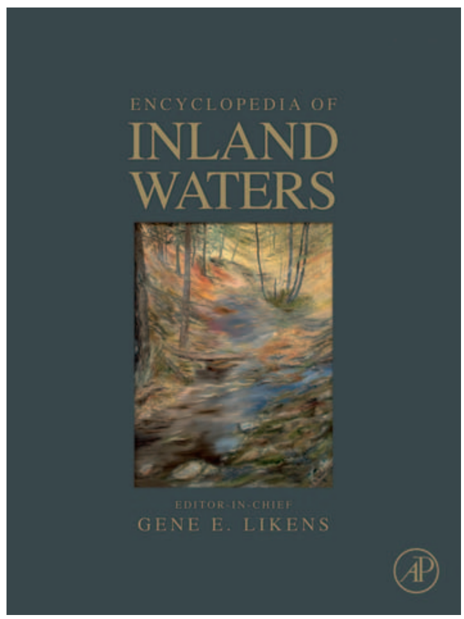

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Rivers

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What is a River?

There is no strict definition to distinguish rivers from streams and therefore the designation 'river' encompasses flowing waters of widely varying size. Flowing waters may be ranked in size by various metrics that include discharge (glossary), catchment area, and length of channel. For example, the discharge of the Amazon River is six orders of magnitude greater than that of a small river. This range of variation is comparable with the range in volume observed among lakes worldwide. Rivers are sometimes defined as 'non-wadeable' flowing waters since this delineation has practical implications for the way sampling activities are carried out. Along the continuum from headwater streams to large rivers, there are gradients in channel slope, width, and depth. Idealized gradients in geomorphology provide a basis for understanding differences in the structure and functioning of streams vs. rivers. For example, the greater width of river channels reduces the importance of riparian inputs while greater depth lessens the influence of benthic processes. Rivers in their natural settings exhibit complex geomorphologies that give rise to a rich variation in channel form and function and provide diverse habitats for aquatic biota.

Hydrology and Geomorphology

Water Sources and Discharge

Water sources to rivers are principally surficial inputs via tributary streams (Table 1). Owing to their small surface area, direct atmospheric inputs are usually minor though groundwater is important in some settings. For comparisons among river basins, discharge is converted to an areal water yield by dividing the volume of discharge by the area of the drainage basin. Water yields vary widely depending on the amount of precipitation relative to evapotranspiration (glossary). South American rivers such as the Amazon and Orinoco are notable for their high water yields, exceeding 1000 mm year^{-1} (Table 2). Arid and semi-arid regions are characterized by low precipitation relative to evapotranspiration and water yields less than 100 mm year^{-1}. Arid regions occupy about one-third of the world's land area, including portions of several major river basins such as the Murray-Darling (Australia), Colorado (North America), Nile (Africa), and Ganges (Asia) Rivers.

Variation in river discharge arises from short-term, seasonal, and long-term variability in precipitation and evapotranspiration within the drainage basin. Over short time scales (days–weeks), discharge is affected by rain events associated with frontal passage. Though infrequent in occurrence, event-related discharge may account for a large proportion of the annual total. The frequency and magnitude of storm events is therefore an important factor influencing interannual variation in discharge. Event-driven and seasonal variations are superimposed upon long-term (decadal-scale) climatic cycles (e.g., El Niño Southern Oscillation), which may bring about extended periods of above- or below-average discharge. The combined effects of climatic variations occurring over multiple time scales results in a wide range of discharge conditions, which may exceed three orders of magnitude for a given site. Variation in discharge is typically larger that the variation in the concentration of dissolved and particulate substances such that the export of materials from the basin (flux rate) is principally determined by discharge.

Seasonal variation in rainfall and evapotranspiration give rise to predictable annual patterns in river discharge that are characteristic of climatic regions (Figure 1). In temperate-humid climates, rainfall may be distributed relatively uniformly throughout the year but seasonal changes in evapotranspiration give rise to variation in discharge. Warmer months are associated with high evapotranspiration, resulting in less runoff from the catchment and lower river discharge relative to colder months. Snowmelt may also contribute to a spring discharge pulse in climates that allow for winter accumulation of snow (including tropical rivers with mountainous catchments). The north-flowing rivers of Canada and Russia are representative of this hydrologic regime in exhibiting high year-round discharge but with a pronounced winter-spring peak. In tropical-humid climates, evapotranspiration is less variable throughout the year but rainfall is often strongly seasonal, particularly in regions affected by monsoons. Wet seasons are associated with elevated river stage and discharge and may be accompanied by extended periods of floodplain inundation. Most South American and African rivers are representative of the tropical unimodal hydrologic regime, which is characterized by an extended period of elevated discharge and floodplain inundation during the rainy season. Arid and

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Table 1 Distinguishing characteristics of rivers, estuaries, and lakes

	Rivers	*Estuaries*	*Lakes*
Water movement	Unidirectional, horizontal	Bidirectional, horizontal	Vertical
Water forces	Gravitational	Tidal	Wind-induced
Water-level fluctuations	Large (seasonal)	Variable (daily, storm events)	Small (seasonal)
Water residence time	Days–weeks	Weeks–months	Months–years
Water sources	Runoff	Runoff, marine, precipitation	Runoff, groundwater, precipitation
Stratification	Rare	Common (salinity)	Common (thermal)
Transparency	Low (nonalgal particulates)	Variable (particulates, dissolved color)	High (algae, dissolved color)

