Chapter 2

The River Ecosystems and their Natural Flow Regimes

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The ecosystem provides a conceptual framework for the study of interactions among organisms (plants, animals and microbes) and their abiotic environment (water, energy, minerals and gases) along with their temporal dynamics (see Likens 1992). The distribution and arrangement of biotic and abiotic elements within an ecosystem is referred to as its structure (Wallace 2007). The interactions between these structural elements involve several ecological processes (such as photosynthesis, nutrient uptake, feeding and decomposition) that lead to flux of energy and biogeochemical cycles. The processes result in ecosystem functions such as the production of organic matter. Tansley (1935) defined ecosystems as ‘spatially explicit units of the Earth’. However, the spatial boundaries of ecosystems are defined somewhat arbitrarily because these are not based on known functional discontinuity between adjacent ecosystems. The problem of determining boundaries for ecosystems is relatively small in case of many aquatic systems (particularly lakes and rivers) where the lateral boundaries are ostensibly apparent (Likens 1992). All ecosystems derive their energy and gases from a common source – the sun and the atmosphere- and the water that continuously circulates through the atmosphere, and interact with each other to different extent in very different ways. The movement of animals across adjacent ecosystems and even on inter-continental scale is an important example of interaction among ecosystems.

Aquatic ecosystems are differentiated from terrestrial ones by the abundance of water in and above the substratum.
that significantly influences all components (energy, gases, minerals) of the abiotic complex and hence, also, the organisms inhabiting them. The aquatic ecosystems invariably depend upon the terrestrial surrounding areas (called catchments or watersheds) through which the water passes (as surface or subsurface runoff) before entering into them. Rivers are distinguished from the lakes by their natural uninterrupted flow with a very short residence time. The drainage basin of a river (including its tributaries) is generally shared by several kinds of aquatic ecosystems which may be physically separated but are usually linked together by the hydrological cycle (Figure 1).

**EVOLUTION OF THE ECOSYSTEM APPROACH TO RIVERS**

As mentioned in Chapter 1, humans have been interested in the rivers for their water and fish since historical times. However, scientific pursuit of rivers is only about a century old. Geographers, geologists, geomorphologists, hydrologists and geochemists studied flows (volume, velocity) and channel forms and dynamics of the rivers and their role in shaping the Earth’s surface and in the flux of sediments, nutrients and pollutants from watersheds to oceans over temporal scales varying from hours to millennia (Lane 1955, Leopold 1973, Schumm 1960, Wolman 1967, Yerke 1971). The science of fisheries itself emerged during the middle of the 19th century, after a rapid decline in fish catch, almost at the same time in North America (1871) and Europe (Italy 1872; Germany 1891). Fish biologists focused largely on the distribution of fish fauna in different habitats of a river (e.g., Hamilton 1822, Day 1875-78, Hora 1928). Fish distribution patterns were studied to classify European water bodies (von dem Borne 1877) and distinguish between river zones in North America (Shelford 1911). Until after the middle of the 20th century, the focus on the management of river fisheries by recognising somewhat characteristic fish assemblages in different river zones from source to mouth continued to influence ongoing river ecological studies (Illies 1955, Huet 1959). Illies and Botosaneanu (1961) observed that assemblages of bottom-dwelling (benthic) invertebrates changed along with changes in fish assemblages in different zones, which differed in their flow, substrate and temperature characteristics. They distinguished two major zones in hill streams: (a) Rhithron - the stretch of the river extending from the source to the point where monthly mean temperature rises to 20°C, and (b) Potamon - the region where monthly mean temperature rises above 20°C. Rhithron was further characterised by a rocky (or boulder and gravel) substratum, fast and turbulent flow and high oxygen concentration whereas the Potamon had slower flow, sandy to silty substratum and lower oxygen concentration.

Invertebrates, algae, macrophytes and microorganisms were also investigated for their distribution patterns, their responses to physical and chemical characteristics of water, and their trophic relationships. These studies were summarised in the first book on river ecology by Hynes (1970). In India also, significant studies were made during the 1950s and 1960s on various kinds of organisms and water quality of several major rivers (for references see, Jhingran 1991, Gopal and Zutshi 1998).
Figure 1. Conceptualised illustration of a river from its source to mouth at the sea, along with various associated aquatic habitats (from Gopal et al. 2010)
The River Continuum Concept

An ecosystem perspective of the rivers emerged rather late; its development can be traced back to the late 1960s in the North American studies which revealed the importance of plant litter as the major source of energy for a diversity of invertebrate organisms in the pristine (undisturbed by humans) streams (Minshall 1967, Kaushik and Hynes 1968). Kaushik and Hynes (1968) reported that the decay of leaves (falling directly or wind blown into the stream) started with the leaching of soluble substances, followed by fragmentation of leaves by invertebrate organisms. The chemical composition of the leaves (nitrogen and lignin content) influenced the rate of decay by various invertebrates (Kaushik and Hynes 1971). Later studies on the decomposition of plant litter brought out the role of microbial communities and other organisms (for details see Allan 1995). Further studies examined the upstream/downstream linkages in relation to the downstream transfer of water by combining the abiotic factors (channel morphology and flows with the structure and function of biological communities. It was observed that most of the organic matter (plant litter) entering the headwaters is processed gradually in the river downstream by larval stages of different groups of insects. The composition of these groups varied along the course of the river: in the upper reaches of a river, shredders and collectors were the main abundant groups whereas in the middle reaches the grazers feeding on periphyton increased substantially. In the lower reaches, as the organic matter is converted to fine particles, collectors become the most abundant (Figure 2).

Based on these observations, Vannote et al. (1980) theorized that ‘biological communities developed in natural streams assume processing strategies involving minimum energy loss. Downstream communities are fashioned to capitalize on upstream processing inefficiencies. Both the upstream inefficiency (leakage) and the downstream adjustments seem predictable’. They proposed the River Continuum Concept as ‘the framework for integrating predictable and observable biological features of lotic systems’ (Vannote et al. 1980). The concept promoted the view of the rivers as linear features delimited by the bed and banks of the main channel dominated by unidirectional flow which linked various sections longitudinally such that each downstream section was dependent upon and influenced by the upstream section.

The River Continuum Concept (RCC) triggered numerous studies many of which supported it, others refuted it and yet others offered many modifications (Statzner and Higler 1985, Sedell et al. 1989). The RCC was developed for relatively smaller streams of lower order that were undisturbed. It focused on changes in the biota and certain processes but did not duly recognise habitat changes and their heterogeneity (see Rice and Roy 2008). The influence of large tributaries, wide floodplains and the interruption of flow by human-made dams could not be explained by the RCC. Cummins et al. (2006) recognised the need to ‘integrate the lateral components of riparian vegetation and small tributaries with the in-channel heterogeneity’.

The Flood Pulse Concept

Studies of large river systems which develop extensive floodplains, brought into focus the importance of the lateral interaction with the floodplains through periodic flood events. The
linkages between floodplains and riverine fisheries were demonstrated by Welcomme (1979). River-floodplain interactions are most intensive in case of the Amazon River which annually rises by up to 18 m submerging vast areas of forest under water for several months. Detailed studies of the Amazonian floodplains, together with those of other large rivers, resulted in the Flood Pulse Concept (FPC) proposed by Junk et al. (1989). The FPC emphasized the role of the flood pulse (a predictable flooding regime) in mobilising material (organic and inorganic) and energy from the floodplain into the main channel, that supports the food webs (including fish) in the rivers (Figure 3). The FPC also emphasized the importance of the floodplain for fish and breeding, nursery and feeding habitats. The postulates of the

Figure 2. Characterisation of the river ecosystem according to the River Continuum Concept (redrawn from http://educationally.narod.ru/freshwaterecostreams/photoalbum.html)
Figure 3. River-floodplain interaction according to the Flood Pulse Concept (reproduced with permission, from Bayley 1995)
FPC have received extensive support from numerous studies in different countries and have been extended to large temperate rivers (Tockner et al. 2000). The FPC thus added the perspective of lateral connectivity to the longitudinal connectivity of the riverine ecosystem.

**Stream-Groundwater Interaction**

For long the connections between the surface flows, subsurface flows and groundwater had been well known. In 1940s the subsurface water was shown to be inhabited by a variety of organisms. Orghidan (1953), based on extensive surveys along the river Danube in Romania, concluded that ‘the contact between stream water and groundwater creates, within the subsurface, a transitional zone’ which forms a unique habitat with characteristic physico-chemical conditions and a diverse group of fauna. He named it as ‘hyporheic biotope’. The importance of the hyporheic zone to the ecology of streams/rivers was highlighted by Stanford and Ward (1988) who described it as a ‘temporary refuge for organisms in times of physical and biological adversity’. Numerous studies during the past few decades characterised the hyporheic zone as a surface water-groundwater ecotone (Figure 4) and described in detail its faunal community and contribution to the functioning of river ecosystems as water, nutrients, organic matter and organisms move across the system (Boulton et al. 1998, 2010, Williams et al. 2010, Robertson and Wood 2010, Krause et al. 2011, Stubbington 2012).

