raise the water table may be one means of conserving satisfactory water conditions. Water may also be specially released from reservoirs to 'irrigate' the floodplain, a procedure planned to protect the alluvial forest within a reach of the Danube which is to be short-circuited by the works at Gabcikovo.

11.4 COMPLEX IMPACTS ON HYDROSYSTEMS

In practice, human impacts on rivers have sometimes given rise to synergistic effects, many of which are delayed in time, and often offset in space. Two examples selected from the Rhône basin are particularly illustrative.

11.4.1 THE METAMORPHOSIS OF THE LOWER AIN

The River Ain is a 200 km long tributary of the Rhône draining a catchment area of 2670 km^2. The mean flow is 120 m^3 s^{-1}. The mountainous nature of the catchment and a high gradient of 0.0015 gives the river a very torrential character. The 10-year flood exceeds 1750 m^3 s^{-1}. Until the beginning of the 20th century, the Ain had developed a braided fluvial style related to the pebbly and sandy bedload supplied by vast spreads of fluvioglacial deposits. Between 1940 and 1960 the style of the Ain was marked by actively migrating meanders. Then a metamorphosis occurred, as a response to a considerable reduction in bedload (Figure 11.2). However, the hydroelectric power dams built in the upstream gorges are less responsible for this change than a long history of channel training to control lateral erosion which was the main source of sediment. For the last 20 years the change has continued, reducing the degree of sinuosity and giving rise to channel deepening, which has reached 2–3m in some sections. Appreciable changes of the hydrological regime have also be influential. In fact the disappearance of major floods since the end of the 1950s, undoubtedly linked with climatic variation, and therefore reversible, has been exaggerated by the deliberate attenuation of small

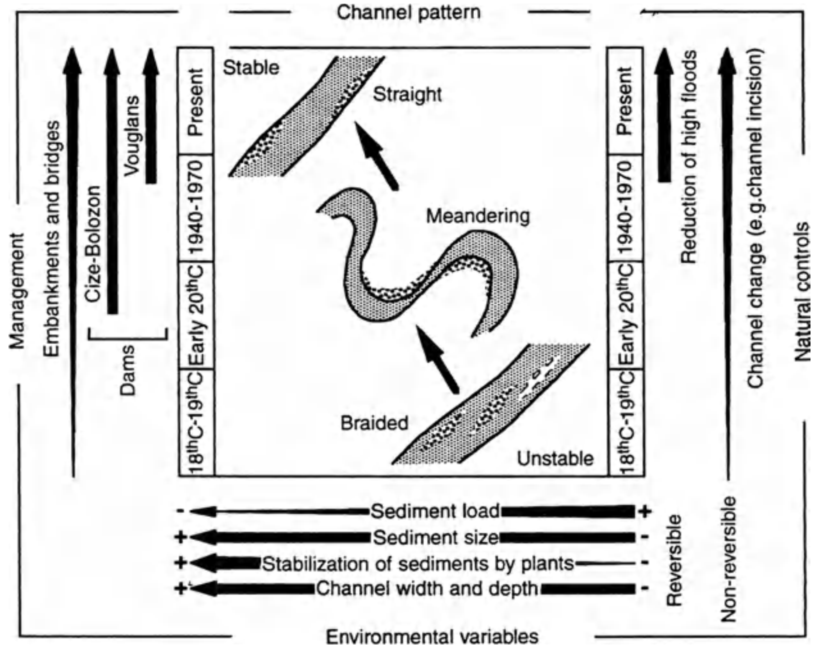

Figure 11.2 Natural and anthropogenic factors in the metamorphosis of the Ain, a tributary of the Upper Rhône (Fagot *et al.*, 1989).

and medium-sized floods by the Vouglans reservoir which was brought into operation in 1968. The reduction in erosive activity and sediment transport by the river has allowed the alluvial forest to encroach into the channel, concentrating floodwaters. This process has intensified the tendency of the Ain to deepen its channel. The main biological impact has been the loss of spawning grounds for grayling.

11.4.2 CHANGES IN THE BRAIDED SECTIONS OF THE UPPER RHÔNE

Until the beginning of the 19th century, the flushing of braided sections by floods had the effect of truncating ecological successions on pebble bars and in secondary channels, where the sandy fill was periodically re-excavated (Figure 11.3). The fact that the vegetation was affected by grazing of large domestic animals made the deposits particularly susceptible to erosion. Submersible embankments constructed between 1880 and 1890 were designed to concentrate the water during low-flow periods, by cutting off secondary channels, in order to permit navigation. These channels continued to receive a permanent input by seepage through the permeable embankments and by overspill during floods. Nevertheless