Table 2 Water and sediment delivery from large river basins of the world

River	*Drainage area (10^6 km^2)*	*Discharge (km^3 year^{-1})*	*Water yield (mm year^{-1})*	*Sediment load (10^6 t year^{-1})*	*Sediment yield (t km^{-2} year^{-1})*
Amazon	6.15	6300	1024	1200	195
Colorado	0.64	20	31	0.01	0.02
Columbia	0.67	251	375	10	15
Congo (Zaire)	3.72	1250	336	43	12
Danube	0.81	206	254	67	83
Ganges–Brahmaputra	1.48	971	656	1060	716
Huang He (Yellow)	0.75	49	65	1050	1400
Indus	0.97	238	245	59	61
Mackenzie	1.81	306	169	42	23
Mekong	0.79	470	595	160	202
Mississippi	3.27	580	177	210	64
Niger	1.21	192	159	40	33
Nile	3.03	30	10	0	0
Orinoco	0.99	1100	1111	150	152
St. Lawrence	1.03	447	434	4	4

Source: Milliman JD and Meade RH (1983) Worldwide delivery of river sediment to the oceans. *Journal of Geology* 91: 1–21.

semiarid regions occur in both temperate and tropical climates and occupy about one third of the world's land area. They are characterized by low precipitation relative to evapotranspiration and include portions of several major river basins, including the Murray-Darling (Australia), Missouri (North America), Nile (Africa), and Ganges (Asia) Rivers. River basins in arid regions exhibit sustained periods of low discharge interspersed with short periods of elevated discharge. For example, the Murray-Darling River is fed by infrequent summer monsoons which, coupled with high rates of evapotranspiration, result in an annual discharge equivalent to only 3% of annual rainfall.

Large river basins may span climatic and topographic regions and exhibit complex hydrologic regimes. For example, the Rhone is a snowmelt-dominated river in its upper, mountainous sections but is influenced by a Mediterranean climate in its lower course. The river exhibits a complicated flow regime with low discharge periods shifting from winter in the upper course to autumn in the lower course and floods occurring in all seasons. Despite the problems inherent in categorizing this continuum of variation, hydrologic regimes are useful for facilitating comparisons among river basins (e.g., in response to land-use and climate change effects).

Flooding

Rivers experience large and rapid fluctuations in surface water elevation (i.e., 'stage') in response to runoff. The rate and magnitude of rise in river stage is dependent in part on the morphometry of the channel (Figure 2). Low banks enable the river to escape the active channel and inundate lateral areas (floodplain). During flooding, the widening of the river lessens the stage response to runoff and reduces water velocity because the force of the water is distributed over a wider area. Flood-prone rivers are common in both temperate and tropical climates and exhibit considerable variation in the extent, timing, and frequency of flooding events. In some settings (e.g., Amazon River) the annual flood pulse is a defining feature of the riverscape, important not only to the life cycles of riverine biota but also in shaping floodplain communities. Floodplains are rare in naturally constricted

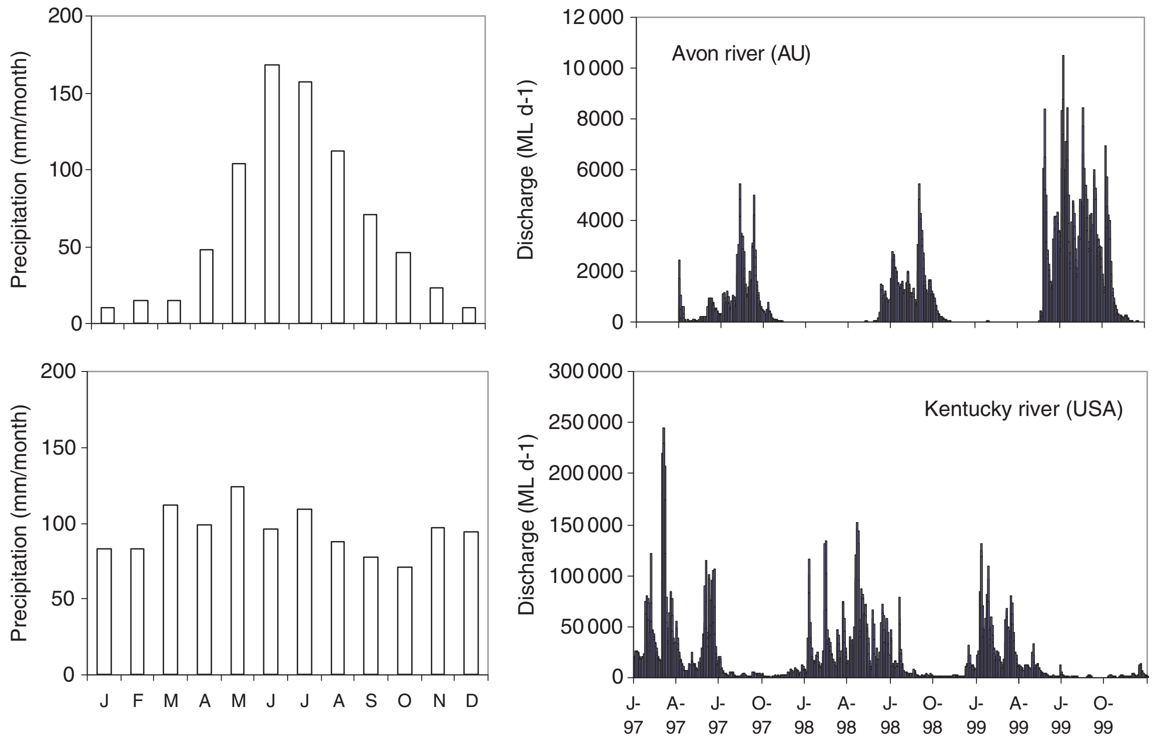

Figure 1 The hydrologic regimes of tropical and temperate rivers reflect differences in seasonal patterns of precipitation and evapotranspiration. The Avon River (Western Australia) experiences high evapotransipration throughout the year and variation in discharge is largely driven by seasonal patterns in rainfall. The Kentucky River (North America) receives similar rainfall throughout the year but variation in evapotranspiration results in similar seasonal patterns in river discharge (offset in northern vs. southern hemispheres).

rivers; or may be disconnected if lateral water regulation structures (i.e., levees) are present. In constricted and levied channels, the effects of runoff on river velocity and stage are accentuated because the ratio of water volume to bottom area increases with rising stage. Thus, the influence of frictional resistance in dissipating energy is lessened with rising stage. Hydrodynamics of river channels are often depicted using simulation models that describe water movements in one, two, or three dimensions (longitudinal, lateral, vertical). These models typically rely on input data describing channel geomorphometry (cross-sectional depictions of river bed and bank elevation) and calibrated using measured surface water elevation and discharge. The models predict surface water elevation under various discharge scenarios and are used to forecast the timing, severity and location of flood events.