![Diagrammatic representation of the hyporheic zone](adapted from Williams 1993)

Figure 4. Diagrammatic representation of the hyporheic zone (adapted from Williams 1993)
The importance of the stream-groundwater interaction brought into focus the three-dimensional nature of rivers, dependent upon the longitudinal, lateral and vertical transfers of material, energy and biota. A fourth temporal dimension was added to consider their dynamics (Ward 1989). It is now well-recognised that the ecological integrity of the rivers depends upon the interactions of hydrological, geomorphological and biological processes over a range of time scales (Calow and Petts 1992, 1994, Petts and Amoros 1996).

**Other Recent Concepts**

During the past four decades or so, many other concepts and hypotheses have been developed to explain the functioning of various river ecosystems. It is necessary to mention here briefly a few of these developments. Many researchers felt that neither the RCC nor the FPC explained fully the ecosystem functioning of all large rivers. Whereas the RCC, based on smaller temperate streams, considered the allochthonous inputs of organic matter from upland areas as major driver of riverine food webs, the FPC demonstrated the role of allochthonous inputs from the floodplains. Thorp and Delong (1994) observed that in some reaches of the rivers autochthonous (within stream) production by algae and macrophytes (particularly in the riparian zone) is the major source of energy for the consumers and accordingly proposed the Riverine Productivity Model (RPM).

Similarly to account for the downstream transport of nutrients with the flow along with their cycling, Webster and Patten (1979) developed the Nutrient Spiraling concept that seeks to integrate the two processes. This is elaborated later in the section on nutrient dynamics.

In view of the large geomorphological and hydrological diversity along the river and its tributaries, the patch theory of terrestrial landscapes was applied to river systems which were also viewed as hierarchical mosaic of patches (Pringle et al. 1988, Townsend 1989). The hierarchical patch dynamics perspective considers each river network as a unique, discontinuum comprised of a longitudinal series of alternating stream segments with different geomorphological structures, from headwaters to mouth (Poole 2002).

Fausch et al. (2002) employed the term riverscape (first used by Ward 1998) to advocate a holistic view of the rivers, "not just of disjunct reaches but of the entire spatially heterogeneous scene of the river environment unfolding through time". The riverscape “encompasses the entire stream network, including interconnections with groundwater flow pathways, embedded in its terrestrial setting ... with considerable animal and human modifications of flow paths likely along the way” (see Hauer and Lamberti 2011). For a recent discussion, see Carbonneau et al. (2011).

More recently, a riverine ecosystem synthesis (RES) model has been proposed by merging the RCC, FPC, RPM and the nested hierarchical patch dynamics (Thorp et al. 2006, 2010). The RES conceptualises rivers as “downstream arrays of large hydrogeomorphic patches (called as Functional Process Zones) formed by catchment geomorphology and climate”. The RES is visualised to provide a framework for understanding broad, often discontinuous patterns along longitudinal and lateral dimensions of river networks and local ecological patterns across various temporal and spatial scales (Figure 5). Figure 6 presents a comparison of the four major concepts.
Figure 5. Schematic view of a river catchment showing various ecological functional process zones (FPZs) from headwaters to the delta (reproduced with permission, from Thorp et al. 2006)

Figure 6. Diagrammatic representation of main concepts for characterising a river ecosystem (adapted from http://paulhumphriesriverecology.wordpross.com)
Rivers are complex and dynamic ecosystems whose abiotic and biotic components change gradually and continuously from the source till the mouth. The nature of a river system is primarily controlled by the interaction between geology, climate and geomorphic features. The flow of water in the river, controlled largely by the climate, is the master variable which together with the sediments derived from the substrate, determines the morphological features of the river’s channel and corridor. Climate also controls the landforms and vegetation communities. Geology influences the drainage patterns, bed materials (through slope and erodibility of the substrate) and water chemistry. Vegetation in the catchment and the river corridor plays a significant role in determining the kind of sediments found in the river bed and floodplain. Fluvial geomorphic processes shape the diversity of physical features along the valley floor. Interplay between these features, sediment characteristics and the flow regimes results in a diversity of habitats, and consequently in a diversity of plant, animal and microbial communities. The geomorphic features are also in turn influenced by the plant communities found which develop along valley floors through biophysical interactions (e.g., sediment trapping, bank stabilisation and organic matter accumulation). Further, geomorphic processes create a variety of habitats within the channel and in the floodplain.

Described below are five major components of the river ecosystem; physical habitat (fluvial geomorphology), flow regime, water quality, biological diversity, and the riparian (including the floodplain) zone, along with their interactions (cf. Rutherford et al. 2000).

**Physical Habitats**

Rivers comprise of a complex array of habitats which vary enormously along extremes of spatial and temporal scales, that are also coupled with geomorphological processes according to their scale (see Kirkby 1990). Here we are not concerned with very large spatial (biogeographic) and temporal (millions of years) scales of developmental processes such as tectonic movements and climatic change which have also influenced the stream biota on the evolutionary time scale (e.g. Hora 1937, 1944). These habitats result from interactions between the structural and hydraulic components of the river channel and the discharge regime (Maddock 1999). An understanding of the physical habitat characteristics and their interaction with the fluvial processes is of utmost importance to the assessment of river ecosystem functions, and for the conservation and management of these ecosystems.

**The River Channel**

On a macro-scale, the river consists of a main channel and its fringes (river bed) bounded by the natural levees on both sides. Beyond the natural levees lies the floodplain which is periodically flooded by over-bank flows. On a meso-scale, the river includes running water, standing water, temporary water, groundwater and terrestrial habitats. The channel bed is modified by the flow-erosion-deposition regime. Many channels are sinuous, eroding into the outer banks of the river bed, depositing on the inner banks and actively meandering or passively responding to confining points of resistant geology. Less sinuous channels
may change by braiding. Sheltered banks may have backwaters and side channels. Along the longitudinal axis, occurs a sequence of ‘pools’ and ‘riffles’. Pools are areas of deep slow moving water, often with fine bed material whereas riffles are shallow water areas with coarser bed material. The location of pools and riffles in a channel changes with the channel morphology and planform. On a micro-scale, further habitat differentiation occurs according to the nature of bed material, vegetation, animals and flow velocity.

The diversity of habitats changes along the river course, from the headwaters to the mouth. Headwater streams are generally straighter; meanders and migration increase downstream and with age. Mountain streams have fast and turbulent flows, are steep and unstable with the bed composed of rocks or gravel with occasional sandy patches, while channels in the flat plains are slow flowing, have beds composed of sand and silt and meander over large areas. Middle and lower reaches are dominated by the transfer and deposition, respectively, of materials.

During the past few decades, rivers and riverine habitats have been classified in several ways. These classification schemes may be categorised according to spatial and temporal scales, or the disciplinary focus (geomorphology, hydrology and ecology/biology) and their combinations (Naiman et al. 1992, Buffington and Montgomery 2013). Many classification schemes are however limited to a section of the spatial length of a river (e.g., only mountain streams). A few of the geomorphological classification schemes are examined here. Hydrological classifications deal with flow regimes and will be described later. However, it is interesting to note that river habitats have also been classified on the basis of depth and flow velocity alone (Hawkins et al. 1993).

Horton (1945) for the first time proposed a classification of river networks based on the links between tributaries. It was improved upon by Strahler (1957; Figure 7). The tributaries of the network are identified into ‘Orders’, starting from those at the top (first order). Two first order channels join to form second-order channels; i.e, the second order channel starts below the confluence of two first-order channels, and continues until it meets another Second order channel. The Order of the channel does not change by the joining of another tributary of lower order. The stream order is usually correlated with drainage area, slope, and channel size. Stream order is not indicative of stream morphology and processes which depend on factors such as channel slope and confinement, the supply of water and sediments, etc. The lower order channels in mountains such as the Himalaya are vastly different from those arising in central Indian highlands or even the Western Ghats in Southern India.

Schumm (1977) considered the entire river basin as one unit, and emphasising the fluvial processes related to sediments, distinguished three zones in a river: (a) the uppermost, primarily eroding, production zone from which water and sediment are derived, (b) the transfer zone through which the sediments are transferred downstream, and (c) the deposition zone where the sediments are deposited. Montgomery and Buffington (1997) recognized three primary channel-reach substrates: bedrock, colluvium and alluvium. They further grouped the reaches into source, transport, and response segments on the basis of the ratio of transport capacity to supply of sediments. Colluvial channels are characterized
by randomly deposited rock debris from adjacent hillslopes and experience weak or ephemeral fluvial transport. Alluvial channels are formed with increasing fluvial energy which transports and distributes sediments to create various forms of channels. Coupling the reach morphology (substrate-based) with reach-level channel processes, they classified mountain streams into seven distinct reach types (Figure 8). These were later identified as ‘process domains’, based on specific disturbance process, channel morphology and aquatic habitats (Montgomery 1999).

