

Rivers and Streams: Life in Flowing Water

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What lies beneath rivers, diverse habitats with broadly varying niches? Communities reflect and influence local, upstream, downstream, and broader landscape conditions.



Introduction

Water current pervades every facet of existence for life in lotic (flowing water) habitats. Maintaining position in the face of flow can be energetically costly but provides access to a conveyor belt-like food-delivery system. Stream and river organisms reflect their localized niche and surrounding landscape both upstream and downstream. River organisms have evolved in diverse and fascinating ways in the varied environments between river source and mouth.

Streams and Rivers: Habitats Partitioned at Different Spatial Scales

Large-Scale Differences: Source to Mouth

The blue line of a river on a map conveniently represents rivers as two-dimensional habitats beginning (usually) in a mountainous region and ending in a far-off sea (or inland basin). But the physical changes in three dimensions along a river's length have important implications for river inhabitants.

River sources are usually small and, in the case of mountain streams, steep and erosional (Montgomery & Buffington 1997). In temperate environments, small streams

tend to be shaded by an interlocking, overhead tree canopy. Such conditions result in cool, well-oxygenated streams that are abundantly supplied with a food base of leaves. Fine particles of organic matter are released as the leaves are broken down by biological communities in the streams (River Continuum Concept; Figure 1; Vannote *et al.* 1980).