Water Movement

Energy is required to move water and in the case of rivers, this energy is derived from gravitational forces acting along an elevation gradient. Rivers are similar to estuaries in that both are flow-dominated (advective) systems; in estuaries, however, the movement of water is bidirectional and driven by tidal forces (Table 1). Water movement in lakes is driven by comparatively weak forces associated with wind-induced vertical mixing. The slope of the channel and the frictional resistance imposed by its boundaries determine the velocity with which water is carried down the elevation gradient. The roughness of the channel reflects the composition of bed and bank materials and the presence of natural and artificial structures (e.g., woody debris, wing dams). Turbulence arises as force is dissipated by frictional resistance. This mixing energy maintains particulate matter in suspension and is sufficient to overcome differential heating of surface and bottom layers. Consequently, thermal stratification is rarely observed in rivers except in cases where impoundments are present.

The length of time that water resides within a given segment of the river determines in part the potential for physical, chemical, and biological processes to act upon the dissolved and particulate constituents in through-flowing water. Because of the unidirectional

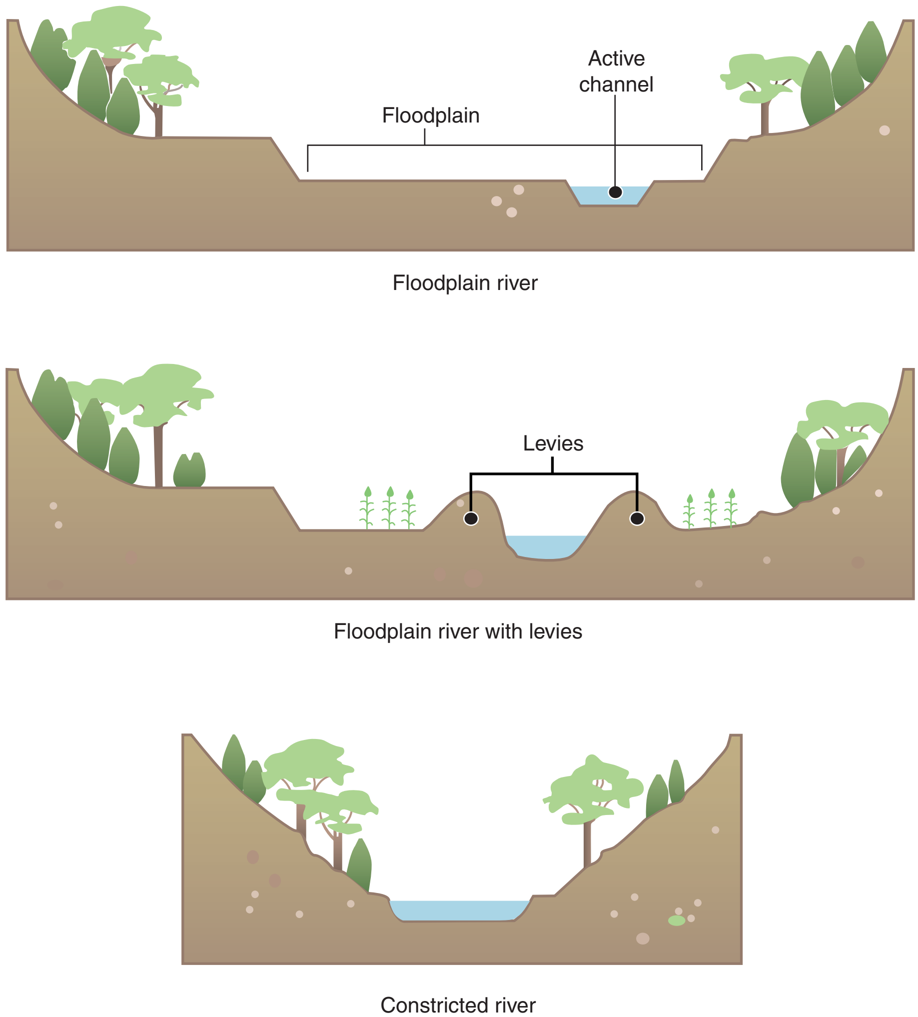

Figure 2 Cross-sectional morphologies of floodplain and constricted rivers. In floodplain rivers, rising river stage results in lateral inundation unless precluded by the presence of levees. Widening of the river during flood events increases frictional forces and reduces water velocity. In constricted rivers, lateral inundation is constrained by steep adjoining slopes resulting in rapidly increasing water velocity with rising river stage. (Illustration by Christopher O'Brion, VCU Design Services).

flow of water, transit time is a useful metric to characterize inter-river differences in the time required for water and materials to travel through a reach of specified length. Tracers such as dyes (rhodamine) or conservative solutes (chloride, bromide) are used to measure transit time by tracking the movement of labeled parcels of water. Tracer additions provide a reach-scale estimate that integrates longitudinal, lateral, and depth variations in water velocity. Application of this technique to larger rivers is problematic owing to the quantities of tracer required and the difficulty of achieving a laterally uniform addition. Transit time estimates may be obtained from hydrologic models using measured discharge and cross-sectional area to infer average (cross-sectional) velocity at multiple points along the channel. The coupling of transit time and nutrient uptake, termed nutrient spiraling (glossary), is a concept that has been widely used as a framework for understanding the interaction between hydrologic and biological processes in regulating nutrient retention. Transit time estimates are also used to design sampling programs in which a parcel of water is sampled repeatedly as it travels down the channel (termed LaGrangian sampling).

