TYPES OF RIVER ECOSYSTEMS

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Summary

Rivers link terrestrial, freshwater and coastal marine systems in an open transport and migration route. The most obvious characteristic of river ecosystems is that of unidirectional flow driven by gravity. River characteristics show gradients over the longitudinal, lateral (transversal) as well as vertical axis, and as these gradients also show time-varying characteristics, they are in fact four-dimensional systems. The major phenomena that structure patterns and processes in the riverine landscape can occur at various time scales (from seasonal to millennial scale).

In the river catchment, several processes lead to differentially structured river sections, varying in geomorphology, hydrology, biogeochemistry and ecosystem variables. Various ecological concepts have been developed to describe these differences in relation to each other, like the River Continuum Concept (RCC), the Flood Pulse Concept (FPC) etc., which play an important role in our basic understanding of river ecosystems. In terms of stream habitats, a hierarchical classification based on spatial and temporal scales is a necessary tool to understand biodiversity. Fluvial and ecological processes are correlated at a range of scales, and the sensitivity to disturbance and recovery times of communities in river systems differ at the various scales. The continuum character of rivers becomes very clear in the case of the construction of dams and embankments (dikes), because these disrupt the longitudinal and lateral continuum, resulting in shifts in abiotic and biotic parameters and processes.

1. Introduction

There is increasing interest in the importance of rivers from hydrological, geomorphological, ecological as well as environmental points of view, and the number of scientific symposia, publications and books on the subject is rapidly expanding (Burns, 2002). These river studies have led to a much better understanding of the main fluvial processes and their structuring role in riverine ecosystems in relation to abiotic factors. By now, a series of ecological concepts have been developed to link data on the structure of, and physical, chemical and biological processes in, pristine rivers and their watersheds. These concepts are valid for an understanding of river systems and their biota when rivers are unpolluted and natural processes are not affected by human-induced disturbances. At the same time, a better understanding of the structure and function of pristine rivers is also required for ecological rehabilitation of disturbed ones.

The present paper is not intended to be comprehensive, but provides a short introduction to river characteristics that determine the structure and functioning of riverine ecosystems, including flow, land-water interface, influx and retention of substances, stream size and disturbance. In addition, it outlines the four-dimensional perspective of river systems and the various ecological river concepts. Finally, it discusses the implications of this four-dimensional perspective and these ecological concepts for river research and management.

2. Characteristics of riverine ecosystems

2.1. Flow

The most obvious characteristic of rivers is that they flow, which distinguishes these lotic systems from lentic (standing or still) water systems like lakes and ponds. Fluvial processes driven by flow act in a nearly linear fashion. Flow is caused by differences in relative altitude in the landscape; its motor is gravity. It is unidirectional but not uniform. The slopes in between the rivers are subject to corrosion, erosion and denudation. Flow is maintained until the river reaches standing (still) water at the erosion base, that is, the sea or a lake. The retention time of water differs greatly between rivers and lakes. Turnover times of water in rivers are short, since rivers are continuously fed by run-off water and groundwater flows, which mean that their water masses are replaced all the time. There is a rapid, variable but continuous throughput of water and materials. The movement of water masses dissipates energy and influences stream morphology, sedimentation patterns and water chemistry. While a water mass is being transported, its chemical and biological conditions can change as a result of processes such as dilution, additions from tributaries, uptake and release of substances, biogeochemical conversions, vaporization etc. These processes are very clearly demonstrated in flooding events initiated upstream (flood wave) as well as in chemical spills and similar discharges into rivers (toxic waves).