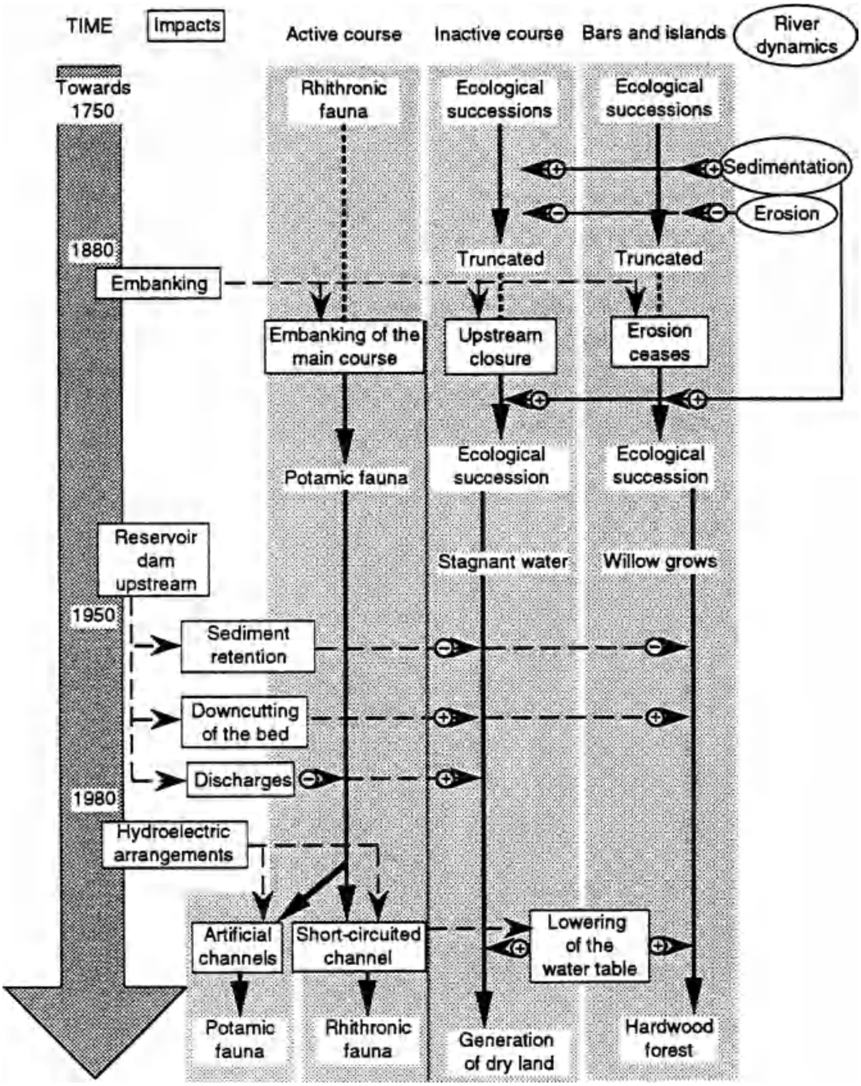

Figure 11.3 Spatial and temporal changes in various impacts on a braided sector of the Upper Rhône and interference with natural processes (adapted after Roux *et al.*, 1989).

these embankments had three effects: (a) they converted rhithronic reaches into potamic ones and reduced the diversity of the environment, increasing the depth and reducing light penetration to the bed; (b) they created lentic conditions in the cut-off arms, which progressively filled with fine mineral sediments; and (c) on the bars, which were thus stabilized, progressive accretion (no longer compensated for by erosion) accelerated ecological succession favouring hardwood species.

The construction of hydroelectric reservoirs upstream helped to accentuate these trends in a less obvious way, by reducing sediment loads. Furthermore, dam operation involves the flushing out of fine sediments deposited in the reservoirs, and this has advanced the siltation of secondary channels with sediments of a very different character to the sands of the natural braided river.

Within the short-circuited reaches, the artificial canal has a potamic nature, the old embanked and by-passed channel has the hydrology of a small river with constant flow (10–120 $m^3 s^{-1}$), which is subjected to random floods. In these latter channels, the fauna is adapted to rhithronic conditions and benefits from relative isolation during flushing operations, which discharges through the canals. As for the islands in the by-passed channels, the vegetation has been affected by lowered water tables causing an accelerated change towards hardwood populations, and even mortality where water levels have not been maintained by artificial bars (Roux *et al.*, 1989).

Fluvial hydrosystems: a management perspective

12

G. E. Petts and C. Amoros

12.1 BACKGROUND

River management should involve resource utilization without deterioration of the natural basis (Mellquist, 1992), a concept promoted in the *Brundtland Report* (1987). In practice, river management involves important choices (Boon, 1992). First, for rivers that are essentially pristine, there is an overwhelming case for *preservation*. The challenge is to allow natural changes within fluvial hydrosystems (those caused by floods, droughts, erosion and sedimentation – and variations in the frequency and duration of these processes with changing weather patterns) whilst protecting the river from artificial influences. In most cases, however, the pressures for land and water development, and the resulting problems of waste disposal, will require management to limit artificial changes within the catchment and to mitigate the impacts of human actions.

Secondly, at the other extreme are rivers or sectors that have become so severely degraded that in the short and medium terms the only management option is to accept *dereliction*. This realization is necessary to direct resources not only to high quality rivers and sectors deserving protection but also to those that have a fair chance of being improved by the third option, *restoration*.

For preservation and restoration to be effective, management must address (a) catchment-scale issues, i.e. the flows (quantity and quality) and sediment loads (Chapters 2 and 3), and (b) local (sector-scale) issues concerning channel dynamics, especially lateral erosion and deposition (Chapters 4 and 5). Particular attention must be given to the maintenance

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of connectivity (a) between sectors, (b) between the different functional units of the hydrosystem and (c) between surface and subsurface environments (Chapter 9) and to the nature of ecological successions (Chapter 10). Management options must also be evaluated in the context of the historical legacy of human impacts throughout the drainage basin (Chapter 11).