Geomorphology

At any point along a river course, channel morphology reflects the interplay between the force of water and the stability of bed and bank materials. Channel form is a quasi-equilibrium condition maintained by the dominant discharge and determined in part by the supply of sediment from upstream. Where rivers are not constrained by natural landforms or

Figure 3 Selective loss of fine materials may over time create channel reaches that are characterized by a predominance of large substrates such as the gravel bars illustrated here. Their presence in the river channel is important to the maintenance of biodiversity as some species colonize hard substrates or exploit interstitial spaces as a means of adapting to flowing environments. Gravel bars and other subsurface exchange zones are also important to ecosystem function such as nutrient retention. Photo of the Rio Apurimac in Peru by A. Aufdenkampe (see related paper by Aufdenkampe *et al*. (2007) *Organic Geochemistry* 38: 337).

water regulation structures, channels migrate laterally (meander) through erosion and redeposition of bank materials. Active channels are characterized by the ephemeral nature of their features (movement of bars and banks) and by their morphological complexity, which may include the presence of pools, riffles, side channels, and meanders (Figure 3). Constrained channels occur where natural landforms or water regulation structures limit lateral mobility. High discharge results in the erosion of bed materials leading to incised (entrenched) channels of low structural complexity and relatively uniform flow conditions. Channel forms and substrate conditions influence the structure and functioning of riverine food webs. For example, where flow conditions favor the deposition of fine materials, the accumulation of particulate organic matter enhances benthic microbial activity. Various schemes have been devised to categorize channel forms, though these efforts are often confounded by the continuous rather than discrete variation in channel features (e.g., width–depth ratio; size distribution of bed materials). Emerging technologies for sensing underwater environments hold much promise for linking biological and geophysical properties particularly in large rivers.

Water Regulation

Human activities have substantially affected the natural hydrologic cycles of rivers throughout the world. Land-use changes have indirect effects on river hydrology by altering the timing and quantity of runoff from the catchment. For example, urbanization creates impermeable surfaces that increase the volume and speed of storm runoff. Direct impacts include the abstraction (withdrawal) of river water for domestic supply and irrigation as well as the alteration of river channels by water regulation structures. Rivers have been altered through the construction of dams, levees and other channel modifications to accommodate local needs for flood protection, hydropower generation and navigation. Channelization (straightening) of river courses facilitates navigation but reduces channel and flow complexity thereby diminishing habitat diversity. Channelized rivers are subject to elevated flow velocities that cause erosion and necessitate bank stabilization. Levees preclude lateral exchange and thereby diminish the role of floodplains in material and energy cycles. In flood-prone rivers, biota are adapted to annual flood pulses that provide access to food and spawning areas within the floodplain. Among the most widespread of human impacts on rivers is the construction of dams, which currently number in excess of 45 000 worldwide. Together, their cumulative storage capacity is equivalent to 15% of global annual river runoff. Over half of the world's major rivers are affected by dams, most of which were constructed in the twentieth century. Dams induce pelagic conditions by increasing water storage and dissipating mixing energy. Pelagic conditions favor sediment deposition and biotic assemblages that differ from those occurring in flowing environments. The severity of water regulation effects varies according to the number and size of regulation structures along the river course. The cumulative effect of dams within a river basin can be gauged from their number and storage capacity expressed relative to river discharge (Table 3). Low dams (height < 10 m) are designed to maintain a minimum depth for navigation during low discharge and

Table 3 Water regulation effects vary according to the number and storage capacity of mainstem dams as illustrated by rivers of the central United States

River	*Mean annual discharge ($m^3\ s^{-1}$)*	*Storage capacity of mainstem impoundments (km^3)*	*Retention effect of impoundments (days)*
Kentucky	234	0.26	12.7
Green	314	1.11	41.0
Tennessee	1880	15.00	92.4
Cumberland	936	1.18	14.7
Wabash	800	0.19	2.8
Ohio	7811	8.92	13.2

The combined storage capacity of mainstem dams on the Tennessee River is equivalent to 26% of the river's annual discharge or approximately 92 days at average discharge. In contrast, the Wabash is a relatively free-flowing river with only a single mainstem impoundment that stores a volume less than 1% of its annual discharge.

thereby regulate stage but do not eliminate flowing conditions. High dams are designed for flood control and water storage. They inundate large areas and effectively create lake-like conditions, in some cases, resulting in thermal stratification of the water column.

Water Quality

Rivers integrate drainage waters from distant points in the landscape that may differ in topography, soils, vegetation, and land use. These differences give rise to widely varying water chemistry within river basins particularly where anthropogenic influences differ among sub-basins. Along the river course, water chemistry changes in response to inputs from these diverse sources and also reflects variable water residence times in channel, hyporheic, and lateral storage zones.

Particulate Matter

High concentrations of suspended particulate matter are a characteristic feature of rivers particularly during periods of elevated discharge. The upward component of water turbulence acts to maintain particulate matter in suspension, resulting in downstream transport. Particulate matter may originate within the channel through erosion of bed and bank materials, resuspension of sedimented materials, and biological production. Most particulate matter, however, is derived from sources outside the river channel that are transported via tributary streams. The rivers of Asia are particularly noted for their high sediment load. It is estimated that the Ganges, Brahmaputra, and Yellow Rivers contribute 20% of the total sediment load transported to the oceans (Table 2). High sediment production is attributed to natural factors affecting surface erosion (soil composition, steep slopes, and intensive rainfall) as well as anthropogenic effects associated with deforestation and urbanization. Riverine suspended matter is predominantly a fine-grained (<0.2 mm) mixture of mineral and organic particulates (e.g., clay and silt). Though recalcitrant, mineral particulates may undergo changes in their chemical composition through the selective sorption and desorption of dissolved substances. For example, proteins and other dissolved organic compounds adhere to the surfaces of mineral particulates, thereby altering both the bioavailability of these compounds and the chemical properties of particulate matter. Phosphate has a high sorption potential and is principally transported with the particulate fraction. The sorption capacity of particulate matter is determined by the number of available binding sites on the surfaces of the particles and their cumulative surface area (a function of particle density, shape, and size).

