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Connectivity of Streams and Wetlands to Downstream Waters: A Review and Synthesis of the Scientific Evidence

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LIST OF ACRONYMS AND ABBREVIATIONS

c	scaling power constant
CWA	Clean Water Act
DOC	dissolved organic carbon
FPOM	fine particulate organic matter
GIS	geographic information system
GPP	Gross Primary Productivity
GW	groundwater flowpath
NPP	Net Primary Productivity
NHD	National Hydrographic Dataset
POM	particulate organic matter
PPR	prairie pothole region
$T1$	major tributary
$T2$	minor tributary
USDA-ARS	United States Department of Agriculture, Agricultural Research Services
U.S. EPA	United States Environmental Protection Agency
USF	unsaturated flow
USGS	United States Geological Survey
WGEW	Walnut Gulch Experimental Watershed

LIST OF UNITS

A	drainage area
C	Celsius
cm	centimeter
d	day
ft	feet
g	gram
ha	hectare
kg	kilogram
km	kilometer
L	liter
m	meter
mg	milligram
Mg	megagram
mi	mile
mm	millimeter
μM	micromolar
N	metric normal temperature and pressure
ng	nanogram
Q	discharge
s	second
t	metric ton
τ_o	shear stress
V	velocity
ω_a	stream power
W	channel width
yr	year

PREFACE

This report was prepared by the National Center for Environmental Assessment, the National Health and Environmental Effects Research Laboratory, and the National Exposure Research Laboratory, in the U.S. Environmental Protection Agency (EPA)'s Office of Research and Development. It reviews and evaluates evidence from peer-reviewed sources published through August 2012. Two previous drafts prepared on 1 February 2011 and 12 July 2011 were reviewed by EPA and Army Corps of Engineers staff. Additional comments were received from scientists in government, academic, nonprofit and private industry organizations listed in the **Reviewers** section who reviewed all or part of the 1 February 2011 preliminary draft. A draft prepared on 11 October 2011 was independently peer reviewed by a panel of 11 topic experts, listed in the **Reviewers** section, on 30 January 2012. Comments from the external peer review and earlier reviews improved the clarity and strengthened the scientific rigor of this report.

Throughout this document, terms are used with their generally recognized scientific meaning. We have provided definitions of technical terms in the Glossary (see Appendix A).

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1. EXECUTIVE SUMMARY

1.1. BACKGROUND

This report reviews and synthesizes the peer-reviewed scientific literature on the connectivity or isolation of streams and wetlands relative to large water bodies such as rivers, lakes, estuaries, and oceans. The purpose of the review is to summarize the current understanding about these connections, the factors that influence them, and the mechanisms by which connected waters, singly or in aggregate, affect the function or condition of downstream waters. The focus of the review is on surface and shallow subsurface connections from small or temporary streams, nontidal wetlands, and certain open-waters. Specific types of connections considered in this review include transport of physical materials such as water, wood, and sediment; chemicals such as nutrients, pesticides, and mercury (Hg); movement of organisms or their seeds or eggs; and hydrologic and biogeochemical interactions occurring in surface and groundwater flows, including hyporheic zones and alluvial aquifers.

The literature review is organized into six chapters. Chapters 1 and 2 contain the executive summary, purpose, and scope of the report. Chapter 3 presents a conceptual framework describing the hydrologic elements of a watershed; the types of physical, chemical, and biological connections that link them; and watershed and climatic factors that influence connectivity at various temporal and spatial scales (see Figure 1-1). This conceptual framework provides background on the structure and function of streams and wetlands viewed from an integrated watershed perspective. In a discussion of connectivity, the watershed scale is the appropriate context for interpreting technical evidence about individual watershed components reviewed separately in subsequent chapters. Chapter 4 reviews the literature on stream networks (lotic systems) in terms of physical (see Section 4.3), chemical (see Section 4.4), and biological (see Section 4.5) connections between upstream and downstream habitats. Two case studies examine longitudinal connectivity and downstream effects in greater detail in regions with well-studied examples of river networks having a large proportion of intermittent and ephemeral streams: prairie streams (see Section 4.7) and arid streams of the Southwest (see Section 4.8). Chapter 5 reviews the literature on connectivity and effects of nontidal wetlands and certain open-waters (lentic systems) on downstream waters. This chapter is further subdivided into two broad categories of landscape settings based on directionality of hydrologic flows: bidirectional settings, in which wetlands and open-waters can have two-way hydrologic exchanges with other water bodies (e.g., riparian and floodplain wetlands and open-waters; see Section 5.3), and unidirectional settings, in which water flows only from the wetland or open-water towards the downstream water (e.g., most wetlands and open-waters outside of riparian