The cumulative effects of human impacts have been particularly severe in Western Europe (Petts *et al.*, 1989b). In summary:

1. Catchment land-use changes have altered the hydrological and sediment transport regimes, and the form and amount of allogenic organic matter entering water courses;
2. Impoundments created by dams, weirs and locks, have transformed the fundamental instream hydraulics;
3. Water is abstracted for domestic and industrial supplies (often to be returned to the same river as waste water but sometimes transported long distances by inter-basin transfers) and for irrigation agriculture – a truly consumptive use (water being 'lost' by evapotranspiration);
4. Industrial, urban and agricultural pollution has led to the accumulation of contaminants in sediments, plants and animals, with concentrations being increased along food chains;
5. Channels have been engineered for navigation and flood control;
6. The linkage between the channel and its floodplain, with its network of channels and backwaters, has been decoupled by regulation;
7. Important changes of the riparian zone, notably the removal of important 'buffer' strips of riparian trees, has resulted from river developments for navigation, from land drainage and agricultural expansion;
8. Floodplains have been developed for urban and industrial uses.

This historic legacy of land and river development is important not only because it highlights the causes of ecological degradation along rivers but also because it identifies constraints to restoration. In most cases, management cannot restore pristine rivers, rather the objective is to enhance the ecological diversity of the remaining river corridor. The term *rehabilitation* is used in this situation.

In rehabilitation, particular emphasis should be placed on encouraging and expanding relict populations/communities once their habitat requirements are known. Where a population is struggling, but surviving, data gathered on the relicts will be of great assistance in defining the requirements of a rehabilitation programme. In any case, river rehabilitation can not be achieved passively; the cessation of a particular use and abandonment of the river or floodplain is unlikely to prove successful. 'Management' involves the maintenance of some *artificial* condition (Mellquist, 1992). The protection or rehabilitation of a river requires active management that not only involves manipulation of the environment and controls on the abundance and distribution of animals and plants, but also imposes and administers controls on human actions.

This concluding chapter summarizes the values of fluvial hydrosystems for ecologically sound – or, at least, ecologically sensitive – environmental management and then examines the applicability of the fluvial hydrosystems approach for the rehabilitation of large alluvial rivers.

12.2 RATIONALE FOR RIVER REHABILITATION

The rationale for rehabilitating fluvial hydrosystems relates especially to their values for biological conservation and, in a socioeconomic context, for enhancing the quality of life and increasing the potential for wealth creation. The World Conservation Strategy (IUCN, 1980) embodies the primary objectives:

- To maintain essential ecological processes and life-support systems;
- To preserve genetic diversity; and
- To ensure sustainable utilization of species and ecosystems.

The strategy focuses on the long-term benefits of biological conservation to humans, emphasizing that nature conservation does not imply the neglect of issues affecting human welfare.

River corridors are particularly important in biological conservation for five reasons:

- They have high biological diversity;
- They have high biological productivity;
- They contain refuge habitats;
- They include refugia from the preindustrial period; and
- They are sources for species dispersal.

The particular value of river corridors is illustrated by the study of Knopf *et al.* (1988) who show that although riparian habitat occupies less than 1% of the western North American landscape, it provides habitat for more species of bird than all other habitats combined.

The second dimension to the rationale for river rehabilitation is that river corridors have a range of socioeconomic values related to their commercial and recreational potential (e.g. fishing, hunting, boating) and their high visual quality (Petts, 1990). Green and Tunstall (1992) showed that river corridors are particularly attractive for casual recreation, receiving more local visits and drawing visitors from a larger area, than does the average small park. The public are attracted to river corridors that are (a) unpolluted, (b) quiet, rich in flora and fauna, and form attractive landscapes; and (c) have basic facilities such as toilets and paths, reflecting important public concerns for the safety of children and general public health. Public perception of a healthy environment is important.

For example, the return of salmon (*Salmo salar*) to the River Taff in Wales is considered to have considerable importance, regardless of any fishery value, because salmon are symbols of clean water (Mawle, 1991). Following a long history of severe degradation caused by gross pollution, a breeding salmon population in the Taff would be a clear demonstration of improved quality.

12.3 THE SCIENTIFIC BASIS

The scientific basis of river rehabilitation is centred on the need to develop models to predict the ecological impacts of human activities, including rehabilitation measures! This requires integration of knowledge from three areas of study and from three levels of investigation. Studies of hydrology, geomorphology and ecology must be fully integrated to develop applicable models of ecosystem, habitat, community and species responses. Information is required on structural relationships and dynamic interactions at three levels of scientific analysis:

1. *Functional* studies which seek to explain the spatial distribution of, and interdependence between, species, communities and habitat patches;
2. *Historical*; and
3. *Palaeoenvironmental* studies which seek to understand the ways that species, communities and habitats change in response to human impacts and climate change, respectively; and to establish the former 'natural' characteristics of fluvial hydrosystems.

The first level of analysis is concerned with understanding short-term process dynamics (e.g. carbon spiralling, trophic interactions, chemical exchanges between water and sediment, etc.) and with describing spatial relationships between individuals, species, communities and habitat patches. Functional studies are important for determining the 'technological' basis for restoration, that is providing the scientific knowledge necessary to define management processes:

- Selection of species, communities and/or habitat characteristics as targets for management;
- Introduction (e.g. fish stocking, reintroduction of otter (*Lutra lutra*), introducing gravel to create bars, etc.);
- Elimination (e.g. culling to control population numbers, controls on invasive plants, etc.);
- Control of key fluxes (e.g. water levels, nutrient supply, primary production, siltation, etc); and
- Controlled disturbance (e.g. river-bank or woodland clearance to rejuvenate succession, artificial 'floods' to scour channels or inundate riparian wetlands).