Particulate matter is the principal factor regulating water transparency in rivers, although light absorption by dissolved organic compounds may be important during periods of low discharge. When present in high concentrations, mineral particulates may have deleterious effects on filter-feeding organisms by interfering with feeding mechanisms or simply diluting the intake of the more nutritious organic fraction. This fraction includes phytoplankton and bacteria although these typically account for a small proportion of particulate organic matter. The bulk of the particulate organic matter is nonliving detrital material of terrestrial and aquatic origin. This material is of variable age and in varying stages of diagenesis, having been acted upon by both terrestrial and aquatic decomposers.

Dissolved Substances

River water contains dissolved inorganic and organic materials derived from mineral weathering and decomposition processes. Their concentration is largely determined by the types of soils and vegetation within the basin and the extent of interaction between runoff and soil. Low concentrations of dissolved substances occur where river basins are characterized by steep slopes and thin soils, particularly where soils are comprised of insoluble materials (e.g., sand, igneous rock). In these basins, river water is dilute (ion-poor) and similar in chemical composition to that of rain water. Gradual slopes and deeper soils allow for longer flowpaths and greater interaction between water and soil. In these settings, there is greater opportunity for biogeochemical processes to influence the chemistry of runoff especially where soils are dominated by easily-weathered materials (e.g., sedimentary rocks such as limestone). Temporal variation in dissolved ion concentrations is typically associated with rain and snowmelt events. High discharge is often characterized by lower concentrations of dissolved substances owing to rapid delivery of water via overland flow, shallow soil flowpaths, and short transit times in tributary streams. At the onset of rising discharge, rain or snow-melt waters may displace older groundwater, resulting in an initial increase in ion concentrations. Thus, the relationship between discharge and concentration is often nonlinear and ion-specific.

Geologic differences among river basins will influence both the total amount of ions present and their relative proportions. Despite these differences, major ions are generally similar and include bicarbonate, sulfate, chloride, and the base cations (Ca, Mg, Na, K). Climatic factors also influence ionic strength and composition particularly in arid regions where evapoconcentration effects are large. A tea-colored appearance is an apparent feature of some ('blackwater') rivers owing to elevated concentrations of dissolved organic compounds. Their presence is associated with characteristic types of vegetation that leach humic and tannic acids and in some cases (e.g., in coastal areas) by the predominance of sandy soils, which have limited capacity to retain these compounds.

Nutrients

Rivers are not simply conduits for transporting watershed-derived materials but rather, riverine processes may exert considerable influence on water chemistry, particularly for those elements whose abundance is low relative to biological demand. Nitrogen is transported in rivers in dissolved inorganic form (NO_3, NH_4) and in dissolved and particulate organic forms. The latter include living cells and detrital matter as well as a diverse array of dissolved organic compounds that are released through exudation, excretion, and decomposition. Nitrate is a highly mobile ion owing to its low sorption potential. Therefore, it is readily transported through soils and is typically the dominant form of N in rivers, where agriculture and urbanization are prevalent. Elevated NH_4 concentrations may occur below wastewater discharge points. Dissolved organic N assumes greater importance in rivers with minimal human influence. Unlike N, phosphorus is principally transported in the particulate fraction. Concentrations of dissolved P (including PO_4 and other reactive forms) are low owing to biotic uptake and high sorption affinity for mineral particulates (e.g., clay). Sorption processes are reversible such that particle-bound P may desorb and enter the bioavailable pool. Anthropogenic impacts are associated with increases in the total amount of P and the proportion that is in the dissolved fraction. Within rivers, inorganic forms of nitrogen, phosphorus, and silica may be transformed to particulate organic forms (e.g., in algal and bacterial cells). Dissolved silica is converted to its biogenic form by diatoms, a common component of benthic and pelagic algal communities in rivers (See **Algae of River Ecosystems**). Biogenic silica is relatively recalcitrant to remineralization (compared with N and P) such that autotrophic uptake results in progressive depletion of dissolved silica along the river course. Denitrification results in the loss of nitrogen to the atmosphere (as N_2) and is an important process determining N delivery from catchments.

Dissolved Gases

Dissolved gases, particularly oxygen and carbon dioxide, are of interest because their concentrations in river water are influenced by biological processes of photosynthesis and respiration. The solubility of dissolved gases is temperature dependent and therefore it is useful to express concentrations as a percent saturation; that is, relative to the expected concentration for a solution in atmospheric equilibrium. Departures from equilibrium concentrations occur when the rate at which gases are exchanged with the atmosphere is slow relative to rates at which gases are produced or consumed through biological activity. Atmospheric exchange is governed by the concentration gradient across the air–water interface, boundary layer thickness (a function of wind speed), the ratio of river surface area to volume, and factors related to agitation and turbulence of water (e.g., presence of waterfalls). Gas exchange occurs more rapidly in shallow and turbulent rivers relative to deeper, slow-moving rivers. In many rivers, dissolved oxygen is undersaturated while CO_2 is supersaturated (**Figure 4**). These departures from equilibrium reflect the heterotrophic nature of rivers in which community respiration exceeds autotrophic production. Respiration is supported in part by inputs of dissolved and particulate organic matter of terrestrial origin. Decomposition of terrestrial organic matter within the river results in a net production of CO_2 (i.e., in excess of photosynthetic C demand) and a net release of CO_2 from water to air. Diel variations in dissolved oxygen can be used to estimate production