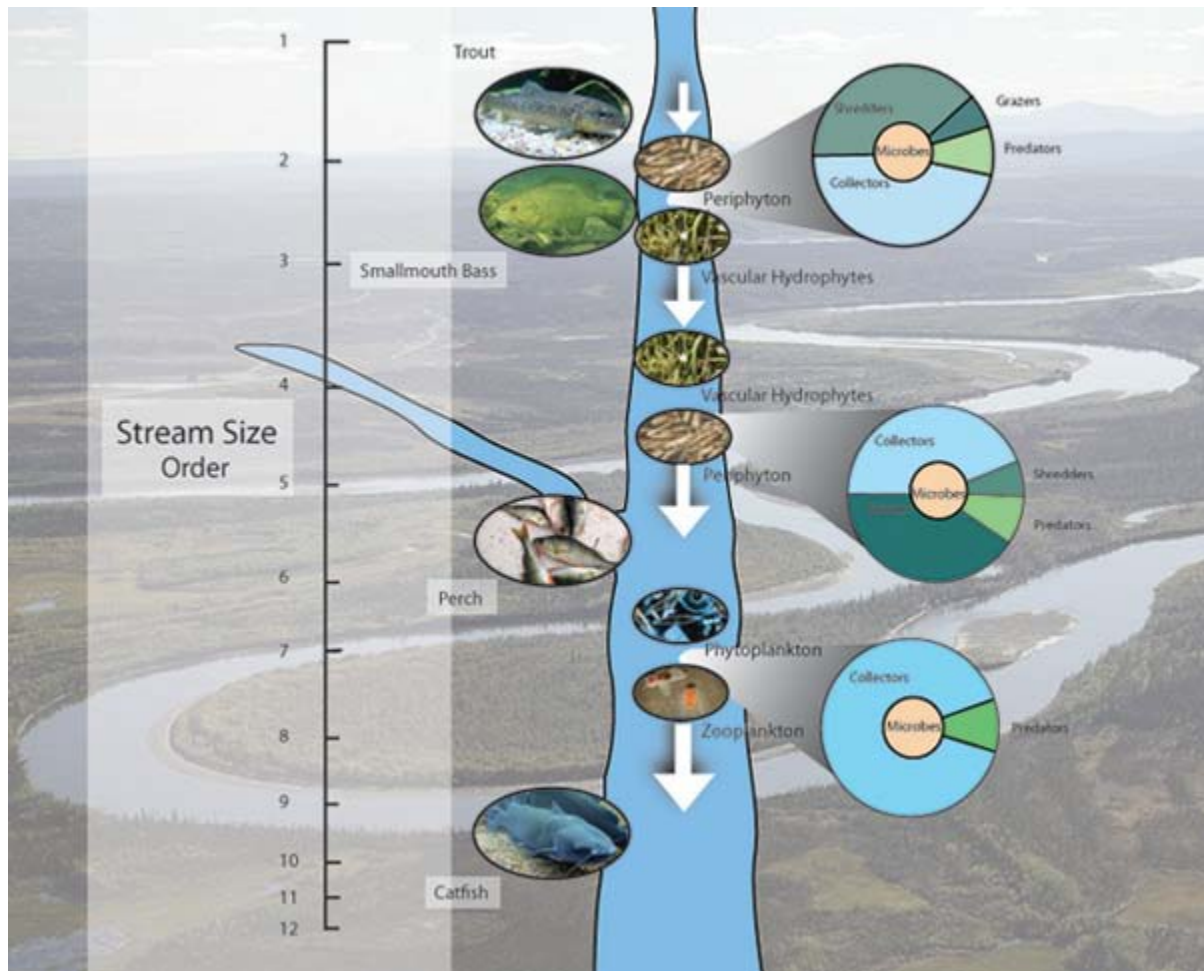


Figure 1: The river continuum concept is a conceptual model that predicts biological community responses to physical changes along the lengths of rivers.
 The river continuum concept is a conceptual model that predicts biological community responses to physical changes along the lengths of rivers.
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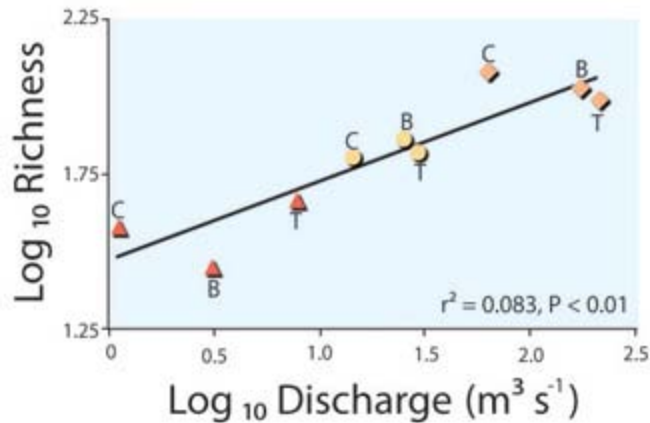


Figure 2: The species discharge relationship illustrated using samples from the upper (triangles), middle (circles), and lower (diamonds) reaches of three tributaries (B, C, & T) of the Mobile River in southeastern USA

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At some point along their path to the sea, rivers have typically gained enough water and width to preclude interlocking tree canopies. This open-canopy state frequently coincides with somewhat lower gradient landscapes. Streams at this point are warmer and less abundantly supplied with leaves than was the case upstream. These larger streams remain well oxygenated because air is entrained by turbulent flow in riffles. Open canopy, and fairly shallow water, means that light can reach the river benthos, increasing in-stream primary productivity.

Very large rivers are usually low gradient and very wide, resulting in negligible influence of riparian canopy in terms of shading and leaf-litter input. Water currents keep fine solids in suspension, reducing light penetration to the benthos. Organic matter in suspension is by far the largest food base in these very large rivers.

Changes in physical habitat and food base from river source to mouth profoundly influence biological communities. Aquatic ecologists classify benthic macroinvertebrates into functional feeding groups: shredders that eat leaves, collectors consuming fine particulates, grazers that scrape periphyton from substrates, and predators of animal prey (Cummins & Klug 1979). Smaller temperate streams tend to be co-dominated by shredders primarily consuming leaf litter and collectors consuming particles (Figure 1). As canopies open in larger streams, grazers become common with increased periphyton production. With less canopy cover in wider streams, shredder abundance is reduced. Collectors utilize particles in streams of all sizes, but they dominate benthic communities in larger streams where suspended organic matter is common. Predators represent a small but important fraction of benthic communities in rivers of all sizes.

The fish zonation concept (Thienemann 1925, cited by Schmutz *et al.* 2000) generalized Western European river habitats based upon a predictable sequence of dominant fish species (Huet 1959). Analogous fish community responses to river slope and size have been found in African, South American, and many North American streams (McGarvey & Hughes 2008). Larger rivers can accommodate larger fish as well as small fish, and

so the size range of fish increases as rivers become deeper. River discharge is the volume of water passing a particular location per unit time. The species-discharge relationship is analogous to the species-area relationship and describes how fish diversity increases with river size (Figure 2; McGarvey & Milton 2008).

The river continuum and fish zonation concepts are idealized models of river systems that provide theoretical frameworks for hypothesis generation and comparisons to particular situations. For example, when rivers pass through lakes, water temperatures, the food base, and downstream communities are all modified (Ward & Stanford 1983). Many stream sources lie above the treeline, have reduced organic matter input, and differ from the predictions of the river continuum concept. Anthropogenic influences frequently increase particulate matter loading to streams, increasing filtering collector component of benthic communities.