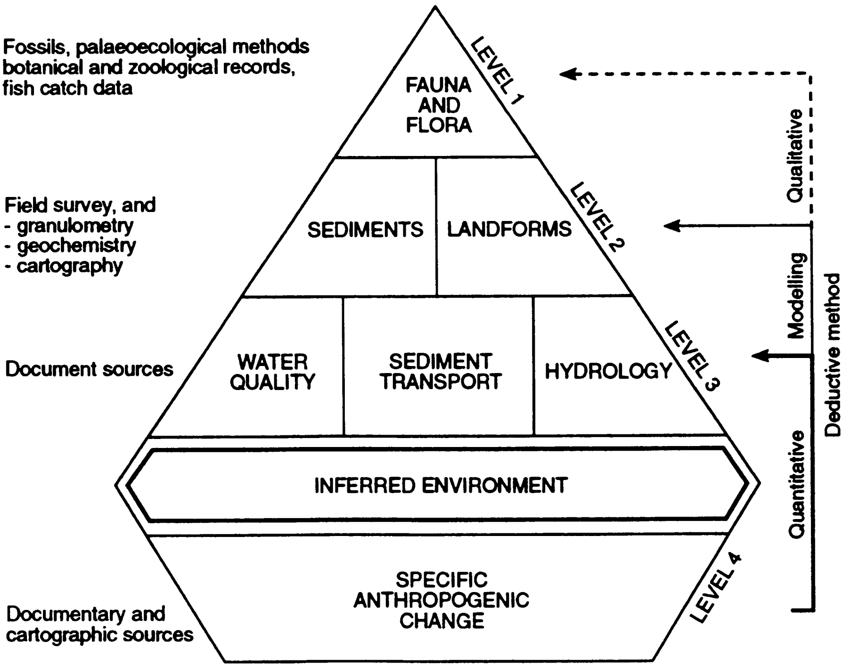


Figure 12.1 The four-level inferential approach to historical analyses of fluvial hydrosystems (from Petts *et al.*, 1989b).

The second and third levels define the context within which rehabilitation programmes must be set. The most productive approach to reconstructing the sequence of changes experienced by fluvial hydrosystems over historic and palaeoenvironmental time-scales is inductive (Thornes, 1987), in which the direction of investigation is the reverse of the direction of causation (Figure 12.1). The use of a deductive method is prohibited by the complexity of physical, chemical and biological dynamics and their interactions.

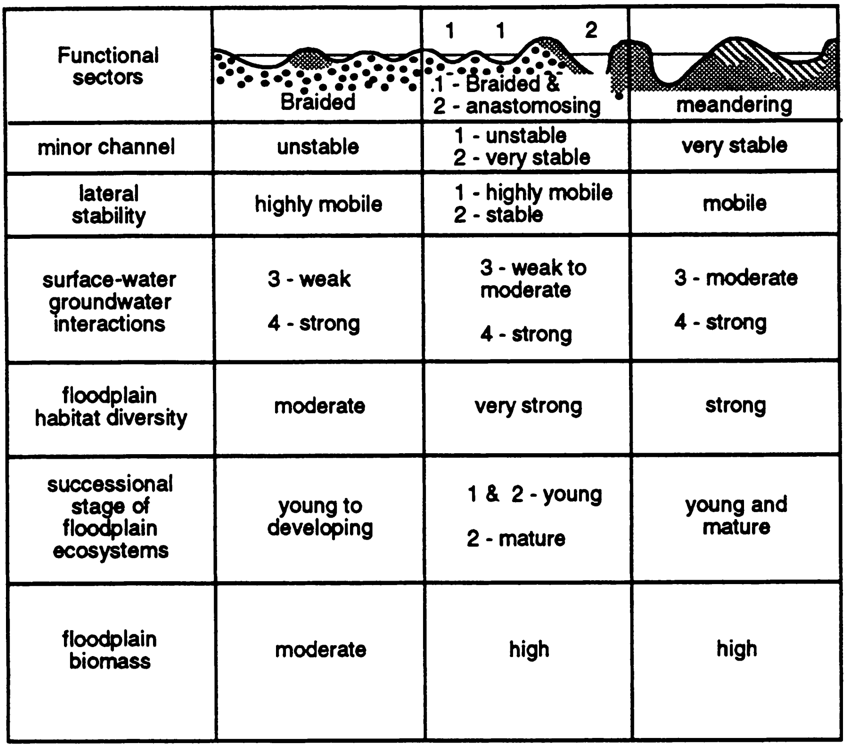
Information on the physical and biological characteristics of rivers in the past can be derived for a number of specific time periods from maps, plans, photographs and documents, and from landforms and stratigraphic units dated by tree-ring analysis, archaeological evidence etc. Studies of sediment cores from cut-off channels, including granulometry, geochemistry, pollen, diatoms, and invertebrates, can be especially useful. With the inductive method, field observations, evidence of former biological populations (Level 1), fluvial sediments and landforms (Level 2) are used to make inferences about the process dynamics of the environment (Level 3). Historical studies benefit in most cases from more or less detailed documentary evidence concerning the precise nature and timing of anthropogenic changes (Level 4). Application of the inductive method to analyse historical changes along large alluvial rivers is developed by Petts *et al.* (1989b), and exemplified for the Rhône by Amoros *et al.* (1987b) and for the Trent by Petts *et al.* (1992).