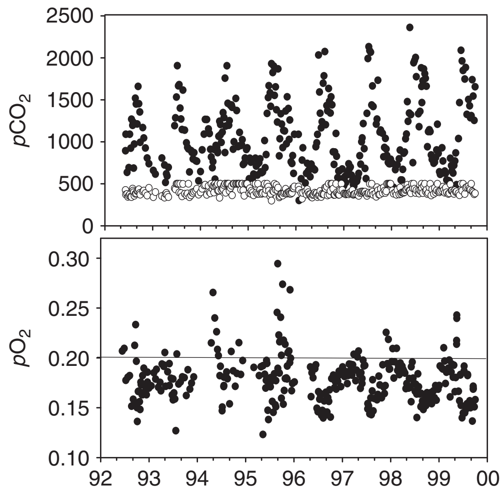

Figure 4 Partial pressure of dissolved carbon dioxide and oxygen in the Hudson River (NY, USA; atmospheric levels of CO_2 indicated by open circles). Persistent supersaturation of pCO_2 and undersaturation of pO_2 are indicative of net heterotrophic conditions whereby respiration exceeds net primary production (adapted from Cole and Caraco 2001, Marine and Freshwater Research).

and respiration provided that re-aeration rates can be reasonably estimated. Although undersaturation of dissolved O_2 is common, severe depletion (i.e., hypoxia – glossary) is rare in riverine environments because turbulent mixing promotes reaeration. Organic matter inputs from poorly-treated sewage effluent were once a wide-spread problem that resulted in chronic and severe oxygen depletion in rivers. Modern wastewater treatment plants are designed to minimize the biological and chemical oxygen demand of effluent.

Pollutants

Rivers integrate runoff over large areas of the landscape and therefore their pollutant loads reflect the cumulative effect of basin-wide releases. Macropollutants include a relatively short list of agents present in concentrations on the order of parts per million ($mg\ l^{-1}$) while micropollutants includes a much larger inventory of chemicals that occur at very low environmental concentrations (ppb or ppt; $\mu g\ l^{-1}$ or $ng\ l^{-1}$). The most common macropollutants are compounds of N and P, which originate in runoff from agricultural areas and from contamination by wastewater (including treated effluent and urban storm water overflow). Nitrogen and phosphorus often limit primary production in lakes and estuaries though their role in regulating the trophic state of rivers is less clear. Many rivers experience nutrient enrichment but biotic responses to elevated nutrient levels (i.e., eutrophication) may be muted by factors that constrain primary production (principally light and residence time). Other macropollutants include sulfate, chloride, and base cations; these are associated with atmospheric deposition, mining, wastewater, and de-icing. Their effects on river biota are less well studied compared with pollutants associated with eutrophication. Micropollutants are a diverse group of chemicals that have deleterious effects at low concentrations. They vary in their reactivity, mode of toxicity, and persistence in the environment and include inorganic pollutants such as metals as well as synthetic organic compounds (e.g., pharmaceuticals, detergents, pesticides). In rivers, the high throughput of water favors the rapid removal of pollutants in the dissolved form. Many pollutants, however, bind to particulates or enter the food chain, where they may persist over long periods of time in sediments and long-lived species such as fish. Regulatory policies aimed at mitigating pollution must take into account proximal effects on river biota as well as distant effects on receiving waters such as estuaries. In some cases (e.g., nutrients), the latter may exhibit greater sensitivity than rivers owing to their longer water residence time.

Biology of Rivers

Rivers owing to their diverse size, channel forms, and biogeographic settings differ greatly in their species assemblages. Constituent species include river specialists that rarely occur outside of flowing waters and habitat generalists that occur in both lentic and lotic waters. In coastal areas, marine species are seasonally important members of river food webs. Salmon and other anadromous fishes (glossary) serve as vectors for distributing marine-derived resources through drainage networks. Species inhabiting rivers face challenges imposed by the unidirectional flowing nature of their environment. Strategies include current avoidance in sheltered areas (along channel margins, behind debris dams or in interstitial spaces), and specialized adaptations such as attachment to hard substrates. Riverine species also share the benefits provided by water flow which supplies particulate matter to filter-feeding organisms, replenishes nutrients and oxygen at the cell boundary layer, and, during floods, allows periodic access to floodplain habitats.

Primary Producers

Attached algae (i.e., periphyton), phytoplankton, and macrophytes contribute to autotrophic production in rivers; their relative importance varies in accordance with river hydrogeomorphology. In shallow, fast-flowing rivers, benthic algae predominate particularly where rocks and woody debris provide stable substrates for colonization. Benthic algal abundance is determined by the availability of suitable substrates, light conditions (the extent of riparian shading), and flow regime (the frequency and severity of scour events). Nutrients and grazers may be important in some settings particularly where nutrient loading is associated with riparian disturbance and loss of canopy shading. In deep, slow-moving rivers, phytoplankton are often the dominant primary producers. Their abundance is principally determined by light availability. The average light intensity experienced by phytoplankton circulating within the river channel is determined by water transparency and the depth of the channel. Nutrients and grazing may be important particularly in regulated rivers and during low discharge conditions. Low flow velocities favor the accumulation of phytoplankton biomass owing to reduced washout (advective loss) and increased water transparency (due to sedimentation of nonalgal particulates). Phytoplankton communities are composed of taxa similar to those found in lentic environments but may also include detached benthic algae. Dominance by diatoms is often reported and may reflect their ability to tolerate the low light conditions in rivers (having a high light utilization efficiency) and the benefits of active mixing (to offset high sinking velocities). Channel morphometry is an important factor determining the species composition and areal coverage of submergent and emergent aquatic vegetation (Figure 5). Constricted and channelized rivers have steep shoreline areas, which provide little suitable habitat, whereas floodplain and low-gradient rivers allow for greater colonization in shallow-water areas. Substrate stability is likely a key factor determining the extent and persistence of macrophyte beds since perenniating structures (e.g., tubers, rhizomes) are vulnerable to displacement during periods of elevated discharge.