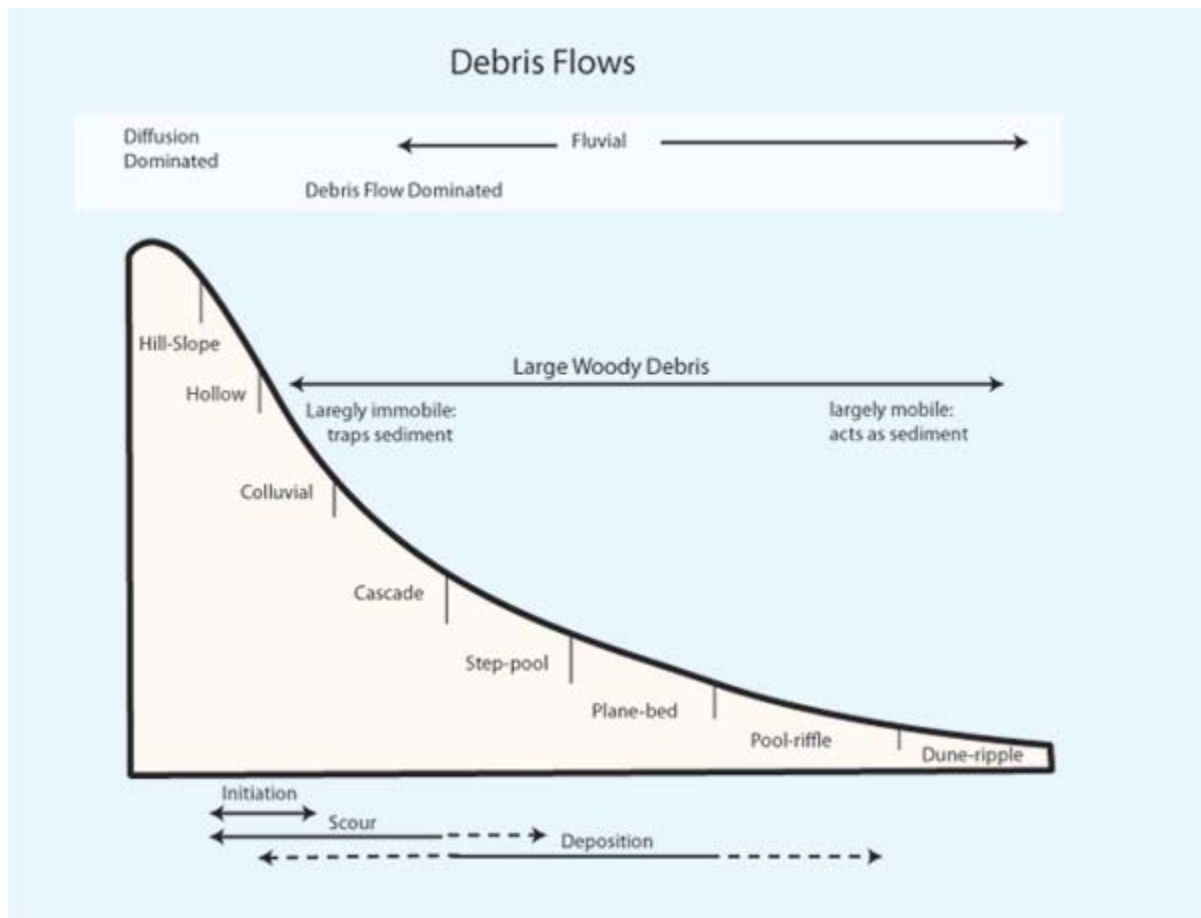


Figure 3: Generalized model of stream gradient and associated river-bed forms from steep mountain streams through low-gradient rivers (Montgomery and Buffington 1997)
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Local-Scale Structure: Pools, Riffles, Meanders, and the Hyporheic Zone

Local stream conditions vary substantially depending on gradient, stream size, and location along a stream continuum. A stream's gradient profile can be generalized as gradually changing from steep to low gradient as we move from high to low elevation and from small to large rivers (Figure 3; Montgomery & Buffington 1997). Steep mountain streams cascade over large pieces of rocky substrate with almost constantly turbulent flow. When a steep stream is confined by valley walls, a series of pools separated by near-vertical steps can form. These step pools repeat at a frequency of approximately one to four channel widths.