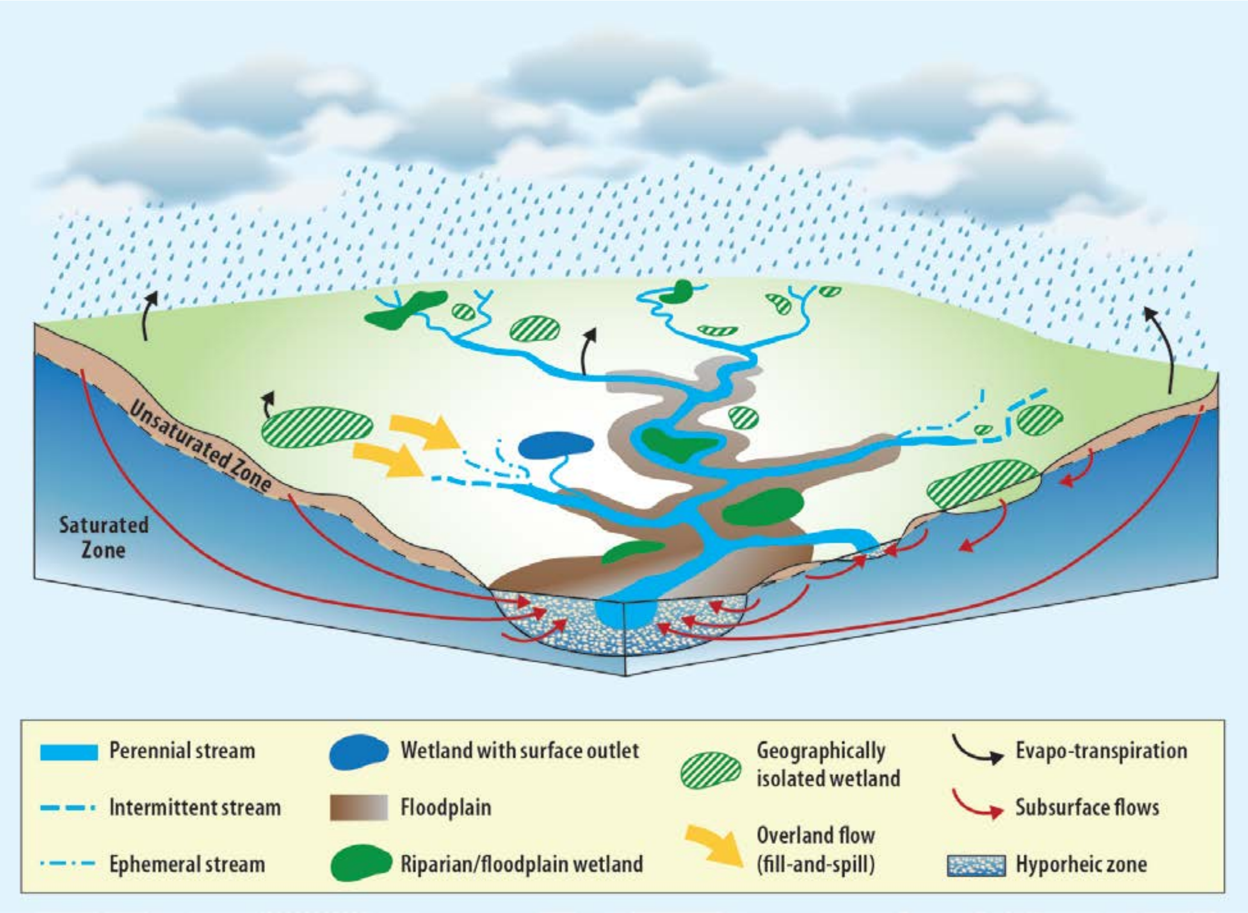


Figure 1-1. Overview of watershed elements discussed in this review. This is a simplified overview of the watershed elements and connection pathways discussed in this review. Blue lines represent stream and river channels, which include ephemeral, intermittent, and perennial tributaries to a river mainstem, shown at the center of the diagram. In addition to surface flows through stream channels, water and materials can move into streams and rivers through overland flow, shown here in yellow, and groundwater flows, shown here in red. Flowpath details (e.g., bidirectional exchanges between channels and hyporheic zones, confining layers, etc.) are omitted for clarity.

areas and floodplains; see Section 5.4). Directionality of hydrologic flow was selected as an organizational principle for this section because hydrologic flow direction has a dominant role in determining the types of connectivity and downstream effects (if any) of wetlands. Importantly, our use of these landscape settings based on hydrologic directionality should not be construed as suggesting directionality of geochemical or biological flows. In addition, the terms "unidirectional" and "bidirectional" describe the landscape setting in which wetlands and open-waters occur, and do not refer to wetland type or class. Four case studies from the literature, representing different landscape settings and geographic regions, examine evidence pertaining to connectivity and downstream effects of oxbow lakes (see Section 5.6), Carolina and Delmarva bays (see Section 5.7), prairie potholes (see Section 5.8), and vernal pools (see Section 5.9) in greater detail. Chapter 6 discusses key findings and major conclusions of the review, which also are included at the end of each review section and in the next section of this executive summary.

1.2. SUMMARY OF MAJOR CONCLUSIONS

Based on the review and synthesis of more than 1,000 publications from the peer-reviewed scientific literature, the available evidence supports three major conclusions:

1. The scientific literature demonstrates that streams, individually or cumulatively, exert a strong influence on the character and functioning of downstream waters. All tributary streams, including perennial, intermittent, and ephemeral streams, are physically, chemically, and biologically connected to downstream rivers via channels and associated alluvial deposits where water and other materials are concentrated, mixed, transformed, and transported. Headwater streams (headwaters) are the most abundant stream type in most river networks and supply most of the water in rivers. In addition to water, streams transport sediment, wood, organic matter, nutrients, chemical contaminants, and many of the organisms found in rivers. Streams are biologically connected to downstream waters by the dispersal and migration of aquatic and semiaquatic organisms, including fish, amphibians, plants, microorganisms, and invertebrates, that use both up- and downstream habitats during one or more stages of their life cycles, or provide food resources to downstream communities. Physical, chemical, and biological connections between streams and downstream waters interact via processes such as nutrient spiraling, in which stream communities assimilate and chemically transform large quantities of nitrogen (N) and other nutrients that would otherwise increase nutrient loading downstream.

2. Wetlands and open-waters in landscape settings that have bidirectional hydrologic exchanges with streams or rivers (e.g., wetlands and open-waters in riparian areas and floodplains) are physically, chemically, and biologically connected with rivers via the export of channel-forming sediment and woody debris, temporary storage of local groundwater that supports baseflow in rivers, and transport of stored organic matter. They remove and transform excess nutrients such as nitrogen and phosphorus (P). They provide nursery habitat for breeding fish, colonization opportunities for stream invertebrates, and maturation habitat for stream insects. Moreover, wetlands in this landscape setting serve an important role in the integrity of downstream waters because they also act as sinks by retaining floodwaters, sediment, nutrients, and contaminants that could otherwise negatively impact the condition or function of downstream waters.

3. Wetlands in landscape settings that lack bidirectional hydrologic exchanges with downstream waters (e.g., many prairie potholes, vernal pools, and playa lakes) provide numerous functions that can benefit downstream water quality and integrity.