Figure 5 Aquatic macrophytes are common in rivers though usually they are restricted to channel margins and backwater areas, where flow conditions are reduced. Photo of Beaver River in the Adirondack Mountains of New York State (USA) by P. Bukaveckas.

Invertebrates

The diversity and productivity of invertebrates has received considerable attention in studies of riverine foods webs. For example, nearly one-third of Hynes' classic *Ecology of Running Waters* is devoted to benthic macroinvertebrates. Invertebrates are important to trophic energetics because they link primary sources of energy (autochthonous production and allochthonous inputs) to higher trophic levels such as fish. Pelagic invertebrates (zooplankton) are commonly found in regulated and deep rivers and at times in large numbers. Their abundance is determined by in situ production within the main channel and contributions from areas of reduced water velocity (Figure 6). Inputs from upstream reservoirs may also be important in some systems. River zooplankton assemblages are dominated by rotifers and small-bodied forms of cladocerans (e.g., *Bosmina*) and copepods, whereas larger zooplankters (*Daphnia*) are generally associated with lentic environments.

Benthic invertebrates are important components of river food webs and are widely used in habitat assessments owing to their sensitivity to water quality conditions. These include crustaceans such as amphipods and crayfish, mollusks (snails and bivalves), and a great variety of insects (dragonflies, damselflies, stoneflies, mayflies, midges, blackflies, caddisflies). The aquatic insects in particular draw attention to the productive nature of riverine environments through periodic emergence of adults in large numbers. Invertebrates may be grouped according to their feeding habits as predators, filtering and gathering collectors, deposit feeders, scrapers, and shredders. The River Continuum Concept predicts shifts in food resources and feeding habits along a gradient of stream order. In low- and middle-order streams, shredders and grazers rely on leaf litter inputs and benthic algal production whereas in rivers, collectors and filter-feeders utilize suspended particulate matter. Productivity is determined by water temperature, food quantity and quality and the presence of suitable habitat (e.g., hard substrates and snags). A variety of invertebrates, particularly oligochaetes, amphipods, chironomids and microcrustaceans, occur in large numbers in the subsurface zone (hyporheos; glossary) where they find refuge from predation and currents.

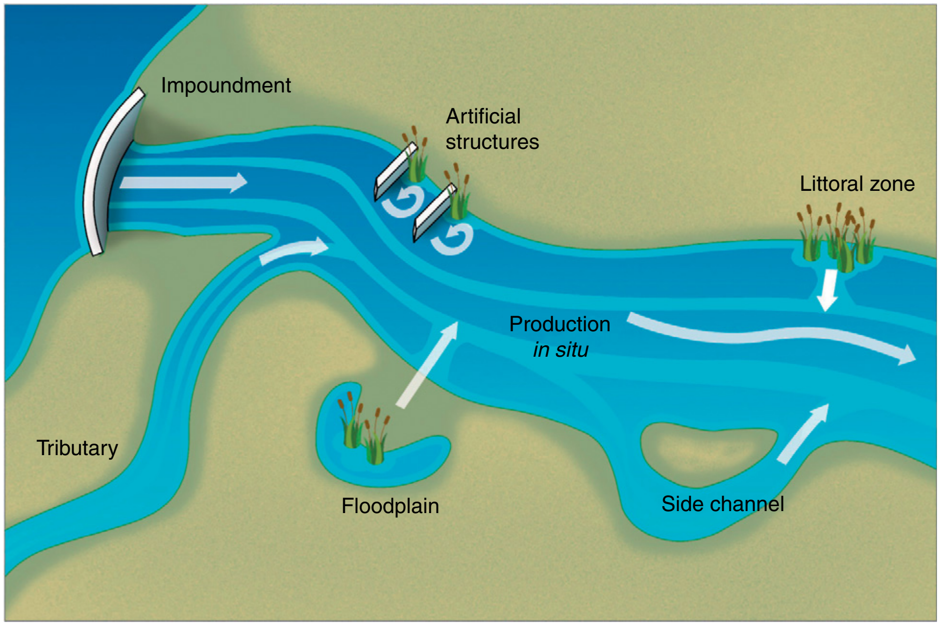

Figure 6 Sources of plankton to rivers include *in situ* production as well as inputs from tributaries, impoundments and near-shore areas of reduced water velocity (Illustration by John Havel and Christopher O'Brion).

Fishes

Fish are typically the top predators in river food webs and, like macroinvertebrates, are often used as 'bio-indicators' for habitat assessment. Many studies have focused on species that are important to commercial or recreational fisheries. However, quantitative estimates of abundance are difficult to obtain particularly in large and deep rivers. The lack of production and biomass estimates with which to compare against similar data for lower trophic levels greatly limits our understanding of food-web energetics. For example, the utility of using phosphorus or chlorophyll as a predictor of fish biomass, which is well-known for lakes, remains largely untested in rivers. In contrast, factors influencing the diversity and species composition of river fish communities are generally well studied. In both temperate and tropical rivers, the numbers of species increase with the size of the drainage basin. The dendritic form of river networks may foster high diversity (relative to contiguous water bodies of comparable area) by providing diverse habitat conditions and through isolation of populations in distant portions of the drainage basin. In many regions, rivers are ancient features of the landscape, thus providing opportunities for speciation among reproductively isolated populations. Anthropogenic influences generally act to make fish assemblages more similar within and among basins and lead to loss of biodiversity. In many rivers, the presence of water regulation structures has had a negative impact on species that prefer flowing conditions and in some cases, has restricted their ability to access former spawning areas. The introduction of nonnative fish species has also substantially altered fish communities in many rivers. As for other river biota, discharge is the key environmental factor structuring communities. In floodplain rivers, fish seek refuge from current velocities and utilize food resources in inundated areas. In levied and naturally constricted rivers, high discharge may cause high mortality, particularly of larval stages, due to elevated current velocities in the channel.