Most fluvial geomorphological studies have been devoted to river segments only. A river segment is a part of the river demarcated by topographic discontinuities in the structure of the bed, slope, river discharge and sediment quantities. It may be hundreds of kilometers long and several channel planforms (shape viewed from above) can be defined within a segment. These planforms usually remain in dynamic equilibrium for thousands of years (Frissell et al. 1986, Gregory et al. 1991, Rademakers and Wolfert 1994). Leopold and Wolman (1957) distinguished between three planforms - straight, meandering and braided river segments, based on a combination of several hydraulic factors (slope and discharge, sediment load and grain size, channel roughness, width and depth ratio, and riparian vegetation. Meandering channels are sinuous single channels with a series of point bars, deep pools and eroding meander bends. Braided rivers comprise of several channels separated by gravel bars or sand bars (or islands). Anastomosing (multi-thread channels separated by islands cut from the floodplain) and wandering channel (intermediate between meandering and braided) forms were recognised later.
Emphasising upon the importance of sediment load of the river, Schumm (1977) related the channel pattern and stability to size of sediment (sand, silt, clay fractions) and the mode of transport (suspended load, mixed load, bed load), and proposed a conceptual framework for classification of alluvial rivers Schumm (1977, 1985) (Figure 9). This scheme has been refined and elaborated to cover a wider range of rivers by Church (1992, 2006; Figure 10). Buffington et al. (2003) and Buffington (2012) presented another framework categorising channel patterns from the interactions between topography (different valley types), substrate (alluvial, bedrock, colluvial), streamflow and sediment supply (Figure 11). Similarly, Miall (1996) based his classification primarily on sediment characteristics, to group the streams into three classes (1) gravel dominated, (2) sand dominated high-sinuosity and (3) sand-dominated low sinuosity. These were further categorised into 16 Styles based upon predominant flow characteristic (e.g. flashy, ephemeral, sheet flood, sand-bed rivers).

Some useful classification schemes have described the spatial and temporal scales of patterns and processes of fluvial systems in terms of a hierarchy of scales. Frissell et al. (1986) presented a hierarchical framework for streams according to geomorphic features and events, and spatio-temporal boundaries by distinguishing between the stream system,
Reach is defined as a part of the river segment between breaks in channel slope, local side slopes, valley floor width, vegetation and/or bank material (Frissell et al. 1986). It is usually defined by its longitudinal characteristics or gradients. A subsystem of a reach determined by bed topography (lateral gradient), water depth and current velocity and position relative to the main channel is identified as an ‘ecotope’ (Frissell et al. 1986).

Paustian et al. (2010) recently revised their earlier hierarchical classification, developed in 1992, for river channels in Alaska (from mountains to the coast). They recognise Process groups based on differences in hydrologic function, landform, and channel morphology; Channel types (within a process group) based mainly on channel width, and/or incision depth, gradient and channel pattern, and further differentiation of phases, that results in more than 50 types. Similar hierarchical classification have been proposed in other regions as well (for details see, Buffington and Montgomery 2013).

Rosgen’s (1994) hierarchical classification of natural rivers, though developed for the mountain regions, is the most well known and widely used system. It lays great emphasis on
Figure 10. Alluvial river channel forms and their principal governing factors (redrawn from Church 2006)
Figure 11. Stream channel types and their characteristics as a function of topography, streamflow, and sediment supply (redrawn from Buffington and Montgomery 2013)

Figure 12. Hierarchical organization of a stream system and its habitat subsystems. Linear spatial scale is appropriate for second- or third-order mountain streams. (reproduced with permission, from Frissell et al. 1986)
dimensional properties of the river channels to define eight primary stream types at reach scale, using a hierarchical decision tree and features like channel threads, dimensional properties of entrenchment ratio, width-depth ratio and sinuosity. Sediment size and channel slopes are used to classify these types into 94 subcategories (Figures 13 and 14).

- Entrenchment Ratio, ER = W fpa/W bkf
- Bankfull Width/Depth Ratio, W-D Ratio = W bkf/ d bkf
- Sinuosity = $S_{valley}/S_{channel}$
- Channel Bedslope $S_{channel}$

The classification scheme, however, has not been applied to or evaluated for large and tropical floodplain rivers.

Whiting and Bradley (1993) considered mainly bed mobility to classify headwater streams into 42 classes on the basis of physical processes and their relative rates (erosion potential of hill slopes, dimensional properties, morphological features including channel gradient, channel width, valley width, median sediment size and mode of fluvial transport).

Whereas, the majority of river classifications have focused on mountain regions and headwaters, lowland rivers with vast floodplains have received relatively little attention. The importance of the river-floodplain interactions to the physical processes, morphology, and the quality and diversity of habitats (both in the channel and the floodplain) is being realised.

Figure 13. Longitudinal profile, channel cross-sections, and plan-view patterns of major stream types (reproduced with permission, from Rosgen 1994)
Figure 14. Rosgen’s classification of stream types. (reproduced with permission, from Rosgen 1996).

As a function of the “continuum of physical variables” within stream reaches values of Entrenchment and Sinuosity ratios can vary by +/- 0.2 units; while values for Width/Depth ratios can vary by +/- 2.0 units.
only in recent years. Melton (1936) had distinguished between floodplains formed by meandering (lateral accretion), overbank (vertical accretion), or braiding processes. Woolfe and Balzary (1996) proposed a classification based on the prediction of the sedimentation and erosion regimes. They recognised eight categories that relate the rates of channel to floodplain aggradation and degradation (rate of change of channel elevation and rate of change of floodplain elevation).

Nanson and Croke (1992) classified floodplains by recognizing that various fluvial processes and changes in stream flow and sediment supply determine characteristic floodplain morphology (Figure 15). They identified three main classes of floodplains: high-energy non-cohesive, medium-energy non-cohesive and low-energy cohesive. These three

![Figure 15. Example of river–floodplain types showing medium-energy, noncohesive environments (reproduced with permission, from Nanson and Croke 1992).](image-url)
classes are further subdivided into thirteen suborders based on geomorphic or fluvial factors: Valley width, Gross stream power, Individual channel width, Specific stream power, Quantity of sediment load, Calibre of sediment load and Discharge (Figure 15).

More recently, Brierley and Fryirs (2005) further recognized that channel–floodplain interactions may be modulated by extrinsic factors (e.g., bedrock outcrops, glacial moraines, relict terraces) in partly confined, semi-alluvial rivers (Jain et al. 2008, Fryirs and Brierley 2010 Brierley et al. 2011). They developed a ‘river style’ framework which uses successional (evolutionary) models to assess channel condition and to inform restoration actions (Figure 16). The ‘river style’ is a process-based description of (1) land type and degree of confinement, (2) river character (channel pattern, bed material, and geomorphic units (type of valley fill, floodplain characteristics, channel-unit assemblages)), and (3) river behavior (associated fluvial processes). According to Buffington and Montgomery (2013), this approach “lacks process-based descriptions for the morphogenesis of a given style (e.g., the flow and sediment transport processes that give rise to a given channel morphology). Instead, morphogenesis is described in terms of observed historical changes in basin characteristics (discharge, sediment supply, riparian vegetation) and the consequent morphologic response within a given channel succession sequence”.

**The Hyporheic Zone**

Another very important riverine habitat is the hyporheic zone – the transitional area between surface, subsurface and groundwater (Figure 4). It comprises of the interstitial, water-
filled space beneath river beds. Most active exchange of water, nutrients and organisms between the river and aquifer occurs in this zone. The extent of the hyporheic zone varies considerably as riverine organisms have been found in groundwater up to 2 km from active stream channels (Stanford and Ward 1988).

The physical habitat of the hyporheic zone is highly heterogeneous (Orghidan 1955; English translation 2010), according to the spatiotemporal variability in hydrology, sediment characteristics and water quality. Buffington and Tonina (2009) show that the hyporheic environments and their spatial variation across the landscape within mountain catchments are easily explained by reach scale channel morphologies (e.g. step-pool, pool-riffle, and braided) and associated fluvial processes. A review of hyporheic zones in the U.K. has concluded that the sediment, nutrients and contaminants delivered to a site from hillslopes or upstream reaches are important for the stability, disturbance and maintenance of hyporheic zone habitats. At reach and site scales, hyporheic exchanges are influenced by topographic features and changes in bed permeability, especially the presence of riffles and sediment heterogeneity. Plan-form irregularities, such as meanders also induce hyporheic exchange. The role of hydrology and sediment characteristics in creating a diversity of hyporheic habitats is further discussed by Stubbington (2012).

Flow Regimes

The flow in a stream is derived from the surface (overland) and subsurface runoff of rainfall and snowmelt from the watershed. It is directly influenced by the climate (mainly precipitation) and the nature of the substratum. The flow of a river, also called as discharge, is expressed by the volume of water that moves over a specified point over a fixed period of time. It is expressed as either cubic feet per second (cusec, cfs) or cubic meters per second (cumec, m³ s⁻¹). Flow is a function of water volume and velocity, and the velocity increases with the volume of the water in the stream.

River flow at any point along the river varies over time and the temporal scales range from minutes (e.g. flash floods) to hours and decades. Some rivers have a naturally constant flow of water with seasonally higher levels. Ephemeral rivers in arid areas flow only occasionally. The variation of discharge with respect to time is best presented graphically by a hydrograph in which the discharge is averaged over time intervals ranging from 1 day to a month (Figure 17). The total flow of a river is often separated into base flow and direct runoff. Base flow is defined as “That part of the stream discharge that is sustained primarily from groundwater discharge. It is not attributable to direct runoff from precipitation or melting snow” (USGS 2005). It is important to note that the base flow differs greatly from direct flow in its magnitude, duration and timing; in most perennial rivers in seasonal climates such as those in South Asia, the base flow continues for several months after the rains have ceased.