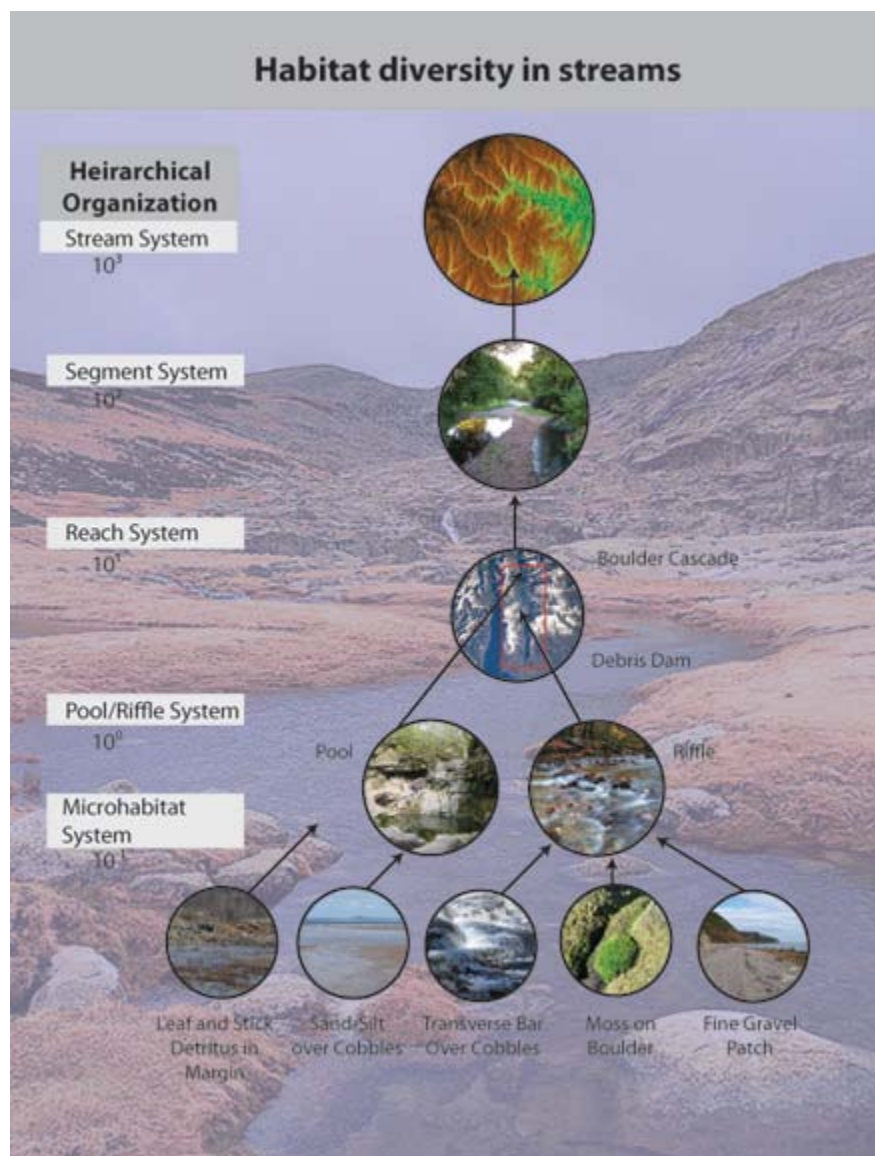


Figure 4: Habitat diversity in streams illustrated from large to micro scale (Frissell *et al.* 1986)

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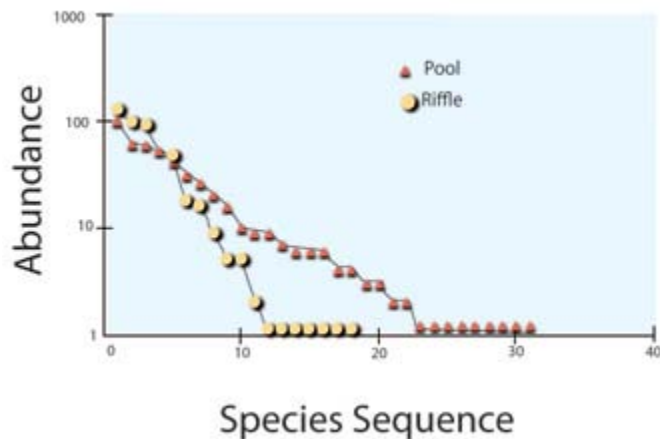


Figure 5: Differences in fish diversity between riffles and pools in rivers in southeastern Brazil

Species are represented, left to right, from most abundant to least. Pool communities have more species (31 spp) than riffles (18 spp), and are more even, as indicated by the lower slope of the pool plot (Langeani *et al.* 2005).