12.3.1 THE FLUVIAL HYDROSYSTEM APPROACH

A fluvial hydrosystem perspective provides a practical approach for ecologically sensitive river management by classifying rivers as a sequence of sectors of variable length from less than 1 km to 50 km or more. Each sector is defined by four sets of criteria, each including artificial influences:

1. *Inputs* derived from the catchment and routed through the channel network upstream. The fluvial hydrosystem is seen as a component of the drainage basin within which the primary controls are climate, geology, relief, and vegetation (land use);
2. *Internal structural controls* within the sector including slope and degree of lateral confinement (by valley sides, river terraces, woodland and channel engineering structures), etc.;
3. *Internal process dynamics* within the sector such as influent or effluent flow conditions, nutrient spiralling dimensions, and morphological dynamics (aggradation and incision), etc.; and
4 *Downstream structural controls* which effectively control baselevel for the adjacent sector upstream, including bedrock controls, channel behaviour (aggradation and incision) and artificial controls such as weirs and bridges.

Each sector comprises a characteristic range of physical habitats. These are the the fundamental units (Chapters 1 and 5) and their different successional stages (Chapter 10); in ecological terms they determine the biotope and biocoenosis of each elementary river landform. Figure 12.2 summarizes the biological features of three functional sectors having different physical characteristics. The figure emphasizes the importance of (a) lateral and vertical connectivity (Chapters 7, 8 and 9) and (b) channel erosion and deposition, which rejuvenates successions and sustains a range of successional stages as well as a diverse range of habitat patches (e.g. gravel bars, sandy levees, backswamps and ponds; Chapter 5). Greatest diversity and productivity occur in hydrosystems characterized by a moderate degree of channel instability. In highly mobile braided channels, ecological successions are truncated and production limited by the morphological instability and high frequency of disturbance.



Functional sectors	Braided	1 1 2 1 - Braided & 2 - anastomosing	meandering
minor channel	unstable	1 - unstable 2 - very stable	very stable
lateral stability	highly mobile	1 - highly mobile 2 - stable	mobile
surface-water groundwater interactions	3 - weak 4 - strong	3 - weak to moderate 4 - strong	3 - moderate 4 - strong
floodplain habitat diversity	moderate	very strong	strong
successional stage of floodplain ecosystems	young to developing	1 & 2 - young 2 - mature	young and mature
floodplain biomass	moderate	high	high

3 : aggrading systems ; 4 : degrading systems

Figure 12.2 Three examples of functional sectors (represented by schematic cross-sections) and the ecological implications of the different channel types (after Amoros *et al.*, 1987b).

12.3.2 PRINCIPLES FOR ECOLOGICALLY SENSITIVE RIVER MANAGEMENT

The applicability of this fluvial hydrosystem perspective in river management is justified by three important principles.

The first principle is that each sector must be viewed in the context of its catchment. The flow regime, the water quality and the sediment loads within a sector are dependent on catchment conditions upstream. Whereas sector-scale management actions can yield important and immediate benefits, in the longer term, successful rehabilitation requires catchment management and planning.

The second principle is that rivers must be viewed as systems in dynamic equilibrium. Within each sector a quasi-equilibrium condition may be defined involving hydrological, geomorphological and ecological interactions. Each sector can be described by a more or less complex arrangement of aquatic, semiaquatic and terrestrial patches. The patches will be of different type (defined primarily by morphological, sedimentological, and vegetational criteria) and different age (reflected by successional criteria for each type). The arrangement of patches within the sector changes over time in response to successional processes and disturbance (by erosion and deposition). Thus, the optimal areas for particular fauna shift to different parts of a sector in response to the build-up of sediments (Bayley, 1991). Over a time-scale of 10–100 years the spatial arrangement of patches may change, but the composition of patches within each sector will remain relatively stable, about an average condition.

The third principle is that lateral exchanges play an important role in sustaining the functioning of river sectors. The role of the ecotone concept (Chapter 9) in river management is to focus attention on the transitional zone, or dynamic boundary, at the land–water interface. Traditionally, management has focused on patches. Conservation has been concerned primarily with the preservation of species within patches by defining more or less artificial boundaries around them. River margins are determined primarily by hydrological variations and geomorphological disturbance, and are highly sensitive to external controls. The ecotone concept emphasizes (a) the importance of river margins for sustaining the functional characteristics of the fluvial hydrosystem and (b) the role of hydrological and geomorphological dynamics in sustaining the structural and functional characteristics of the river margins.

12.4 OPTIONS FOR MANAGING FLUVIAL HYDROSYSTEMS

Management must be based on the best available science (Calow and Petts, 1992, 1994). Despite the long history of scientific endeavour models of fluvial hydrosystems remain imprecise and a precautionary approach must be used when applying apparently 'scientifically sound' tools and approaches. Whilst acknowledging the limitations of our knowledge, enough scientific information is available to begin to address most of the immediate problems. The fluvial hydrosystem approach provides a framework to structure the consideration of the management options.

At one end of the spectrum, management to protect a pristine river from development may require non-use of a natural resource – implicitly accepting that non-use is an acceptable form of use. In some cases, the protection of a river from hydropower development, for example, may be seen as a trade-off, the preservation of one being acceptable because of the intensive development of another (e.g. Ledec and Goodland, 1988). At the other end of the spectrum, river management is required to limit or mitigate the impacts of water division for power generation, domestic supply or irrigation, the complete alteration of a river's hydrological and water-quality regimes by large-scale impoundments, or the controlled discharge of waste waters. On a smaller scale, management must consider options for minimizing the adverse ecological effects of removing channel bed sediment to improve navigation, weed cutting for flood control, 'protecting' a river bank to prevent erosion, embanking to prevent floodplain inundation, or removing riparian vegetation to improve access.