Every river is characterised by its specific flow regime, that is the temporal pattern of flow variability which depends upon the climate and watershed characteristics such as rock structure, basin morphometry, vegetation and soils. The flow regime is described by five common hydrological attributes: the magnitude, duration, frequency, amplitude, rate of
change and timing of flow during the annual cycle (Figure 17). As we shall see later, each of these attributes, besides the daily, seasonal and annual patterns of stream flow, determine many of the physical and biological properties and processes of a stream (Gordon et al. 1992). Poff et al. (1997) proposed the natural flow-regime paradigm which postulates that the structure and function of a riverine ecosystem are dictated by the pattern of temporal variation in river flows, of which the magnitude, frequency, seasonal timing, predictability, duration and rate of change of flow conditions are the primary components. Poff et al. (1997) also recognised ecologically relevant flow events namely, low flows, extreme low flows, high flow pulses, small floods, and large floods which could be distinguished by the variation in the primary flow components.

There has been considerable interest in the classification of hydrological variability at scales ranging from river basins to national, regional and global. Olden et al. (2012) have reviewed these hydrologic classifications and differentiated between deductive approaches, which are based on those aspects of the environment assumed to influence stream flow, and inductive approaches which use the discharge time series data to analyse the emergent properties of the flow regimes.

Beckinsale (1969) defined various flow regimes on the basis of Köppen’s climatic classification (Köppen 1936) but recognized their dependence on the interactions between climate, geology, vegetation, soil and basin morphology. Flow regime classifications based on basin characteristics assume that catchments with similar physical properties produce similar hydrological responses (Acreman and Sinclair 1986) but climate being the first order control upon runoff, flow regimes are likely to vary within a basin. Statistical measures can however reveal differences between catchments or between locations on the same stream, and changes due to natural trends or human interventions. Haines et al. (1988) used extensive hydrological data for a global classification of rivers, based on differences in river
regimes. He distinguished 15 groups based on average flows expressed as percentages of the mean annual flow (Figure 18). Within USA, Poff (1996) identified seven permanent and three intermittent flow types on the basis of parameters for flow variability, predictability and low-flow and high flow extremes. Kennard et al. (2010) analysed the hydrologic regimes for Australia and recognised 12 classes of flow-regimes which differed in the seasonal pattern of discharge, degree of flow permanence, variation in flood magnitude, and flow predictability and variability.

Figure 18. Average flow regime patterns for 15 groups identified globally. Bands of +/- one standard deviation are also shown. (reproduced with permission, from Haines et al. 1988)
Within South Asia, although there are numerous hydrological studies, but hydrological data are classified and highly restricted in availability. Hence flow regimes have not been investigated in detail. The Himalayan rivers are perennial as they receive glacial meltwater during the summer, but their flow regimes are characterised by peak flows derived from southwest monsoonal precipitation in the headwater areas. The peninsular rivers exhibit large variability and usually have two peak lows associated with the southwest and northeast monsoonal precipitation.

Recently the flow regimes of 28 rivers across Nepal were analysed in detail using hydrological data for 12 to 26 years (Kansakar et al. 2002, Hannah et al. 2005). Several types of flow regimes were distinguished on the basis of timing (3 levels) and the magnitude (low, intermediate and high). The timing of the peak moves within a July-September period depending largely upon the advancement of the monsoon, and the magnitude is influenced by topography. Hannah et al (2005) identify the following major flow regime types: (a) Low, marked August peak regimes across far-western Nepal and in some eastern basins with a short summer monsoon and snow and ice-melt; (b) Low, July–August peak regimes in the central to eastern High Mountains and High Himalaya and the eastern Middle Mountains where the summer monsoon arrives earliest; (c) Low–intermediate, August–September peak regimes in the central Middle Mountains due to an extended summer monsoon and greater groundwater contributions; (d) Intermediate–high magnitude regimes along the Middle Mountains–High Mountains boundary with July–August peaks in western–central areas and marked August peaks at higher elevations in eastern–central and eastern Nepal (Figure 19 ).
The analysis of river flow regimes has become more extensive with the growing recognition of the influence of hydrological variability at very small spatial and temporal scales, on ecological processes and various groups of organisms. A variety of methods and hydrological indices have been used to analyse the variability and changes in the flow regimes. Richter et al. (1996) listed 33 individual metrics (and 33 associated measures of variation) for characterizing human modification of flow regimes (Table 1). In a recent study in China, natural flow regimes in the Huai River Basin have been categorised into six classes (low or high discharge, stable or variable, perennial or intermittent, predictable or unpredictable) by analysing 27 years of data with 80 hydrologic metrics by hierarchical clustering techniques. The subject is discussed further in several recent publications (e.g., Lytle and Poff 2004, Bragg et al. 2005, Assani et al. 2006, Oueslati et al. 2010, Bejarano et al. 2010, Carlisle et al. 2010, Snelder and Booker 2013).

Table 1. Hydrological parameters for defining the flow regimes
(adapted from Richter et al. 1996)

<table>
<thead>
<tr>
<th>IHA statistics group</th>
<th>Regime characteristics</th>
<th>Hydrologic parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group 1: Magnitude of monthly flow</td>
<td>Magnitude, Timing</td>
<td>Mean flow for each calendar month</td>
</tr>
<tr>
<td>Group 2: Magnitude and duration of annual extreme flows</td>
<td>Magnitude, Duration</td>
<td>Annual minimum 1-day means Annual maximum 1-day means Annual minimum 3-day means Annual maximum 3-day means Annual minimum 7-day means Annual maximum 7-day means Annual minimum 30-day means Annual maximum 30-day means Annual minimum 90-day means Annual maximum 90-day means</td>
</tr>
<tr>
<td>Group 3: Timing of annual extreme flows</td>
<td>Timing</td>
<td>Julian date of annual 1 day maximum Julian date of annual 1 day minimum</td>
</tr>
<tr>
<td>Group 4: Frequency and duration of high and low flow pulses</td>
<td>Magnitude, Frequency, Duration</td>
<td>No. of high flow pulses each year No. of low flow pulses each year Mean duration of high flow pulses each year Mean duration of low flow pulses each year</td>
</tr>
<tr>
<td>Group 5: Rate and Frequency of change in flow</td>
<td>Frequency, Rate of Change</td>
<td>Means of all in creases between consecutive daily means Means of all decreases between consecutive daily values No. of rises (in flow) No. of falls (in flow)</td>
</tr>
</tbody>
</table>
**Water Quality**

Other physical characteristics of the river also change with distance from the source. As most rivers arise at high altitudes, the temperature usually increases downstream. In the upper reaches, gaseous exchange, unhindered by stratification and positively encouraged by turbulence, mixing and cascades, keeps the water always saturated with oxygen, whereas downstream oxygen deficits increase with greater frequency and duration. Similarly, the chemical characteristics of water also change, with gradually increasing concentration of various nutrients, as a variety of dissolved and particulate substances and plant litter enter the stream with the run-off. Geological, geochemical and vegetational characteristics of the watershed directly govern the water quality. For example, the water of river Yamuna differs from that of river Ganga due to the nature of their respective catchments. Several processes within the river affect the water quality (for details, see Chapman 1996). They include: oxidation of organic matter, water turbulence, evaporation, adsorption on sediments, nutrient uptake by plants (and algae), chemical transformations in the sediments particularly under anoxic conditions. Among major human activities, which affect water quality, are the discharge of domestic wastewaters, industrial effluents and cooling waters, damming the rivers, navigation, dredging and catchment-based activities, especially agriculture using a variety of agrochemicals.

**Biotic Communities**

The diversity of physical habitats within a stream channel and its riparian and floodplain areas is further enhanced by the components of water quality that are influenced by river basin characteristics. Accordingly, riverine ecosystems support a very high diversity of biota. Practically all groups of organisms – from microorganisms to mammals, are represented in riverine environments, and many organisms occur exclusively in rivers. Biological communities however vary along the course of the river. Whereas fish, some birds and mammals can swim against the current, most of other organisms, unless anchored to the channel bed, drift downstream. Some fish occur even in torrents (Hora 1928). Shallow, slow moving streams, the sides of channels where flow velocity is negligible, and shallow pools and riffles are rich in species of various taxa.

Numerous studies have been made on the distribution, abundance, ecology, biology and other aspects of various organisms which inhabit rivers throughout the world. A recent book by Dudgeon (2008) provides a comprehensive account of biota and ecology of rivers in the tropics. In India, riverine fishes have been investigated for over a century, and the biota of Rivers Ganga, Yamuna and Kaveri in particular have been surveyed extensively. The large diversity of organisms is usually categorised into functional groups: the producers (or autotrophs) which include algae and higher plants (macrophytes) and the consumers (or heterotrophs) which include all animals feeding directly or indirectly upon the organic matter derived from the producers. The latter also include microorganisms.

**Microphytes (Phytoplankton and Benthic Algae)**

Microphytes are microscopic photosynthetic organisms of freshwaters, generally referred to as algae. They are either planktonic (freely suspended in the water column) or attached
to various substrates. The planktonic forms are unicellular or colonial, though fragments of filaments are also common. The attached forms occurring on the stream bottom are often referred to as benthic and include epilithic (on rocks or stones), epipsammic (on sand) and epipellic (on clay and organic matter) forms. Forms attached to substrates that are suspended in water (submerged stems, twigs, leaves, etc.) are periphyton.