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In low- to moderate-gradient streams with loose rocky substrates, cobbles and boulders are mobilized during high-flow events and deposited across the width of river channels forming high-gradient riffles (Figure 4). Riffles are separated by pools, forming riffle-pool sequences recurring about three to five times the width of the river (Hynes 1970, Montgomery & Buffington 1997). During typical base-flow conditions, riffles are erosional habitats with fewer deposited fine particles between substrates. Particulate deposition increases as water velocity slows in pools. Riffle macroinvertebrate communities are typically more diverse than communities in pools. The pattern in fish communities is reversed, with pool fish communities tending to be more diverse than those in riffles (Figure 5; Gelwick 1990, Langeani *et al.* 2005).

Larger alluvial rivers in their natural state are diverse habitats with side channels, sand and gravel bars, and islands that are formed and reformed on a regular basis (Figure 6; Ward & Tockner 2001). In low-gradient flood plains, unconstrained rivers form meanders that shift and move as bed materials are eroded and redeposited. Dramatic changes can occur rapidly during flood events.

Streams exchange water, nutrients, and organisms with surrounding aquifers. The interstitial, water-filled space beneath river beds, where most active aquifer-river water exchange occurs, is termed the hyporheic zone, and is an important habitat for a number of aquatic organisms (Figure 7; Gibert *et al.* 1994 and references therein). The limits of the hyporheic zone vary, and riverine organisms can be found in groundwater up to 2 km from active stream channels (Stanford & Ward 1988).

Gradients in physical characteristics, including flow, depth, substrate characteristics, and light penetration, exist across river channels. These physical differences within a

river result in a diverse range of potential niches for aquatic organisms. Because of the heterogeneous nature of riverbeds, the distributions of fish, invertebrates, and algae, tend to form a patchy mosaic that shifts and responds dynamically to high-water events (Townsend 1989). One result of this patchiness is that samples of river organisms are notoriously variable.