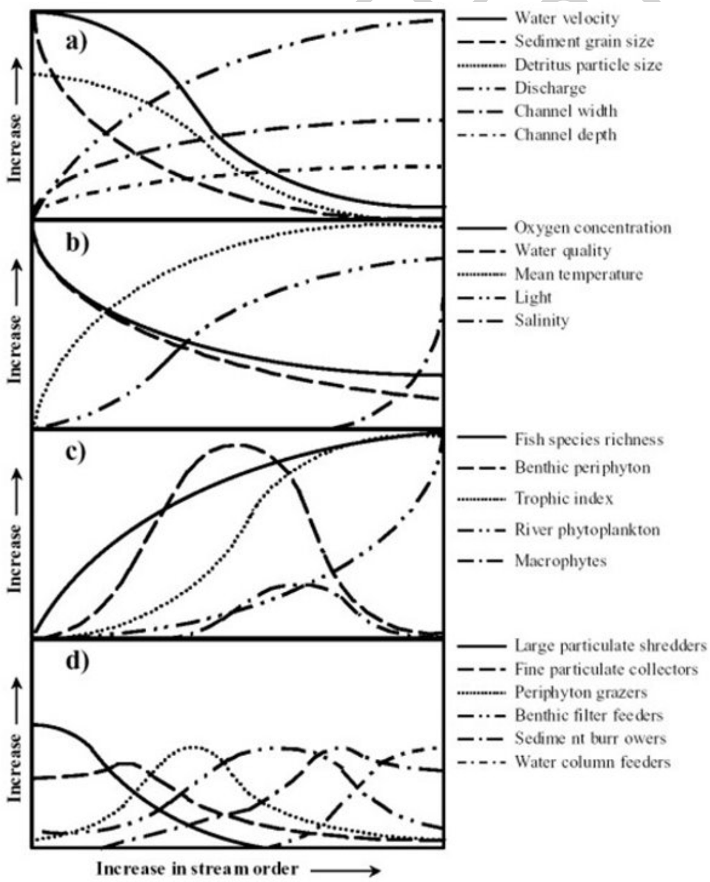

Figure 1. Theoretical relation between stream order and various physico-chemical and biological parameters in a temperate river (Adapted from Küster, 1978; Klee, 1985; Minshall et al., 1985).

The development of biota depends on the retention time of the water mass. In short rivers, this retention time may be too short for plankton development, allowing little succession to occur. With increasing retention times, phytoplankton diversity and biomass increase (Figure 1), although light is often limited by advective flows and turbidity. Although zooplankton in rivers is similar to that in lakes, smaller forms are more numerous in rivers. Zooplankton only develops well at low water velocity, which means that it shows an inverse relation with flow rates. As a consequence, zooplankton is more dominant in side channels where the velocity is low, or in the lower reaches of a river. Clay turbidity can suppress zooplankton development by reducing food availability and preventing food uptake.

The linear riverbed only represents a small portion of its total watershed. At watershed scale, chemistry, hydrology and sediment delivery are more or less controlled by biogeochemical processes and differ from those in other basins (Sweeney, 1992; Osborne & Kovacec, 1993; Allan & Johnson, 1997). Typical characteristics of river systems include a high and rapidly changing level of spatial heterogeneity, as well as great variability and individuality of physical, chemical and biological characteristics. Substrate and morphology in the channel also show dynamic changes, with biota supported by flows of mostly allochthonous organic matter, imported into the river from the catchment area and moving downstream (Wetzel, 2001). Thus, upstream communities influence downstream communities. However, migration in river systems is characterized by two opposing phenomena, viz., downstream and upstream transport by propagules, drift and swimming.

2.2. Stream order

Strahler (1957), following up the pioneering work of Horton (1945), proposed a classification system that starts from the smallest permanent streams, which are said to be of the first order. Two of these can combine to form a wider stream, called a second-order stream. Two streams of order (n) combine to form a stream of order (n+1). The trunk stream is not changed and remains of the same order as long as there are only additions by lower-order streams, but if a tributary of the same order joins it, the order is increased. This Horton-Strahler system is the most widely used, although some deficiencies of and alternatives to this method were discussed in Gordon et al. (1992). Stream order is positively correlated with the logarithm of catchment area and stream length (Wetzel, 2001), and has been found to be negatively correlated with the logarithm of the total number of tributaries and the mean slope. Many ecological studies have also correlated stream order with river characteristics such as input of particulate matter, primary and secondary production, species richness and abundance of functional groups (Figure 1).

2.3. Stream size

Benthic invertebrate and fish communities clearly differ between smaller streams and floodplain rivers (Ryder & Pesendorfer, 1980). Although fish production is not very different between these types, and can vary from moderate to high (average 50 g Dry Matter (DM) m^{-2} y^{-1}), fish communities in smaller streams tend to include warm as well as cold-water species, with numerous adaptations to a turbulent environment. By contrast, fish communities in floodplain rivers include mainly warm water species, with numerous adaptations to a turbid environment. Zoobenthos production is low to moderate in smaller streams (4-25 g DM m^{-2} y^{-1}) and moderate to high (more than 25 g DM m^{-2} y^{-1}) in floodplain rivers. Benthic invertebrate habitats also differ between smaller and larger rivers. In small streams, the riparian zone is narrow and rocky, varying from gravel to bedrock and flooding is brief but catastrophic (increasing the disturbance factor). Rivers in floodplains can change their course, unlike non-floodplain rivers. Floodplain rivers are characterized by a wide floodplain, which may include swamps, sand, snags and backwater sloughs, and flooding is prolonged and beneficial. This is clearly reflected in the zoobenthic community structure and feeding guilds. In smaller streams, there is a great diversity of shredders and scrapers in the channel, with relatively high abundances, feeding on microbially colonized litter fall and periphyton. These guilds are absent from the floodplain rivers. Nevertheless, diversity in the floodplain river is very high, with zoobenthos mainly consisting of gathering and filtering collectors in the channel and shredders and gathering collectors in the floodplains. Their food is dominated by dissolved organic matter (DOM), fine particulate organic matter (FPOM) and the microbes characteristic of wetlands and floodplains.