The phytoplankton comprise largely of chlorophyceae (green algae), cyanophyceae (blue-green algae) and bacillariophyceae (diatoms). They are common producer components in rivers (see Wetzel 2001) although some researchers stress that there is no true plankton (often called potamoplankton) in the rivers and its presence is derived from either the benthic populations that slough off periodically from the substrates or the influx from the adjacent standing water bodies which get connected with the river (Rojo et al. 1994). Phytoplankton are in general absent in the upper reaches with rapid turbulent flow because they are continuously flushed downstream with the flow, but in the slow flowing streams, in pools of standing water within the river channel especially in wider valley reaches, and during low flow period, they develop large populations. The reservoirs constructed on the rivers are another major source of phytoplankton which sometimes develop dense blooms there. Owing to their very low gradient, slow flow and high levels of nutrient enrichment, most rivers of the Indian subcontinent are rich in phytoplankton diversity (for references see, Gopal and Zutshi 1998). Shukla and Asthana (1995) recorded 577 species of algae (151 green algae, 198 bluegreen algae and 223 diatoms) from River Ganga in the plains alone.

Diatoms are invariably the most abundant forms in the rivers and are the dominant group in benthos and periphyton, from which they enter the water column. Benthic diatoms are usually the only forms in the headwater streams with boulders and gravel substrates. Filamentous and periphytic algae occur commonly in shallow pools, waterlogged areas, sand bars, moist banks, and on the substrates such as wood or vegetation in the streams. The distribution of benthic algae depends upon complex interactions between hydrological (flow velocity and depth), water quality (turbidity and nutrients) and biotic factors. Depth and turbidity (caused by sediments) are directly related to light penetration in water and its affect on photosynthesis. Nutrients promote the growth of various algae differently, and diatoms are quite sensitive to eutrophication. Hence, the diatoms which are nearly cosmopolitan in distribution, have been widely used in many countries across the world, for the assessment of anthropogenic impacts on water quality (e.g. Prygiel and Coste 1993; Kelly et al. 1995, Bona et al. 2008, Stevenson et al. 2010). A study of the diatoms in upper Ganga river is included in this book (Nautiyal 2013) to show their variability in different reaches and with flow conditions.

**Macrophytes**

Macrophytes is the term given to all macroscopic plants of aquatic environments. Besides flowering plants, they include, large algae such as *Chara* and *Nitella*, liverworts and mosses, and ferns. Among them, mosses and liverworts develop abundantly on the exposed river beds during low flow periods. These are common near springs, in sheltered areas of large boulders, and on river banks. *Chara* and *Nitella* occur in shallow, sluggish clear water rivers and in side channels, oxbows etc.
Macrophyte communities develop with the reduction in flow velocity and change in the substratum. They vary according to flow rate, substratum, trophic status and general catchment characteristics (Holmes and Newbold 1984). Water movement has a significant effect on macrophyte growth, typically promoting both abundance and diversity of macrophytes at low to moderate velocities, but reducing growth at higher velocities. Macrophyte beds reduce current velocities both within and adjacent to the beds, facilitating increased sedimentation and reduced turbidity (Madsen et al. 2001). While the reduced turbidity increases light availability to macrophytes, sediment deposits on their surfaces retard their growth. In plains, the macrophyte communities are quite diverse and exhibit elaborate zonation. Haslam (1978, 2008) has discussed in detail river vegetation and its role in the riverscape. River macrophytes include quite a large variety of forms: submerged and floating-leaved species occur mostly in shallow water areas and reservoirs (2–3 m deep) if the water is clear. Emergent reeds and cattails are abundant and common along river banks. Reeds and canes (*Phragmites* and *Calamus* species) often form tall stands along fast flowing streams as well. Shrubs and trees are common in the riparian zone (on river banks).

Free floating plants do not occur through large masses of plants such as water hyacinth can be observed stranded along banks or floating down the streams in many rivers of South Asia and other tropical countries. Free floating plants often form large stands along sheltered banks or in pools when the river is not flowing.

It is important here to mention an interesting family of flowering plants – the Podostemaceae (48 genera, 270 species) which occurs throughout the tropics. The members of this family are annual or perennial, aquatic herbs, resembling lichens or bryophytes. They grow attached to rocks or boulders in streams, mostly in rapids and under waterfalls. The plants have no roots but only a minute stem and leaves which are shed when the plants are exposed. They photosynthesise under water, and flowers develop when the water level drops. In India, 19 species occur in Maharashtra, Karnataka, Tamil Nadu, Kerala, Andhra Pradesh, Madhya Pradesh, Orissa, Assam, Meghalaya, Arunachal Pradesh and Uttarakhand (Nagendran et al. 1976). Most species that occur in Kerala are endemic (Mathew and Satheesh 1997). This group of plants is the most threatened amongst aquatic plants, by the construction of dams.

**Zooplankton**

Planktonic animals primarily include representatives of three groups – Cladocera, Copepoda and Rotifera. Similar to the phytoplankton, these organisms are also readily flushed downstream with the flow. However, significant populations survive in sheltered areas near river banks, in pools and shallow sluggish channels. As described earlier in the context of the River Continuum Concept, zooplankton populations develop with the gradual breakdown of the allochthonous organic matter in the upper reaches with very low flow velocities.

The growth and diversity of zooplankton populations are influenced greatly by the allochthonous inputs of organic matter, e.g. in the form of sewage or from the river’s interaction with its floodplain. Numerous studies are available on zooplankton diversity and abundance in different river stretches throughout south Asia.
**Benthic Fauna (Macroinvertebrates)**

The animals living in, on, or in association with various bottom substrates sediments, stones, logs, plants, in the streams and rivers comprise mostly of invertebrates. Because of their relatively macroscopic nature (>2 mm), these are usually referred to as benthic macroinvertebrates. They vary greatly in their form and tolerance to environmental conditions, and depend upon allochthonous or autochthonous organic matter in different stages of decay for their food. Because of their very limited mobility, they are affected to a great extent by the physical and chemical conditions of their habitat.

The benthic macroinvertebrate fauna is composed largely of the larval stages of several orders of insects, crustaceans, molluscs and nematodes although many other groups are also represented. Benthic macroinvertebrates are among the most extensively investigated fauna, other than fish in the streams and rivers throughout the world. The species composition, density and abundance of different groups varies considerably between rivers and along the course of the river in relation to water quality (Chapman 1996). In earlier studies, the variations were attributed to water temperature along the elevational gradient and accordingly, three zones namely crenon, rhithron and potamon – were recognised with different benthic assemblages (Illies and Botosaneanu 1963). Robinson et al. (1993) also observed water temperature to be a major factor for differences in benthic fauna between stream types. However, a detailed analysis of benthic fauna in fourteen streams at different latitudes from Alaska to New Zealand showed that hydraulic characteristics of the rivers (estimated from measurements of current velocity, depth, substrate roughness, surface slope, and hydraulic radius) have a predominant influence on the patterns of benthic macroinvertebrate community except under extreme environmental conditions (Statzner and Higler 1985, 1986). Recently, Eady et al. (2013) grouped the macroinvertebrate assemblages in a South African river according to their preference for variability in water temperature into specialists (greater variability) and generalists (less variability).

Benthic macroinvertebrates constitute a major source of food for many fishes, and therefore, the abundance and distribution patterns as well seasonal variations are greatly affected by, among other factors, the fish community in the rivers (e.g., Winemiller et al. 2006),

Benthic fauna have been investigated in many rivers in south and southeast Asia especially because of their importance in monitoring water quality in general and organic pollution in particular (e.g., DeKruijff et al. 1992, Sivaramakrishnan et al. 1996). However, these studies do not provide any information on the stream hydraulics and even the substrate characteristics. A recent study of the upper Ganga river basin is summarised as a case study in this book (Nautiyal 2013).

Mention must be made here also of the invertebrate fauna of the hyporheic zone that was described earlier. Most of our understanding of the hyporheic fauna is based on studies in Europe Australia and North America. Whereas some of the benthic fauna use the hyporheic zone as a refugium during the dry period, others are regular inhabitants and
adapted to the specific environmental conditions (Figure 4 Williams 1993, Wood et al. 2010, Stubbington 2012).

**Fish**

Fishes are a major and economically most important component of river biota. Fishes are also among the most studied components of the riverine fauna (for a detailed account see Welcomme 1979, 1985). The distribution of species however varies considerably in different parts of the world and within a river system. Fish assemblages are governed by climate, geographical isolation, several abiotic factors (e.g., stream width, water depth, channel slope, current velocity, and substrate diversity) and associated composite variables such as stream order, distance from sources and basin area (Matthews 1998, Tejerina-Garro et al. 2005, Hoeinghaus et al. 2007a,b, Oberdorff et al. 2011) besides biotic factors (e.g., predation, competition, and disease). Asian rivers are rich in fish diversity, and many fish species are endemic to different regions (e.g. Western Ghats) or rivers (see Jhingran 1991, Kano et al. 2013).

Within the river system, species composition and diversity varies according to the altitude and temperature, water quality (particularly salinity) and food resources. Many fishes inhabit the rapids due to their unique physical adaptations. Hooks, spines or suckers, which enable them to fasten themselves to rocks and vegetation, are common. Small sizes and elongated shapes that allow them to live among rock crevices and rooted vegetation are also common, as are humped shapes that allow for dwelling in the bottom. Pools and riffles in high gradient streams attract different species complexes. Riffles are rich in invertebrate food organisms, and well adapted to survive in strong currents due to well-aerated waters. Small species or juveniles of larger fish live among the rocks. The quieter waters of pools are inhabited by less energetic swimmers, who take shelter in areas of slack flow, and larger fish, that feed on the drift of organisms dislodged from the riffles. Fish in this area may bury their eggs in gravel pockets or may attach the eggs to rocks or submerged vegetation. Some salmonid fish have their spawning habitats in the hyporheic zone (Malcolm et al. 2004). Some species scatter their eggs which drift downstream until they reach sufficient size to migrate laterally into floodplain nurseries.