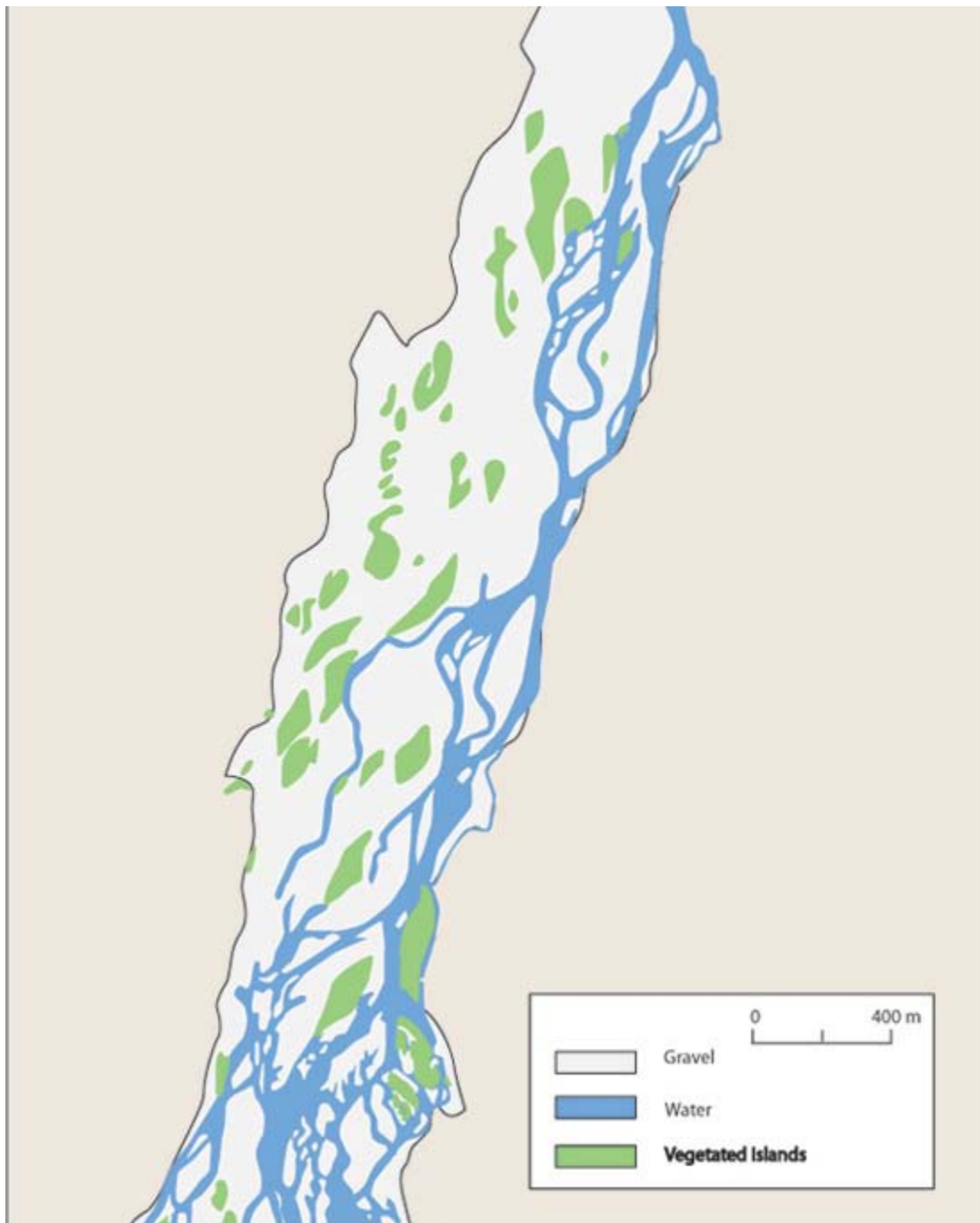


Figure 6: Map of the floodplain of a large low-gradient river in Italy showing the braided channel, deposited gravel, and vegetated islands

Many, if not most, large rivers have been channelized and contained, such that the natural state shown in this diagram is no longer the norm (Ward & Tockner 2001).
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Small-Scale Differences: Microhabitats

Organisms distribute themselves at even smaller spatial scales than those described above. The size and texture of river substrates influence invertebrate abundance and species richness (Downes *et al.* 1995). Invertebrate communities respond to different combinations of velocity, depth, and substrate roughness (Brooks *et al.* 2005). As is true in other habitats, the distributions of river organisms are additionally influenced by biological interactions.

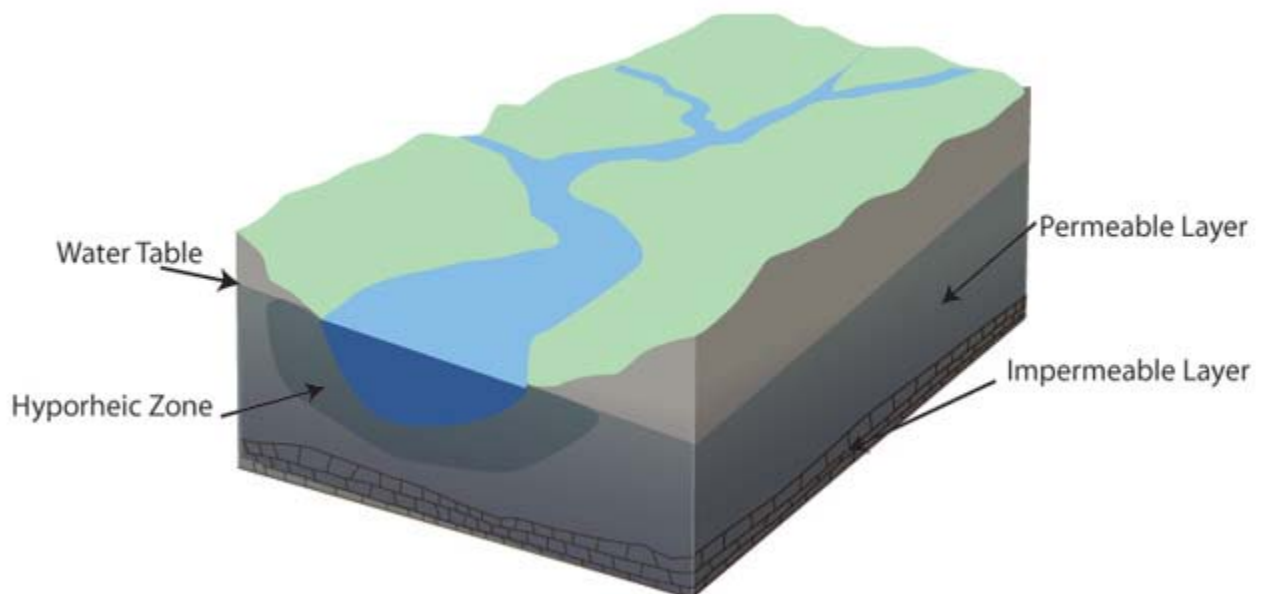


Figure 7: A river's hyporheic zone consists of water in the interstices below a riverbed. This zone is biologically active, and can function as a refuge for organisms during high-water events.
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Exchange with Surrounding Environments