2.4. Land-water interface and other characteristics

The ratio of bank length to water area in rivers is extremely high compared to that in lakes, which means that there is an intensive exchange with the terrestrial environment. The land-water interface, or ecotone, is important because of the input of organic matter, shade and nutrients from the riparian vegetation (Naiman & Décamps, 1990). By contrast, the processes and biogeochemical flows in lakes are more closed, and are dominated by autochthonous processes. Whereas vertical processes dominate in lakes, horizontal processes dominate in streams and rivers.

The river is a continuum with discontinuities, which are ecologically connected by networks (Schönborn, 1992). Vital characteristics of river ecosystems are temperature, oxygen concentration, pH, hydrodynamic processes (flow, floods), morphodynamic processes (sediment transport, formation of river bed features) and habitat structure (Kern et al., 2002). Acid streams harbor macroinvertebrate communities that differ from those of alkaline streams, a difference which is larger than that caused by other stream characteristics (Hildrew & Giller, 1994).

2.5. Influx and retention of organic matter

The ecological functioning of a river is governed by abiotic processes. Going downstream, the abiotic characteristics form a gradient of increasing discharge, temperature, nutrient and sediment content and of decreasing particle size in the sediment (Figure 1). In addition, fluctuations in time are caused by daily and seasonal cycles and annual variations.

Functional processes are characterized by a flux of substances from the river catchment to the mouth of the river, which is influenced by influx, production and respiration processes and retention. Rivers transport inorganic substances like nutrients and minerals and particulate inorganic matter, as well as organic substances like particulate organic matter (POM), dissolved organic matter (DOM) and organisms. The river channel is fed by the input of organic material from the riparian vegetation, the primary production of biomass and the exchange of nutrients, minerals, organic matter and organisms between the river itself and the floodplains. There are two retention mechanisms: (a) physical retention by natural obstacles (e.g. beaver dams), sedimentation and vegetation on the riverbanks and floodplains and (b) biological retention by uptake in the food web. Variations in time and space in the influx and retention of substances as well as abiotic characteristics over the longitudinal axis of the river cause differences in the distribution of species, which are reflected by gradients of plankton, macroinvertebrates and zones of fish and benthic fauna from upstream to downstream. Gradients in discharge and flood duration are also recognizable over the transversal axis of the river and its floodplain. Biota have adapted to various situations and react differently to dynamic changes (Junk et al., 1989).

2.6. Natural disturbance regime

Natural disturbances (fluvial dynamics) play an important role in maintaining a diversity of habitats in riverine ecosystems by forming a variety of patch types and succession stages (Ward et al., 2002). Riverine ecosystems show dynamic longitudinal changes in flow, chemical conditions and biota due to rapid changes caused by precipitation events within the drainage basin. The differences in biota depend on their physiological and behavioral adaptations to extremes in cyclic variations of environmental factors. High discharges causing floods can occur in more or less predictable patterns, e.g. in spring, but sometimes they are very extreme or occur in other periods as well, and similar phenomena can be seen in relation to extreme droughts. Because the biota cannot adapt to such unpredictable phenomena in space and time, these floods or droughts act as disturbances.

After a disturbance, succession occurs as a sequence of appearances of animals and plants with different life strategies, which can be classified into: (a) opportunists (r-strategists), which are species with high growth rates and considerable colonization capacities; (b) periodical strategists, which are species that are adapted to particular periodical, e.g. seasonal, variations in their environment; and (c) equilibrium strategists, which thrive best under more or less constant environmental conditions. The relative importance of these groups depends on the regularity of the flooding events, but also on the location in the river system. In a transverse sequence across the floodplain, there are localities that are permanently under water, localities that are flooded temporarily, e.g. once a year, and localities where water is an exception.

Timing of floods is a factor often ignored when only flooding frequencies are used to explain the zonation. A flood in summer has a totally different effect than a flood in winter (Brock et al., 1987). Dister (1980) noted that data on the flood tolerance of tree species often appear to be contradictory because authors fail to indicate the timing of the floods relative to growth and resting periods. In addition, the duration of flooding is also important.

Temporary, periodic or episodic streams demonstrate the effects of drought disturbance. Drought can be considered a serious disturbance, because the continuity of water flow is interrupted. Emergence of the riverbed is a highly selective factor for the biocenoses. Once again, timing is important and erratic droughts have a much greater impact on the communities than periodic droughts.

There is therefore a clear difference in species composition between temporary and permanent streams, with the number of species in temporary streams mostly being smaller than that in permanent streams. Temporary streams tend to harbor highly tolerant euryoecious species, but also specialists possessing behavioral and physiological adaptations to survive droughts and to recolonize the stream after the water returns.