A common feature of many fishes is their regular migration over distances ranging from a few meters to thousands of kilometers and on time scales ranging from daily to annual. Some fishes migrate within the freshwater reaches of the river (potamogromous) whereas others migrate between the river and the sea (diadromous). Among the latter kinds, some are normal residents of freshwaters and annually move downstream to estuaries or the sea for breeding (catadromous) and some reside normally in the sea water but breed in freshwater and hence, annually migrate upstream to the freshwater areas (anadromous). Among the potamodromous fishes, four main behavioural guilds are recognised by Welcomme (2000).

(i) **White fish**: large strong migratory fish from many different species which move large distances with river channels between feeding and breeding habitats and are intolerant to low levels of dissolved oxygen. The Indian major carps fall under this category.
(ii) Black fish: These fish move only locally from floodplain water bodies onto the surrounding floodplain when the area is inundated. They return to the pools during the dry season. They are adapted to remain on the floodplains at all times and often have auxiliary respiratory organs that enable them to breathe atmospheric oxygen, or have behaviours which allow them access to the well oxygenated surface film. These fish include the clariid catfish of Africa and the anabantids of Africa and Asia.

(iii) Grey fish: an intermediate type between the migratory and floodplain loving species, they migrate over short distances, usually from the floodplain during high water for breeding, to the main river channel where they shelter in marginal vegetation or in deeper pools during the dry season. They are less capable of surviving at extremely low oxygen levels but have elaborate reproductive behaviour which enable them to use the floodplain for breeding. Tilapias, many small characins and cyprinids belong to this group.

(iv) River residents: They inhabit local areas of the main channel, migrate very little, are relatively uncommon and are usually confined to larger rivers. They include the African Mormyrid and Amazonian deepwater gymnotid fishes.

**Birds**

While birds receive great attention in wetland environments, the occurrence of riverine specialists is rarely noticed. Buckton and Ormerod (2002) who assessed their species richness in relation to latitude, altitude, primary productivity and geomorphological complexity, recorded 60 species of passerines and non-passerines to be dependent wholly or partly on production from river ecosystems. Most interesting is the fact that of these 28 species occur in Asia, and the riverine landscapes of the Himalayan ranges have the greatest richness (13 species; see also Tyler and Ormerod 1993 for riverine birds of Nepal). Riverine-bird richness peaks globally at 1300–1400 m altitude, and most species occur typically on small, fast rivers where they feed predominantly on invertebrates (Buckton and Ormerod 2002). Recently, Sullivan et al. (2007) observed that channel slope, drainage area and in-stream habitat conditions were major variables that influenced riverine birds.

**Other Fauna**

Among other vertebrate animals, amphibians and reptiles (together referred to as herpetofauna) are common in many river reaches. Gharial (*Gavialis gangeticus*), the mugger (*Crocodylus palustris*) and freshwater turtles (*Asperidetes gangeticus, Lissemys punctata, Chitra indica, Batagur kachuga, B. dhongoka, Pangshura tentoria and Hardella thurgii*) are important river residents (Taigor and Rao 2012). Frogs and toads and a few species of snakes are common in shallow water bodies in the floodplain.

Several mammals are residents of river ecosystems. In South Asia, river dolphins are important mammals which are now declining and threatened. The Gangetic dolphin (*Platanista gangetica*), a blind mammal which uses echolocation to detect food and navigate in the river, occurs in the Ganga-Brahmaputra-Meghna river system and Karnaphuli-Sangu
river system in India and Bangladesh (Smith et al. 1994, Sinha 1997). It also known to occur in Nepal. The Gangetic dolphin which occurs also in the River Indus and some of its tributaries in Pakistan, is considered as a distinct subspecies. Another dolphin, the Irrawaddy dolphin (Orcaella brevirostris) occurs in Southeast asia (River Mahakam of Kalimantan (Indonesia), the Ayeyarwady (formerly Irrawaddy) of Myanmar (formerly Burma), and the Mekong Delta of Laos, Cambodia, and Vietnam (http://wwf.panda.org/what_we_do/endangered_species/cetaceans/about/irrawaddy_dolphin/).They are also reported from brackish water bodies, such as Chilika Lake (India) and Lake Songkhla (Thailand). This species is also highly vulnerable. Another of its population in the Philippines is critically endangered.

Among other mammals, mention may be made of the otters of which only Eurasian otter (Lutra lutra) occurs in south and southeast Asia. The smooth-coated otter, Lutragale percipelleta, occurs in headwaters of River ganda and its many tributaries as well as in River Chambal. Eurasian beaver (Castor fiber) is also known to occur in some parts of Asia. Another large mammal dependent on riverine floodplains in south Asia is the rhinoceros (Rhinoceros unicornis) which is again an endangered species. Manatees, capaybara, muskrat, coypu, and hippopotamus are other well known riverine mammals.

**Microorganisms**

Microorganisms (protozoans, fungi, bacteria and viruses) are an important component of all ecosystems. Most of them contribute to the decomposition of plant litter and other organic wastes. Aquatic fungi of rivers and wetlands are quite diverse (Shearer et al. 2007, Wurzbacher et al. 2010). Few pathogenic forms such as Streptococci and coliform bacteria, which cause human diseases, attract greater attention and are the subject of innumerable studies on water quality assessment and monitoring.

**Riparian Zone and The Floodplain**

The riparian zone is the area of fluvial landforms that is inundated or saturated by the bankfull discharge (Hupp and Osterkamp 1996). It is also referred to as stream bank or ‘riparian buffer zone’. Whereas the riparian zones along small, incised headwater streams are generally narrow strips (a few meters wide), they may occupy fairly large areas in the floodplain rivers with very low gradients as the distinction between the riparian zone and floodplain becomes unclear (Figure 20). According to some, the floodplains are covered within the riparian zone. As Naiman and Decamps (1997) state, ‘the riparian zones of large streams are characterized by well-developed but physically complex floodplains with long periods of seasonal flooding, lateral channel migration, oxbow lakes in old river channels, a diverse vegetative community, and moist soils’ (Malanson 1993).

The riparian vegetation may be trees, shrubs or grasses. Higher vegetation density provides greater stability to the river channels. Vegetation increases the threshold for erosion and failure of bank material. Together with the within-channel vegetation, the riparian vegetation has considerable impact on the hydraulic roughness and the transport of sediments (Gregory and Gurnell 1988). Many recent studies have elaborated upon
The interactions between fluvial processes and vegetation (Van de Lageweg et al. 2010, Osterkamp et al. 2012)

The riparian zones are important habitats for a large variety of biota, particularly birds, amphibia, reptiles and fish. Along narrow channels, the riparian forest shades the stream surface, lowers the temperature significantly and contributes organic matter for various aquatic biota. Beltrão et al. (2009) have reported that the species composition of fish fauna is influenced by the presence and kind of riparian vegetation. The riparian zones serve as important natural biofilters against sediments, nutrients and pollutants, and thereby help improve river water quality. The important role of the riparian zones in the structure and functioning of river ecosystems has also been discussed in several publications (Fallon and Smolen 1998, Everest and Reeves 2006).

**ECOSYSTEM FUNCTIONING**

Ecosystem functions are the result of the biological, physical and geochemical processes involving complex interactions between the organisms and their non-living environment that allow for fluxes of energy (energy flow) and matter (biogeochemical cycling). Primary production by plants lays the foundation of all trophic interactions. River ecosystems receive considerable amounts of organic matter produced in their riparian zones, floodplain and terrestrial catchments (allochthonous production), besides the production by microphytes and macrophytes within the river (autochthonous production). Numerous studies have examined the relative importance of autochthonous and allochthonous production in different rivers, and along the course of the river, in sustaining the secondary production, particularly that of fish. As described earlier, the River Continuum concept postulates that the plant litter from the riparian vegetation supports the food chain interactions and biotic
communities which change continuously along the length of the river as the downstream reaches depend on energy subsidies from inefficient organic matter processing in upstream reaches. The Flood Pulse Concept emphasized the dependence of stream biota on periodic energy subsides from adjacent floodplains. The Riverine Productivity Model (Thorp and Delong 1994, 2002) considered that the upstream sources of recalcitrant organic matter are less important than the relatively labile material from instream primary production and locally produced allochthonous inputs. Medeiros and Arthington (2010), in their study of an Australian stream, recorded stronger dependence of consumers on autochthonous sources and on locally produced organic matter from the riparian zone than on other resources. Lau et al. (2009) also found that in small streams of HongKong, the food webs were based on periphytic algae and/or cyanobacteria with leaf litter serving as a minor food, though some variations occurred with stream shading and seasons. In a recent review, Roach (2013) highlighted the role of hydrologic regime, turbidity, concentration of dissolved organic matter, floodplain vegetation, lateral connectivity, and upstream impoundment in influencing the contribution of dominant primary production to consumer biomass in large rivers. A brief look at the food web interactions in the river will help understand the divergence of views.