River Food Webs

Research on river food webs has focused on trophic energetics with the goal of understanding the sources of organic matter supporting secondary production. Several conceptual models have been advanced that relate the abundance of invertebrates and fishes to sources of organic matter from the catchment, the floodplain and the river itself. The most influential of these is the River Continuum Concept (RCC) published by Robin Vannote and his colleagues in 1980 and cited in over 1800 subsequent publications. The utility of the RCC model lies in its holistic view of drainage networks whereby changes in the physical template of the channel (morphometry and substrate composition) with increasing stream order is linked to corresponding changes in food resources and biotic communities. The model emphasizes the importance of terrestrial (allochthonous) inputs in supporting secondary production. Consumers in river environments are thought to benefit from allochthonous inputs to a greater extent than their lentic counterparts due to loading factors that reflect the large ratio of land to surface water area in river basins. Autochthonous inputs were thought to be of minor importance particularly in headwater reaches (where shading by the forest canopy limits primary production) and in large rivers (where turbidity and depth limit algal and aquatic plant growth). This viewpoint is supported by geochemical analyses of riverine particulate matter which show that it is predominantly of terrestrial origin. However, the utilization of allochthonous and autochthonous organic matter is determined not only by their relative availability but also by their suitability relative to consumer needs (e.g., edibility, digestibility, nutritional sufficiency). Allochthonous inputs are comprised of detrital materials low in nutritive value whereas organic matter of autochthonous origin is enriched in mineral nutrients (N, P) and important biochemicals (fatty acids, proteins, etc.). An alternative view of river food-web energetics (Riverine Productivity Model; RPM) is that higher trophic levels obtain a disproportionate fraction of energy (or key dietary factors) from autochthonous sources by selective feeding and preferential assimilation of the more nutritious algal component. Stable and radio isotopes of carbon are used to quantify inputs from various sources (e.g., aquatic vs. terrestrial) provided that the sources differ in their isotopic signatures. Stable isotope data have shown that various consumer groups in rivers rely on algal production despite the quantitative dominance of organic matter that is terrestrial in origin. While the RCC and RPM focus on transport and production within the main channel, the Flood-Pulse Concept (FPC) considers the contribution of floodplain areas in supporting riverine communities. The importance of floodplain resources depends on the duration, aerial extent and timing of floodplain inundation. In tropical regions, flooded areas may far exceed the size of the main channel, thereby allowing riverine consumers to utilize terrestrial resources over extensive areas (Figure 7). The growth of aquatic plants and algae in flooded areas may also augment terrestrial resources if the duration of flooding is sufficiently long and light-temperature conditions are favorable. Temperate rivers also experience periodic floods although these are typically of shorter duration and occur during periods when water temperature is low (e.g., in association with winter rains or spring snowmelt). The three models differ by their emphasis on longitudinal transport of terrestrial organic matter (RCC), autochthonous production within the channel (RPM) and floodplain resources (FPC). They share the common view that an appreciation of river hydrogeomorphology is central to understanding variations in the quantity and quality of food resources and, in turn, the energetic efficiency of river foods webs.

Figure 7 Inundation of the floodplain near a tributary of the Amazon River (Rio Unini). In many rivers, flood events follow a regular annual cycle to which riverine organisms and riparian communities are adapted. Flooding allows access by river organisms to terrestrial food resources in inundated areas. Photo by A. Aufdenkampe.

Global Biogeochemical Cycling

Rivers account for only a small proportion of land area worldwide but play an important role in regional and global biogeochemical cycles. Rivers are the principal means by which terrestrial-derived materials are transported to the ocean. Over 90% of the earth's landmass is drained by rivers; the 100 largest rivers drain 65% of global land area. Rivers are the most powerful erosive force on the planet, substantially modifying landscape features and transporting 20 gigatons of sediment to the coastal margin annually. The input of dissolved and particulate organic carbon from rivers is sufficient to account for the estimated replacement times of oceanic dissolved organic carbon (ca. 4000–6000 year). Much progress has been made in recent years to assess material export from rivers, but few studies have examined within-river processes and their significance in regional and global biogeochemical cycles. Work by Jeff Richey and his colleagues has shown that waters of the Amazon release 13 times more carbon through out-gassing (evasion) of respired CO_2 than is exported to the ocean. The respired carbon originates from terrestrial sources and suggests that the overall carbon budget of the rainforest is more closely balanced than would be inferred from terrestrial biomass accumulation and fluvial export losses alone. The cumulative effects of human activities within river basins have given rise to global-scale alterations in water and material fluxes. Anthropogenic inputs have enhanced the delivery of nitrogen and phosphorus by rivers to coastal environments and led to widespread problems with eutrophication. The combined storage capacity of the world's dams has increased water storage and sediment retention thereby partially offsetting erosion losses associated with watershed disturbance.

Glossary

Discharge – The volume of water moving past a given point in the river per unit time (typically, $l\ s^{-1}$)

Evapotranspiration – The movement of water from the Earth's land surface to the atmosphere via evaporation and plant transpiration.

Nutrient spiraling – The uptake and release of dissolved nutrients during downstream transport.

Anadromous – Fishes that live predominantly in marine waters but are seasonal residents of freshwater streams and rivers during spawning and larval development.

Hypoxia – A reduced concentration of dissolved oxygen in a waterbody.

Hyporheos – The zone beneath and lateral to the river bed where river- and ground-water mix.

See also: Algae of River Ecosystems; Chemical Fluxes and Dynamics in River and Stream Ecosystems; Currents in Rivers; Restoration Ecology of Rivers; Streams and Rivers as Ecosystems.

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