There are five general groups of options for river rehabilitation:

1. Water quality improvements involving point and non-point pollution controls;
2. Manipulating river flows;
3. Structural modifications to improve instream, riparian and floodplain habitats;
4. Biological controls, such as vegetation planting or control of invasive weeds, and fish stocking or selective fishing; and
5. Controls on human access and activities.

In general terms, the first two require catchment management and the last three relate to management plans at the sector scale. In any case, management plans must seek to achieve the best practicable solution to a problem by considering all reasonable combinations of options.

12.4.1 WATER QUALITY

That at least a tolerable water quality exists, or can be achieved and sustained is a prerequisite for the success of any rehabilitation programme (Dobbs and Zabel, 1994). Proposed water-quality standards for fisheries in England and Wales are given in Table 12.1. Considerable lengths of river throughout Europe remain unsuitable for physical and

Table 12.1 Water quality standards adopted by the European Community (Directive 78/659/CEE)

Parameter	Salmonid waters	Cyprinid waters
pH	6–9	6–9
Dissolved oxygen (mg l^{-1})		
50% of the time	>9	>8
100% of the time	>7	>5
Action must be taken	6	4
BOD (mg l^{-1})	<3	<6
Unionized ammonia (mg l^{-1} NH_3)		
50% of the time	0.025	0.025
100% of the time	0.005	0.005
Total ammonia (mg l^{-1} NH_3		
50% of the time	<1	<1
100% of the time	<0.04	<0.2

biological rehabilitation because of inadequate water quality. For example, in England and Wales in 1990, fish were absent or occurred only sporadically along nearly 4500 km of main river, representing about 12.5% of the total length of main river.

Since the mid 1960s advances in water-treatment technology, higher standards and better monitoring (Parr, 1994) have decreased the input of labile organics from sewage works and improved industrial effluent discharges. On the River Trent in Nottingham, for example, between 1964 and 1984, biological oxygen demand fell from 15 mg l^{-1} to less than 4 mg l^{-1} (Brewin and Martin, 1988). Despite improvements in the quality of point-source discharges, on most rivers current problems relate to non-point sources and to the high frequency of pollution incidents. Further progress in water-treatment technology and stronger legislation are required if the full potential of river rehabilitation is to be realized.

12.4.2 DISCHARGE

The influence of hydrology involves both water-level (frequency and duration of inundation or dewatering) and water volume (frequency of floods and duration of 'normal', and extreme, low flows). The allocation of water resources to maintain an 'ecologically acceptable' flow regime (e.g. Figure 12.3) is vital for river rehabilitation but also a source of major conflict, not only between water users but also between the different objectives for rehabilitation (Stalnaker, 1994; Petts and Maddock, 1994).

(a) Minimum flows

The maintenance of minimum flows has become a major problem because of abstractions, interbasin transfers and water-storage projects. Along rivers affected by artificially low flows, the implementation of control rules to maintain flows has demonstrated ecological value. Weisberg *et al.* (1990) for example, demonstrated the value of maintaining summer minimum flows reducing the dewatered area of channel bed, increasing flow velocities and diversifying instream hydraulic conditions for benthic invertebrates.

A physical habitat stimulation model (PHABSIM) has been developed to provide a hydraulic framework for describing lotic ecosystems in a way that can be used to predict the effects of water resources development on the habitat of aquatic biota (Stalnaker, 1994). PHABSIM uses relationships between a species of interest and a range of variables describing instream habitat (e.g. velocity). It is assumed that each species exhibits discrete and quantifiable preferences which can be described as habitat suitability curves. The model simulates the area of suitable habitat within a representative or critical reach, providing a single composite

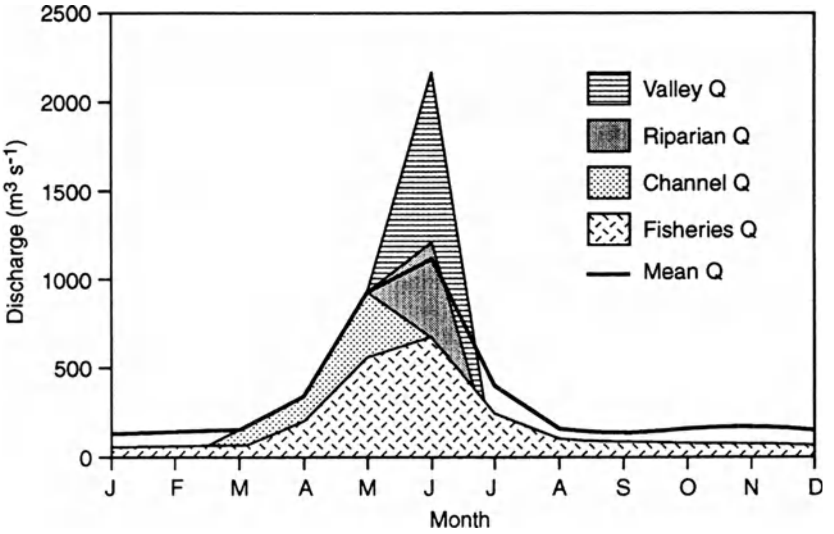


Figure 12.3 Composite minimum streamflow hydrograph for the Salmon River, USA (after Hill *et al.*, 1991) incorporating minimum flows for fish, to maintain channel form, to sustain riparian communities, and to retain the mosaic of habitat patches across the valley floor.

value of habitat for a reach composed of a number of cells, or microhabitats, of different depths, velocities and channel character (substrate and cover). Examples of the application of PHABSIM in the UK are given by Petts and Maddock (1994) and Petts *et al.* (1995).