Rivers exchange water, materials, energy, and nutrients in a reciprocal manner with the surrounding environment. River-water quality, sediment characteristics, and biological communities, all reflect characteristics of the upstream and even the downstream environment. Conversely, local environments are thermally influenced, sculpted, watered, and nutritionally supplemented by rivers and streams.

Soil deposition by rivers onto their floodplains has influenced the course of human agriculture and the distributions of human populations since antiquity. River influence is

strongest on the immediately-adjacent habitat called the riparian zone. Biological communities in riparian zones are unique and distinct from those beyond the immediate influence of rivers. In some biomes (e.g., deserts, grasslands), river corridors are the most vegetated habitats that exist and provide essential habitat for a range of organisms. Riparian woods serve as important wildlife migration corridors linking fragmented forests (Lees and Peres 2008).

Upstream migrations of anadromous fish species bring marine-derived nutrients to the lotic environment (Wold & Hershey 1999). Fish carcasses increased insect abundance eight-fold in one experiment (Wipfli *et al.* 1998). Aquatic insects in turn transfer nutrients linking food webs between rivers and their riparian zones (Nakano & Murakami 2001). Larval aquatic insects spend weeks, more typically a year, or even longer in streams before adult emergence. The synchronous insect emergences sought by trout anglers, and indeed by trout, are sometimes large enough to be detected by regional weather radar (Figure 8) and provide vital nutrition for fish, terrestrial invertebrates, birds, and mammals. Terrestrial insects falling into streams constitute important parts of the diets of stream fish, making up as much as 50% of the diet of Dolly Varden Char (*Salvelinus malma*) in one study (Nakano *et al.* 1999).