**Food Web Interactions**

The food web interactions in rivers are quite complex because of the diversity of food (phytoplankton, periphytic and benthic algae and macrophytes, and both autochthonous and allochthonous organic matter) and the feeding habits of consumers (Figure 21). The herbivores include some zooplankton, benthic copepods, some fish and also large herbivores like rhinoceros. The interactions between the river and the floodplain (described below) bring in further complexity with the involvement of terrestrial consumers whereas in the deltaic region, the interaction with the sea extends the food webs to include marine organisms. As mentioned earlier, many migratory fish move to upstream to breed in freshwater habitats which provide food as well to them and the young ones. The organic matter transported by the rivers to the oceans, particularly from the coastal marshes and mangroves, sustains coastal fisheries.

The benthic macroinvertebrates may be grouped into many feeding guilds. Shredders which have large and powerful mouth parts, feed on non-woody coarse particulate organic matter (CPOM, such as tree leaves) and break them into pieces. Suspension feeders feed on fine particulate organic matter (FPOM) from the water. Some gatherer-collector organisms actively search for FPOM under rocks and in sluggish-flowing habitats. Another group of invertebrates feeds on periphyton and other organic particulates by scraping, rasping, and browsing. Many others are predators on other invertebrates. Among the zooplankton, rotifers and cladocerans feed on fine particulate matter or phytoplankton whereas the copepods feed on detrital particles and periphyton.

Fish can also be placed into feeding guilds (see Welcomme 1985, 2000). Planktivores feeds on phyto- or zooplankton or both. Herbivores-detritivores are bottom, feeders which ingest both periphyton, submerged mactrophytes and detritus. Surface and water
column feeders capture surface prey (mainly terrestrial and emerging insects) and benthic invertebrates moving downstream with the flow. Benthic invertebrate feeders prey primarily on immature insects, but also consume other benthic invertebrates. Predators consume fishes and/or large invertebrates. Omnivores ingest a wide range of plant and animal food, including detritus. There are also parasitic fishes which live on other fishes. An important aspect of fish feeding behaviour is the change in their food habits/preferences with age and season. Generally, the temperate streams have more benthic invertebrate feeders whereas the tropical river systems have numerous detritus feeders (Figure 22).

The availability and kind of food are important factors affecting fish communities. In small streams, food items are limited to insects, small amounts of vegetation and to allochthonous material falling into the water from the land. As food is relatively scarce, specialisations to benefit from specific food types are common and resource partitioning is very high (McNeely 1987). In floodplain rivers, food is apparently not a limiting factor during

Figure 21. A generalised foodweb in a flood plain river (redrawn from Winemiller 2004)
the flood period as most fishes move to the floodplain areas for feeding and spawning. There are many predators and specialised forms as well whereas the generalised feeders consume a wide variety of foods. In the Amazon floodplain fishes are known to feed on forest fruits, seeds and seasonally flooded vegetation (Goulding 1980, Araujo-Lima et al. 1998, Saint-Paul et al. 2000). A recent study has shown that many fish in the Mekong river also utilise a very wide range of fruits, fresh leaves, flowers and even bark and roots of plants from the seasonally flooded forests (Baird 2007). Such studies on feeding habits of fish in the floodplain forests have not been made in other Asian countries. It may however be safely concluded that the stream food webs are based on both autochthonous and allochthonous sources which influence the length of food chains, and indirectly, the biodiversity.

The fish are predated upon by birds and higher carnivores such as gharials and turtles, and mammals like dolphins and otters.
Nutrient Dynamics

Biogeochemical cycling of nutrients and other elements is a major function of ecosystems. The cycling involves the uptake of nutrients and other elements, generally by the plants, from the environment, their transfer to other organisms through the food webs, and various transformations mediated by the microorganisms until their return to the environment. Because the continuous flow horizontally, between the river channel and floodplains, the nutrient cycling in streams is also accompanied by a downstream transport, it is therefore termed as nutrient spiralling (Webster and Patten 1979, Newbold et al. 1981, 1982, Newbold 1992, Essington and Carpenter 2000). Nutrient spiralling measurements provide data on nutrient uptake rate and the efficiency of nutrient processing in the stream ecosystem. Because of their over-riding importance for the plant and animal growth, other biological processes and water quality, phosphorus and nitrogen have received much greater attention from stream ecologists (Mulholland et al. 1985, Ensign and Doyle 2006). Nutrient transport may occur in the particulate or dissolved form, but the uptake is always in the dissolved state. The hyporheic flow plays a major role in the processing of the nutrients which is affected by the substrate composition and channel type also besides the interactions between light availability and channel morphology (Marti and Sabater 1996). Consumer organisms reduce recycling of nutrients within periphyton mats and increase the particulate transport of nutrients (Wallace et al. 1982, Grimm 1988). The temporal pattern of nutrient cycling varies with the seasonal flow conditions as the nutrients may be processed or transported depending upon the discharge. Increased water residence time facilitates surface-subsurface exchanges and promotes removal of nutrients from the water column. The nature of the substrate (clay and organic matter) and availability of oxygen are also important factors influencing nutrient processing and their removal from the water column. The capacity of rivers to process and retain nutrients, and the effects of physical and chemical alterations caused by human activities on them at different scales, have been examined in some detail by Marti et al. (2006). Various studies show that the nutrient enriched streams have lower phosphorus retention efficiency than pristine streams, and that the discharge has little influence on it. Therefore, both small and large rivers may be impacted by human activities in terms of their nutrient retention capacity (Marce and Armengol 2009).

RIVER-FLOODPLAIN INTERACTIONS

The entire river basin bounded by its watershed boundaries is a landscape unit within which rivers interact with their floodplains, lakes, wetlands and upland terrestrial ecosystems. Rivers transport sediments, nutrients and propagules and distribute them to different parts of the basin. The rivers also exert some influence on the microclimate and the vegetation of their basins. The amount and quality of the run-off from the basin into the rivers is influenced by topographic, edaphic and biological characteristics of the watershed. Further interactions occur with the agency of animals and humans.

Rivers do not remain confined, particularly in the lower reaches (low gradient and/or higher order), to the space delimited by natural levees. High flows that exceed the channel capacity spill over the levees flooding areas on either side — the floodplains. Hydrological
processes in the watershed and the rate of downstream discharge determine the depth, duration and frequency of inundation of the floodplain which periodically becomes a part of the river.

Flooding forces the exchange of materials and energy between the river and its floodplain (Figure 23). The importance of these exchanges between the river and floodplain has been investigated in great detail in the context of fisheries (Lowe-McConnell 1987; Welcomme 1979). Riverine fishes migrate to the floodplain for spawning. Young larvae and fry grow there feeding on a variety of food (plankton, invertebrates and detritus). Many other animals breed and pass some stages of their life cycle in different parts of the floodplains.

As the floods abate, receding waters carry with them organic matter, propagules and nutrients from floodplains to the river proper. Thus, the structure and function of downstream communities is influenced by not merely the direct upstream–downstream transport processes as envisaged by the continuum concept (Cummins et al. 2006), but more strongly by the river–floodplain interactions as elaborated by the flood pulse concept (Junk et al. 1989).

Various parts of the floodplain are subjected to differential flooding and vary in character between lentic and lotic with time. As most plant species are adapted to a specific hydrological pulse and because different parts of the floodplain experience hydrological pulses of different nature (geomorphic variation and topographic gradient), large biodiversity is obtained in floodplains. Nutrient cycling within the floodplains is dominated by flooding from the river, runoff from upland forests, or both, depending upon stream order and season. Vegetation exerts significant biotic control over intrasystem cycling of nutrients, seasonal patterns of growth and decay. Floodplains influence the rivers in other ways also. They lie between the rivers and upland areas, and therefore, water, sediments, and nutrients must pass through them before entering the river. The biological communities
in the floodplain control the fate of these substances (Lowrance et al. 1984). Water infiltrates through the soil to the groundwater or moves laterally to the stream. Sediments get trapped and accumulated in the floodplain, causing topographic changes. Organic matter also gets settled and decomposed with time and supports many detritus feeding organisms. The nutrients undergo various transformations that reduce their flux to the rivers. Other interactions also occur between the floodplains and uplands, and therefore, floodplains are considered as ecotones (Wissmar and Swanson 1990; Pinay et al. 1990). Many terrestrial animals from uplands periodically utilise the floodplain resources and numerous insects pass early stages of their life cycle in the floodplain. Similarly, some aquatic animals (especially waterfowl) depend upon the terrestrial landscape at some stages in their life cycle. For detailed discussion of these interactions, see Ward (1989).

**INTERACTION OF FLOW WITH OTHER ECOSYSTEM COMPONENTS**

The role of flow in affecting all physical and biological processes in the rivers had been recognised long ago by Ambühl (1959). Numerous studies since then have established flow as the master variable which regulates all components, processes and functions of the riverine ecosystems. Further, the temporal variability of flow is an important characteristic that determines the ecology of rivers, particularly the floodplain rivers (Puckridge et al. 1998). The place of flows in various interactions in the river ecosystem are shown in Figure 24 (Gilvear 2002). The effects of different components of the flow regimes are noted briefly in Table 2.