(b) High flows

In rivers regulated by dams, an important option exists for rehabilitation, that is the programmed release of a predetermined discharge, for a given duration. Such releases can be used to maintain a desired channel condition and to sustain riparian and floodplain environments.

Channel maintenance flows (Reiser *et al.*, 1989) serve the function of natural high flows: maintain channel geometry, flush fine sediments and control vegetation growth. One method of determining the characteristics of channel maintenance flows is to utilize historic streamflow records to develop statistical relationships between a hydrological parameter, such as flow frequency or duration, and the observed flow at which adequate flushing is achieved. Three examples are the 1.5 year flood (often taken to approximate the 'bankfull discharge'), the 5th percentile flow duration, and 200% of the average annual flow). Attention must also be given to the timing of flows in relation to the life-history requirements of aquatic biota (Chapters 7, 8 and 9).

Overbank flows that inundate and disturb riparian and floodplain areas are required to maintain the range of habitat patches that comprise the river corridor (Chapters 5, 9 and 10). The maintenance and control of water level is particularly important to conserve and rehabilitate floodplain wetlands and woodlands (e.g. Bren, 1988; Dister *et al.*, 1990). Modelling approaches to measure riparian response to altered flow regimes have been initiated by Stromberg and Patten (1990).

Water level manipulation may be achieved by using gated or ungated weirs, but these alter the instream flow conditions. Where weirs are in place, and are required to maintain the river for navigation or hydropower production, water-level regulation may provide an important tool for maintaining or enhancing fish and wildlife resources. Such an approach is being developed, for example, for navigation pools and associated floodplains of the Upper Mississippi System (Lubinski *et al.*, 1991). The advantage of this approach is to allow a high level of management at the sector scale.

12.4.3 HABITAT CONTROLS

A variety of habitats is one of the most important conditions for the existence of well-balanced aquatic communities. Habitat simplification, resulting from river regulation, diminishes the number and diversity of species. Rehabilitation involves the diversification of habitat whilst sustaining other user needs (e.g. erosion control: Jaeggi, 1989; Hey, 1994). A range of design alternatives has been employed (e.g. Brookes, 1989; Swales, 1989; Kern, 1992; Larsen, 1994) including tree planting, instream devices to provide cover, artificial riffles, different channel geometries and realignment to create meanders. Functional research is continuing to elaborate the importance of physical habitats for biota. For example, in conflict with traditional river management practices which seek to remove fallen trees and coarse organic debris from streams and rivers, recent research has demonstrated the biological importance of coarse woody debris in streams and along river margins (Gregory and Davis, 1992; Gurnell *et al.*, 1995). This illustrates the applicability of continuing functional research to river management, in this case emphasizing the ecological value of rehabilitating a river's natural budget of coarse organic debris.

A case study of strategies for conserving the fish fauna of the Danube (Schiemer and Waidbacher, 1992) illustrates the practical approaches that may be applied to river management. They identify the first priority as the maintenance and improvement of the remaining free-flowing sectors of the river by:

- Increasing the morphological diversity of the river bed near the banks;

- Increasing the area inundated at low flood levels; and
- Re-activating the links between the river and floodplain backwaters by opening upstream connections at mean water level.

Although there are few post-rehabilitation appraisals at this time, many studies have demonstrated the link between physical habitat diversity and biotic diversity. In one recent post-project appraisal, the ecological benefits of instream habitat diversification have been given support. Jungwirth *et al.* (1992) demonstrated the correlation between variance of maximum depths, as a measure of habitat structure, with the number and diversity of fish species. On the fifth-order River Melk, Austria, enhanced habitat diversity by creating shallow water lagoons, marginal gravel bars and riffles resulted in an increase in the number of fish species from 10 to 19, a threefold increase of fish density and biomass, an increase in the annual production of 0+ fish, and an increase in the number of benthic invertebrate taxa from 202 to 272. The newly created riparian habitat provided important refuge habitats during floods, places for hatching and emerging, and nursery grounds for younger benthic instars and fish fry.

12.4.4 BIOLOGICAL CONTROLS

The control of animal and plant populations is often necessary to achieve rehabilitation objectives, both to sustain populations of some species and also to prevent overpopulation of other species particularly favoured by a management regime. Vegetation control is a common practice (e.g. Wade, 1994). Management of unwanted plants includes mechanical, chemical and other controls, different river conditions dictating the type of vegetation control to be applied. Planting is also practised, especially to protect river banks from erosion by boat wash, for example, along the River Thames (Hemphill and Bramley, 1989). Without sustained management, forest expansion from fragmented woods into formerly cultivated land, for example, is typically dominated by monopolistic species and an impoverished flora (Pautou and Décamps, 1985).

Fish culture is an ancient pursuit and fish stocking remains a widespread practice (Dodge and Mack, 1994). In reviewing the main conservation options for managing freshwater fish resources in Britain, including the conservation of threatened species, Maitland and Lyle (1992) identified stock transfer, together with improved legislation to prevent the introduction of potential harmful species, as particularly useful. One task of river rehabilitation is to introduce or enhance species which may quickly become adapted to that particular system. The transfer of adult salmon from overstocked areas to underutilized parts of the same system has also been advocated with the advantage that the progeny will be of 'wild quality' compared with the juveniles produced from hatcheries and released into streams. The stocked race will not be directly analogous to the original race, but it will be a race that adapts well to the contemporary river conditions. It is vital that stock type should be matched as closely as possible, both physically and biologically, to the 'new' river (Thorpe, 1988).