> These functions include storage of floodwater; retention and transformation of nutrients, metals, and pesticides; and recharge of groundwater sources of river baseflow. The functions and effects of this diverse group of wetlands, which we refer to as “unidirectional wetlands,” affect the condition of downstream waters if a surface or shallow subsurface water connection to the river network is present. In unidirectional wetlands that are not connected to the river network through surface or shallow subsurface water, the type and degree of connectivity varies geographically within a watershed and over time. Because such wetlands occur on a gradient of connectivity, it is difficult to generalize about their effects on downstream waters from the currently available literature. This evaluation is further complicated by the fact that, for certain functions (e.g., sediment removal and water storage), downstream effects arise from wetland isolation rather than connectivity. The literature we reviewed does not provide sufficient information to evaluate or generalize about the degree of connectivity (absolute or relative) or the downstream effects of wetlands in unidirectional landscape settings. However, evaluations of individual wetlands or groups of wetlands could be possible through case-by-case analysis. Further, while our review did not specifically address other unidirectional water bodies, our conclusions apply to these water bodies (e.g., ponds and lakes that lack surface water inlets) as well, since the same principles govern hydrologic connectivity between these water bodies and downstream waters.

We provide below an overview of the conceptual framework we used, with further discussion of the key findings for streams, riparian and floodplain areas, and unidirectional wetlands.

1.3. CONCEPTUAL FRAMEWORK OVERVIEW

Connectivity is a foundational concept in hydrology and freshwater ecology. The structure and function of downstream waters are highly dependent on the constituent materials contributed by and transported through water bodies located elsewhere in the watershed. Most of the materials in a river, including water, sediment, wood, organic matter, nutrients, chemical contaminants, and certain organisms, originate outside of the river, from upstream tributaries, wetlands, or other components of the river system, and are transported to the river by water movement, wind, or other means. Therefore, streams and wetlands fundamentally affect river structure and function by altering transport of various types of materials to the river. This alteration of material transport depends on two key factors: (1) connectivity (or isolation) between streams, wetlands, and rivers that enables (or prevents) the movement of materials between the system components; and (2) functions within streams and wetlands that supply, remove, transform, provide refuge for, or delay transport of materials.

We define connectivity as the degree to which components of a system are joined, or connected, by various transport mechanisms. Connectivity is determined by the characteristics of both the physical landscape and the biota of the specific system. Isolation is the opposite of connectivity; it is the degree to which system components are not joined. Both connectivity and isolation have important effects on downstream waters. For example, stream channels convey water and channel-forming sediment to rivers, whereas wetlands that lack output channels can reduce flooding and store excess sediment. Transport of materials connects different ecosystem types at multiple spatial and temporal scales. For example, streams flowing into and out of wetlands or between lakes form continuous or seasonal connections across ecosystem boundaries. Similarly, aquatic food webs connect terrestrial ecosystems, streams, wetlands, and downstream waters.

Water movement through the river system is the primary, but certainly not the only, mechanism providing physical connectivity within river networks. Water movement provides a “hydraulic highway” that transports physical, chemical, and biological materials associated with the water (e.g., sediment, woody debris, contaminants, organisms). Because the movement of water is fundamental to understanding watershed connectivity, we begin the review in Section 3 with an explanation of the hydrologic foundation of river systems, and we define many of the terms and concepts used throughout this report.

Numerous factors influence watershed connectivity. Climate, watershed topography, soil and aquifer permeability, the number and types of contributing waters, their spatial distribution in the watershed, interactions among aquatic organisms, and human alteration of watershed features, among other things, can act individually or in concert to influence stream and wetland connectivity to, and effects on, downstream waters. For example, all else being equal, materials traveling shorter distances could enter the river with less transformation or dilution, thus increasing a beneficial or harmful effect. In other cases, sequential transformations such as nutrient spiraling (defined and discussed below) connect distant water bodies and produce beneficial effects on downstream waters. Infrequent events that temporarily connect nearby or distant streams or wetlands to rivers also can have large, long-lasting effects. Most of the major changes in sediment load and river channel structure that are critical to maintaining river health—including meanders of rivers in floodplains and creation of oxbow lakes—are a result of large floods that provide infrequent, intense connections with more distant streams and riparian or floodplain waters.