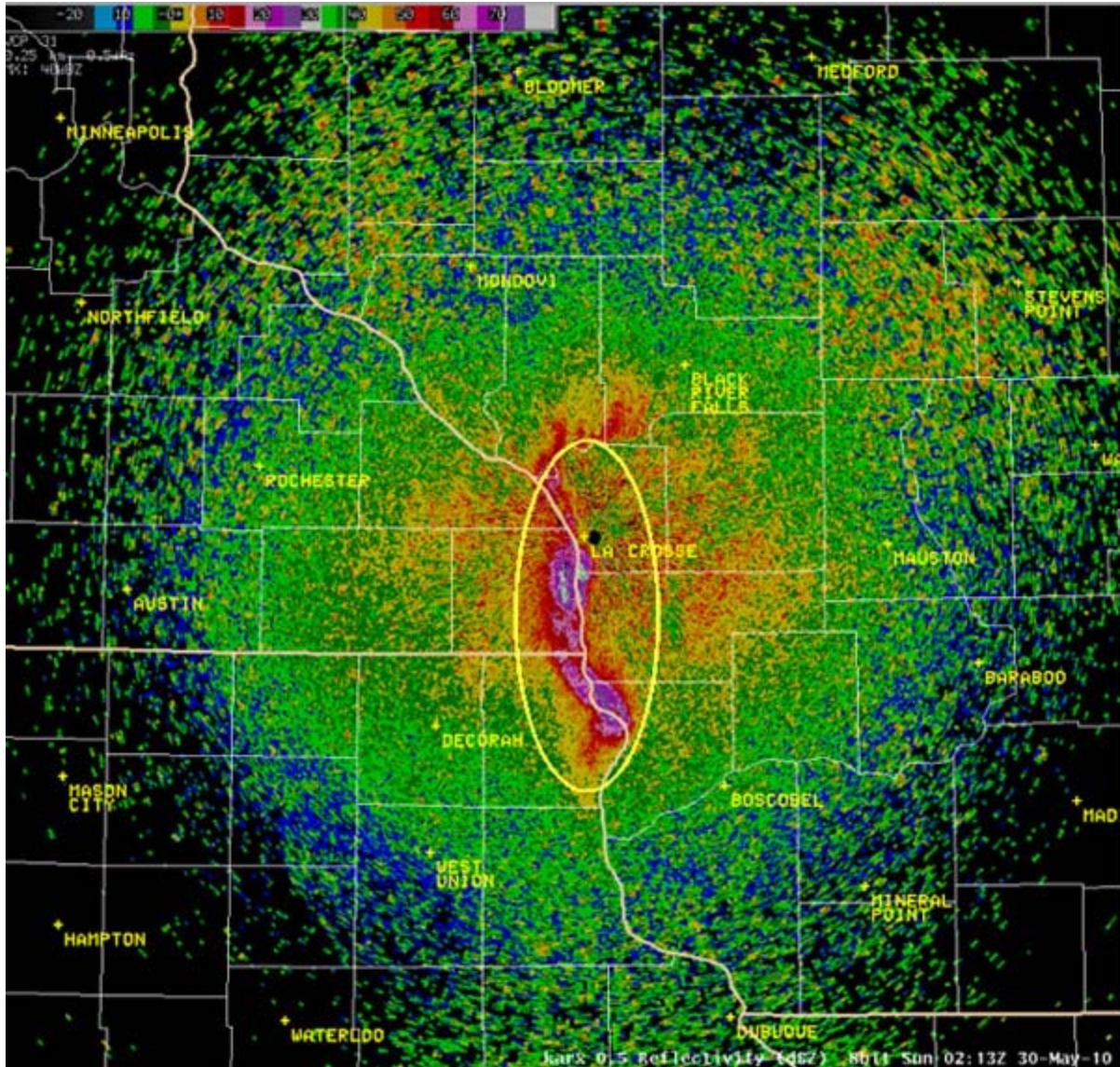


Figure 8: A mayfly mass emergence or hatch from the Mississippi river captured by the National Weather Service Doppler radar in La Crosse Wisconsin (USA) in May 2010

The adult mayflies in flight are represented by the bright pink, purple, and white.

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Tree limbs that fall into streams and rivers increase habitat heterogeneity. Submerged woody debris persists for long periods in streams and rivers, with a calculated half-life of ~20 years (Hyatt & Naiman 2001). Woody debris can stabilize river beds, modify erosion and deposition, create essential fish habitat, and help form pools that retain organic matter, extending the availability of seasonal food resources. Experimentally-manipulated woody debris was shown to increased both macroinvertebrate and fish colonization (Angermeier & Karr 1984).

Stormwater runoff from surrounding landscapes carries particles into streams. The particles include soil as well as plant and animal detritus. Organic particles in the runoff contribute to the food base in stream and river ecosystems.

Disturbance and Community Interactions

Heavy rainfall and snowmelt can greatly magnify the volume of stream water in a relatively short period of time. Rapidly flowing water can carry large quantities of sand and gravel, effectively sand-blasting surfaces and removing the periphyton layer. It is not unusual to see macroinvertebrate abundances reduced by half or more following such high-water events.

Reviewers of the river literature have generally concluded that disturbance is of greater importance than species interactions in streams (Lake 1990, Resh *et al.* 1988). This conclusion does not imply that community interactions are unimportant — and well-studied examples abound in the scientific literature — but the impacts of disturbance are generally considered to be of greater magnitude. Importantly, river organisms have evolved with a context of natural disturbance, and communities persist in spite of it.

Human Influences

Humans have rapidly introduced a wide array of disturbances to which river organisms have had no previous exposure during their evolution. We have dammed, channelized, diverted, drained, filled, and polluted streams and rivers. We have removed riparian vegetation, paved extensive portions of river catchments, and isolated river systems from their floodplains. Water is transferred among river basins and river organisms are exchanged among continents. Our influence on rivers has been so pervasive that one research group (Vörösmarty *et al.* 2010) estimated that fully 65% of the river water discharging to our oceans is associated with threatened habitats.

Our influences on river systems alter the nature of rivers and affect all of the processes described above. It is important to note that because river systems are well studied, environmental engineers have a sound, scientific basis for designing river restoration projects. The general frameworks described above, along with others beyond the scope of this article, provide scientific benchmarks against which to measure the success of restoration efforts.

Summary

The science of life in flowing water is well developed and active. River research is multidisciplinary in nature and draws from many branches of biology, chemistry, physics, and engineering. Because the vast majority of streams and rivers are in some way managed by human populations, our impacts on these systems can be extensive, as is our potential to improve stream habitat quality. Career opportunities for the next generation of river scientists exist in a wide variety of fields, and these new river scientists will have important influences on the health of rivers in the years to come.

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