12.4.5 CONTROLS ON HUMAN ACTIVITIES

Overfishing can be a major problem in some river fisheries, but controls on catches, access (especially seasonal restrictions and controls on the numbers of fishers), and fishing methods have been found successful (Petts *et al.*, 1989b). Similarly, controls on riparian land uses (such as grazing and access for recreation) may need to be controlled to restore riparian vegetation successfully (Risser and Harris, 1989). Grazing retirement can have particular benefits for remnant areas of native vegetation and Armour *et al.* (1991) highlight the value of grazing controls in riparian areas for fish habitat. On the floodplain of the River Seine, grazing of the marshes and wet grasslands by animals adapted to this type of environment, such as Highland Cattle and Carmargue horses, has stabilized the ecological succession and prevented the development of shrubs and trees, thereby sustaining the diversity of wetland patches (Lecomte and Neveu, 1986).

12.5 CATCHMENT MANAGEMENT

Some of the major impacts causing ecological changes within a sector of a river relate to catchment land use practices, influencing runoff and water quality, and river management (e.g. dams, removal of coarse woody debris) in remote sectors upstream or downstream. For example, for restoring migratory fish stocks, catchment management is necessary because sector-scale management, even if target habitats – such as spawning areas – are defined and given special protection, would be inadequate. The obvious example is Atlantic Salmon (*Salmo salar*) which has quite specific environmental requirements (Table 12.2). Inadequate discharges or water quality at any point along a river may severly constrain opportunities for rehabilitation as would the impedence to free passage caused by weirs, dams and impoundments.

Table 12.2 Environmental factors limiting Atlantic salmon populations (based on Banks, 1991)

The life cycle	Limiting factors
Adult return	Water quality in the estuary River water quality Obstructions to passage Flow quantity Quantity–quality interrelations to produce the right combinations at the right seasons
Spawning	Availability of suitable gravel (quantity and quality) Adequate flows during spawning season
Nursery areas	Availability of suitable habitat (quantity and quality) Reliability of flows Adequate water quality
Smolt migration	Presence of diversions and abstractions Obstructions to passage Adequate downsteam water quality

12.5.1 BUFFER ZONES

Buffer zones along channels in headwater catchments can play an important role in reducing the pollution of watercourses. Riparian buffer zones act as a filter for particulates and storage for solutes between the hillslope and the river channel (Large and Petts, 1994). The primary retention processes involved are:

- Interception of sediment-bound nutrients, especially phosphorus, and other contaminants, such as pesticides, transported by surface runoff;
- Uptake by vegetation or microbes of soluble nutrients (particularly nitrate); and
- Association of solutes with organic and inorganic soil particles.

In temperate zones, organic riparian soils can significantly reduce the concentration of nutrients in groundwater, as long as the root zone is not bypassed by deep groundwater flow or pipe drainage.

12.5.2 CONSERVATION CORRIDORS

The importance of river corridors for nature conservation is well established (Naiman and Décamps, 1990; Boon *et al.*,1992). Corridors not only provide ecotonal habitats between the terrestrial and aquatic ecosystems, they also provide a network of routeways through a drainage basin. A restored river corridor should:

- Provide sufficient space for species;
- Be sufficient to protect habitat quality and wildlife from adverse impacts of adjacent land uses; and

- Have adequate connectivity to allow freedom of movement throughout the available stream network.

Most mammal, reptile and amphibian species have been shown to concentrate within 60 m of a river bank (Brinson *et al.*, 1981). Van der Hoek (1987) recommended a 150 m-wide buffer zone to improve groundwater quality, improve floristic diversity and to protect vulnerable and rare plant species but even 5–15 m riparian strips can provide valuable habitat for fauna (e.g. Budd *et al.*, 1987). Floodplain management need not create simple corridors. A bead-like form can have considerable value, with large areas linked by narrow connections (Large and Petts, 1994). Brinson *et al.* (1981), for example, suggest that 5–6 ha habitat 'islands' can support near-maximum bird diversity. However, where there are important alluvial aquifers and groundwater flow has a major influence on the habitat patch mosaic, a larger buffer zone may be required.

12.6 CONCLUSION

Scientifically based approaches and tools are needed to *limit* impacts of river and catchment development; to *mitigate* the effects of river regulation, abstraction or waste disposal where such actions are accepted as necessary for socioeconomic development; and to *rehabilitate* degraded rivers by stimulating and enhancing natural recovery processes. However, in reality the attainment of these aims is constrained by the goals of socioeconomic development. It is necessary therefore to make a pragmatic choice of the best practicable environmental option (Royal Commission, 1976, 1989; Petts, 1990a). Importantly, such an approach recognizes the time-limited nature of decisions, flexibility in management being important so that the 'best' option can be revised once new knowledge is available.

The analysis of fluvial hydrosystems provides an approach with space- and time-scales appropriate for management, which emphasizes the important relationships between hydrology, geomorphology and ecology. It presents a framework for applying scientific knowledge to the ecologically sound development of water and land resources within river corridors. The management of river sectors provides a pragmatic approach to river rehabilitation. The application of the fluvial hydrosystem approach to the integrated management of all river sectors throughout a drainage network offers the potential for developing catchment management with clear benefits, not only for nature conservation, but also for all river users.

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