We have identified five functions by which streams, wetlands, and open-waters influence material transport into downstream waters:

- Source: the net export of materials, such as water and food resources;
- Sink: the net removal or storage of materials, such as sediment and contaminants;
- Refuge: the protection of materials, especially organisms;

- Transformation: the transformation of materials, especially nutrients and chemical contaminants, into different physical or chemical forms; and
- Lag: the delayed or regulated release of materials, such as storm water.

These functions are not static or mutually exclusive (e.g., a wetland can be both a source of organic matter and a sink for nitrogen) and can change over time (e.g., one wetland can be a water sink when evapotranspiration is high and a water source when evapotranspiration is low). Further, some functions work in conjunction with others. For example, a lag function can include transformation of materials prior to their delayed release. In a particular stream, wetland, or open-water, the presence or absence of these functions depends upon the biota, hydrology, and environmental conditions in the watershed.

When considering effects on downstream waters, it is helpful to distinguish between *actual function* and *potential function* of a stream, wetland, or open-water. For example, a wetland with appropriate conditions for denitrification is a *potential* sink for nitrogen, a nutrient that can be a contaminant when present in high concentrations. This function is conditional; if nitrogen were to enter a wetland (from agricultural runoff, for example), the wetland has the capacity to remove this nitrogen from the water. The wetland will not serve this function, however, if no nitrogen enters the wetland. Even if a stream or wetland is not currently serving an *actual* function, it has the *potential* to provide that function when a new material enters it, or when environmental conditions change. Thus, potential functions play a critical role in protecting those waters from future impacts.

1.4. DISCUSSION OF MAJOR CONCLUSIONS

1.4.1. Conclusion (1): Streams

The scientific literature demonstrates that streams, individually or cumulatively, exert a strong influence on the character and functioning of downstream waters. All tributary streams, including perennial, intermittent, and ephemeral streams, are physically, chemically, and biologically connected to downstream rivers via channels and associated alluvial deposits where water and other materials are concentrated, mixed, transformed, and transported. Headwater streams (headwaters) are the most abundant stream type in most river networks, and supply most of the water in rivers. In addition to water, streams transport sediment, wood, organic matter, nutrients, chemical contaminants, and many of the organisms found in rivers. Streams are biologically connected to downstream waters by the dispersal and migration of aquatic and semiaquatic organisms, including fish, amphibians, plants, microorganisms, and invertebrates, that use both up- and downstream habitats during one or more stages of their life cycles, or provide food resources to downstream communities. Physical, chemical, and biological connections between streams and downstream waters interact via processes such as nutrient spiraling, in which stream communities assimilate and chemically transform large quantities of nitrogen and other nutrients that would otherwise increase nutrient loading downstream.

Key findings:

a. Streams are hydrologically connected to downstream waters via channels that convey surface and subsurface water year-round (perennial flow), weekly to seasonally (intermittent flow), or only in direct response to precipitation (ephemeral flow). Streams are the dominant source of water in most rivers, and the great majority of tributaries are perennial, intermittent, and ephemeral headwater streams. For example, headwater streams, which are the smallest channels where stream flows begin, are the source of approximately 60% of the total mean annual flow to all northeastern U.S. streams and rivers.

b. Headwaters convey water into local storage compartments such as ponds, shallow aquifers, or river banks and into regional and alluvial aquifers. These local storage compartments are important sources of water for baseflow in rivers. The ability of streams to keep flowing even during dry periods typically depends on the delayed (lagged) release of local groundwater, also referred to as shallow groundwater, originating from these water sources, especially in areas with shallow groundwater tables and pervious subsurfaces. For example, in the southwestern United States, short-term shallow groundwater storage in alluvial floodplain aquifers, with gradual release into stream channels by intermittent and ephemeral streams, is a major source of annual flow in rivers.