![Figure 24: The relationships between river flow and other abiotic factors that determine fish populations (reproduced with permission, from Gilvear et al. 2002)](image-url)
Table 2. Examples of changes in biological components with changes in river flow regime
(modified from Bragg et al. 2005)

<table>
<thead>
<tr>
<th>Flow change</th>
<th>Biological changes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Declining flow</td>
<td>Increased growth of macrophytes; filamentous algae may increase or decline; significant changes in phytoplankton (usually an increase) and zooplankton communities.</td>
</tr>
<tr>
<td>Low flow</td>
<td>A rise in water temperature and reduction in oxygen level may cause fish mortality; Reduced reproductive success due to stranding and dewatering Change on migration timing of fishes Fish unable to reach their spawning grounds</td>
</tr>
<tr>
<td>Prolonged low flow</td>
<td>Loss of fish spawning areas, nursery and feeding habitats; Adults may not be able to return to the river In case of nutrient rich habitats, cyanobacterial blooms develop. Overall productivity of the river decreases substantially</td>
</tr>
<tr>
<td>Low winter flow</td>
<td>Macrophytes may die out in cold mountainous areas</td>
</tr>
<tr>
<td>Flow cessation</td>
<td>Some benthic or planktonic species may survive in pools Floodplain areas which get isolated from the main channel, get silted up.</td>
</tr>
<tr>
<td>Alternating decline and increase in flow</td>
<td>Changes in the composition of aquatic vegetation along channel margins and floodplain waterbodies</td>
</tr>
<tr>
<td>Increase in flow</td>
<td>Decline of macrophytes with increase in flow velocity; submerged species may be uprooted and washed out</td>
</tr>
<tr>
<td>Flooding of riparian wetlands</td>
<td>Increase in phytoplankton production. Changes in emergent macrophytes according to flooding conditions; Aquatic vegetation may be lost if subjected to prolonged deep water, sedimentation, and turbidity</td>
</tr>
<tr>
<td>High flow</td>
<td>Fish move upstream with even small increase in flow but downstream movement occurs only at high flows.</td>
</tr>
</tbody>
</table>

Flow regime directly controls the cross-sectional geometry, planform, bed material size and levels of bed, and bank stability of the river channel. The nature of the bed sediments in turn affect the habitat quality for benthic organisms – microphytes and macroinvertebrates, as well as the hyporheic habitats and biota. The composition, species (or generic) richness and density of most benthic macroinvertebrates varies greatly with the sediment size such as cobble, gravel or sand (Quinn and Hickey 1990, Collier and Lill 2008).

Flow regimes affect all kinds of organisms by influencing their reproductive cycle, growth and survival (Figures 25 and 26). In case of plants, germination of seeds and vegetative propagules, growth and survival of seedlings, vegetative growth and multiplication, reproductive process (flowering, seed development), as well competitive interaction
Figure 25. Relationship of hydrological variables with various ecological processes that determine the biodiversity of a riverine ecosystem, and the feedback effects.

Figure 26. Ecological processes which are affected by flow variability.
with other species are influenced by hydrological conditions in a complex manner as the hydrological requirements vary with the stage in the life cycle (see, Gopal 1990). Among the faunal groups also, the production of eggs, hatching, survival of the resting stages, growth and competition among zooplankton are affected by all hydrological variables. The timing, frequency, and depth of water availability is of critical importance to zooplankton and invertebrates, especially in floodplain and seasonal water bodies.

The influence of different characteristics of the flood – timing, amplitude, duration, frequency and rate of water level change- on fishes has been discussed in many publications, particularly in the context of floodplain fisheries. These effects are summarised below from a detailed account by Welcome and Hall (2004).

Timing
Timing of flood is most important to fish from the viewpoint of their breeding. The spawning in many riverine fishes is synchronised with the flood events and the breeding season is well defined according to a particular flood phase. Most of the fishes which annually migrate to their upstream spawning sites from the dry season deeding sites downstream have their reproductive process timed so as to match it closely with the flood. However, the increased discharge may not serve as a cue for spawning in some fishes (Humphries and Lake 2000). In some predatory species, the migration upstream to breeding habitats is so timed with the flood that their larvae can grow large enough to be able to feed upon the prey species by the time they start drifting downstream. Timing of floods is also important for the survival, growth and distribution of the young ones. In some rivers such as the Mekong migration and reproduction are closely linked to the lunar cycle (Leang and Saveun 1955). Grey fish including many cyprinids and characins are also influenced by the flood as their breeding period and the release of eggs are so timed as to enable the fry to be washed onto the floodplain by the flood waters. Various cichlids and smaller siluroids are adapted to changes in the timing of flood as they may breed on several occasions throughout the flood season or even into the dry season.

Timing of floods is also important in relation to the temperature during that period as the latter affects the food availability and the rate of metabolism. In cases such as the Murray-Darling river system where downstream flooding occurs during the winter, fishes do not use floodplains at any stage of their life cycle (Humphries et al. 1999).

Amplitude and Duration
The amplitude of flooding is directly related to the areal extent of the floodplain that receives water as well as the water depth in different floodplain habitats. This has a direct bearing on the primary and secondary production, nutrient dynamics, and the distribution, growth and survival of the fish through provision of food and shelter. The amplitude of flooding is also related to the duration of flooding as the areas of the floodplain closer to the river are flooded for longer period and more frequently than the distant parts of the floodplain. Periodic higher floods renew the fish and other faunas of water bodies separated from the main channel. The duration of flooding affects the time for growth of the fish as
also offers protection from predators. Fish are also affected indirectly through the affects of interaction between amplitude and duration on other organisms. Long duration flooding of low amplitude has very different consequences for the reproductive success and survival of young ones that short duration flood of high amplitude.

**Continuity, Smoothness and Rate of Change**

Discontinuity in the progression of flood, caused by dry periods or human interventions, also affect the reproduction in fish as the spawning may occur after the first flood but the eggs and larvae are unable to colonise the floodplains because of lower water levels. The smoothness of the rise and fall of floodwaters as opposed to flashiness also affects the migration and reproduction in many fishes. Sharp fluctuations in water level cause mass destruction of eggs besides affecting the benthic macroinvertebrates and other organisms which serve as important food for the fish. Similarly, the rate of the rise and fall of the water level is also important for many organisms. Rapid rise in water level can submerge nests of bottom breeding species to a depth where turbidity and sediments will affect them. The laevae and eggs may get swept away with the rapid currents. Rapid recession of the flood often results in stranding of fish in the temporary pools on the floodplain and consequent high mortality.

Extreme flood events that occur at irregular intervals have severe damaging effects on the physical habitats (erosion, sediment deposition, change in channel course, breaching of river banks, etc) and all organisms which get flushed out, stranded on uplands and suffer high mortality. Similarly, most fish are adapted to dry season low flow conditions by seeking refuge in the channel pools, floodplain water bodies or the riparian vegetation. Abnormal drying or flooding during the dry season also has serious impacts on the habitats and the survival of fish.

It is important to note that the effects of flow regime are also modified by other environmental factors such as temperature and light, organic matter and sediments, and the oxygen levels that all interact among themselves. For example, Robinson et al. (1993) reported that the interaction between flow regime and temperature affected the life history of benthic organisms and in turn determined the seasonal patterns of their colonization in different stream types. In china, Li et al. (2012) have reported that an increase in water temperature along with a decline in flow in recent years caused a decrease in the macroinvertebrate abundance and richness during winters. Recently, Cockayne et al. (2013) observed that the eggs and larvae of golden perch were found during natural flow events with a minimum of 1.5m river rise for 7 days but spawning was associated with the peak and/or recession of the first or second post-winter flow event where water temperatures exceeded 24°C.

**Influence of River Biota on Hydrology**

While most research on river ecosystems is focused on the effects of flow and river habitats on the biota, the influences of biota on the river hydrology and morphology are not well studied. The biotic influences are generally greater in the slow-flowing streams and lower
stretches of large rivers. The importance of the floodplain vegetation as a potential buffer for reducing the movement of sediments, nutrients and pollutants to the river channel and the role of riparian vegetation as a control on bank stability as well supporting fish has been described above. A review by Clarke (2002) shows that the instream macrophytic vegetation has a significant effect on flow, sediment and nutrient dynamics though increased frictional resistance to flow and through flow diversion may have a short-to-medium-term influence on instream channel geomorphology. Further influences occur also on the nutrient dynamics.

Several animals actively modify the river habitats, and are often called as ‘ecosystem engineers’ (Moore 2006). Among the most prominent and better known are the beavers which fell riparian trees to build dams behind which a pond is created. The ponds become silt traps and sometimes burst open to cause significant floods downstream (Rosell et al. 2005, Butler and Malanson 2005). The change in the habitat alters the composition of fish populations (Collen and Gibson 2001). Many species fish (e.g., salmon) dig nests on stream beds for laying their eggs. Digging has a variety of impacts on benthic habitats, macroinvertebrate and periphytic communities (Moore 2006). Displacement of fine sediments alters the substrate for the benthic biota. Among invertebrate fauna, predatory stoneflies (Zanetell and Peckarsky 1996) and crayfishes (Usio and Townsend 2004) create significant disturbance of the bottom sediments (bioturbation) that in turn affects the primary producers and other organisms. Even molluscs influence the riverine habitats as their shells accumulate in the sediments and provide habitats for a variety of organisms especially during the low flow periods.

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