In fact, four categories of species can be distinguished in temporary streams: a) highly tolerant euryoecious species, b) temporary water specialists, c) species that survive in the dry stream bed as eggs, larvae or dormant adults, and d) species which continue to live actively in remaining pools or groundwater, under stones or in the sediments or as terrestrial organisms, such as flying insects (Legier & Talin, 1973; Williams & Hynes, 1977; Wright et al., 1983; Smith & Pearson, 1985).

The longitudinal zonation is disturbed in rivers if the upstream sections dry out. This tends to result in mass mortality of species, while some species from the upstream parts may move to downstream reaches with permanent water, increasing the number of species there (Gibon & Statzner, 1985).

The dry streambeds undergo colonization by terrestrial organisms such as insects and terrestrial plants and the remaining wet parts by animals living in still water ponds. Drought avoidance strategies and survival adaptations can also be found among fish, varying from migration, via survival in remaining pools, to very high reproduction rates to compensate for mass mortality.

Some fish species migrate to these temporary rivers in spring, spawn there and migrate downstream before the drought. Succession during refilling after drought can take more than a year, with different species or taxonomic groups usually returning at different rates. Colonizing diatoms are followed by green filiform algae and Cyanobacteria, while the return of herbivorous insects is followed by predatory species. Aquatic vegetation can return after 2-3 weeks. However, the rate at which species return may show large variations, depending on their adaptations to drought events.

Species that survive may return within a few days, while non-adapted species may only recolonize after 4-6 weeks or more (Schönborn, 1992). Recolonization takes place by means of drift, upstream migration, vertical migration from the hyporheon and through oviposition by flying insects.

Williams & Hynes (1976) found figures of 41% from drift and 18-28% from other sources. Reduced water levels can also act as a disturbance, because of increased concentrations of substances, increased temperatures and reduced oxygen levels. Recovery times depend on the scale of the system.

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Biographical Sketches

Gerard van der Velde (1946) was involved in the Rhine Action Programme for the Ecological Rehabilitation of the Rivers Rhine and Meuse since 1987. Numerous publications by him and co-authors dealt with various aspects of river ecology.

He was associate professor at the Laboratory of Aquatic Ecology of the Institute for Wetland and Water Research of Radboud University Nijmegen, The Netherlands, and nowadays is working as such at the Department of Animal Ecology and Ecophysiology of the same university. He is visiting professor at the inter-university course on Ecological Marine Management (ECOMAMA) of the Vrije Universiteit van Brussel (VUB), Belgium, where he gives lectures in tropical marine ecosystem management. He is also guest collaborator of the National Natural History Museum Naturalis at Leiden, The Netherlands. He was on the editorial board of Aquatic Botany and Aquatic Ecology, and nowadays on the editorial boards of Biological Invasions, Crustaceana, and Chemistry and Ecology. He participates in the Netherlands Centre for River Studies(NCR).

His research includes aquatic ecosystems with emphasis on macrophytes, macroinvertebrates, and fish including riverine, estuarine and marine habitats with special attention to connectivity due to short and long-term migrations and biological invasions.

Rob S.E.W. Leuven (1957) studied biology (aquatic ecology, fisheries and aquaculture) and wrote a PhD-thesis on the impacts of acidification on aquatic ecosystems in the Netherlands. At present, he is associate professor at the Department of Environmental Science(Institute for Wetland and Water Research) and chair of the Environmental Education Examination Board of the Radboud University Nijmegen (The Netherlands). He is member of the Dutch Commission for Environmental Impact Assessment and of the Program Committee of the Netherlands Centre for River Studies.
His teaching activities are concerned with river ecology and management, integrated water management and nature conservation. He was involved in the European TEMPUS and Erasmus-Socrates programmes.

His research programme focuses on ecological concepts for sustainable river basin management. He was coordinator of research projects commissioned by the European Commission (Interregional Rhine Meuse Activities), Dutch Ministry of Housing, Spatial Planning and Environment, the Dutch Ministry of Traffic and Public Works (Directorate General Water Management), World Bank (Partners for water programme), governmental advisory boards and non-governmental organisations.

Ivan Nagelkerken (1970) is assistant professor at the Department of Animal Ecology and Ecophysiology, Institute for Wetland and Water Research, Radboud University Nijmegen (The Netherlands).

He studied aquatic ecology at this University and marine biology at the University of Groningen, The Netherlands. He was for a long time park manager for the Curaçao underwater park and studied coral diseases and coral reef fish at the Netherlands Antilles in the Caribbean. Since 2000 he is involved in studies on riverine, estuarine and marine ecosystems at the Radboud University Nijmegen and especially in connectivity studies.