c. Even infrequent flows through ephemeral or intermittent channels influence fundamental biogeochemical processes by connecting the channel and shallow groundwater with other landscape elements. Infrequent, high-magnitude events are especially important for transmitting materials from headwater streams in most river networks. For example, headwater streams, including ephemeral and intermittent streams, shape river channels by accumulating and gradually or episodically releasing stored materials such as sediment and large woody debris. These materials slow the flow of water through channels and provide substrate and habitat for aquatic organisms.

d. Connectivity between streams and rivers provides opportunities for materials, including nutrients and chemical contaminants, to be sequentially altered as they are transported downstream. Although highly efficient at transport of water and other physical materials, streams are not pipes: they are dynamic ecosystems with permeable beds and banks that interact with other ecosystems above and below the surface. The connections formed by surface and subsurface streamflows act as a series of complex physical, chemical, and biological alterations that occur as materials move through different parts of the river system. The amount and quality of such materials that eventually reach a river are determined by the aggregate effect of these sequential alterations that begin at the source waters, which can be at some distance from the river. The greater the distance a material travels between a particular stream reach and the river, the greater the opportunity for that material to be altered in intervening stream reaches, which can allow for uptake, assimilation, or beneficial transformation. One example of sequential alteration with significant beneficial effects on downstream waters is the process of nutrient spiraling, in which nutrients entering headwater streams are transformed by various aquatic organisms and chemical reactions as they are transported downstream by streamflow. Nutrients that enter the headwater stream (e.g., via overland flow) are first removed from the water column by streambed algal and microbial populations. Fish or insects feeding on algae and microbes take up some of those nutrients, which are subsequently released back to the stream via excretion and decomposition, and the cycle is repeated. In each phase of the cycling process—from dissolved inorganic nutrients in the water column, through microbial uptake, subsequent transformations through the food web, and back to dissolved nutrients in the water column—nutrients are subject to downstream transport. Stream and wetland capacities for nutrient cycling have important implications for the form and concentration of nutrients exported to downstream waters.

e. Our review found strong evidence that headwater streams function as nitrogen sources (export) and sinks (uptake and transformation) for river networks. One study estimated that rapid nutrient cycling in small streams that were free from agricultural or urban impacts removed 20−40% of the nitrogen that otherwise would be delivered to downstream waters. Nutrients are necessary to support aquatic life, but excess nutrients create conditions leading to eutrophication and hypoxia, in which over-enrichment causes dissolved oxygen concentrations to fall below the level necessary to sustain most within- and near-bed animal life. Thus, the role of streams in influencing nutrient loads can have significant repercussions for hypoxic areas in downstream waters.

f. Headwaters provide critical habitat during one or more life cycle stages of many organisms capable of moving throughout river networks. This review found strong evidence that headwaters provide habitat for complex life-cycle completion, refuge from predators or adverse physical conditions in rivers, and reservoirs of genetic- and species-level diversity. Use of headwater streams as habitat is especially obvious for the many species that migrate between small streams and marine environments during their life cycles (e.g., Pacific and Atlantic salmon, American eels, certain lamprey species), and the presence of these species within river networks provides robust evidence of biological connections between headwaters and larger rivers. In prairie streams, many fishes swim upstream into tributaries to release eggs, which develop as they are transported downstream. Small streams also provide refuge habitat for riverine organisms seeking protection from temperature extremes, flow extremes, low dissolved oxygen, high sediment levels, or the presence of predators, parasites, and competitors.

1.4.2. Conclusion (2): Riparian/Floodplain Waters

Wetlands and open-waters in landscape settings that have bidirectional hydrologic exchanges with streams or rivers (e.g., wetlands and open-waters in riparian areas and floodplains) are physically, chemically, and biologically connected with rivers via the export of channel-forming sediment and woody debris, temporary storage of local groundwater that supports baseflow in rivers, and transport of stored organic matter. They remove and transform excess nutrients such as nitrogen and phosphorus. They provide nursery habitat for breeding fish, colonization opportunities for stream invertebrates, and maturation habitat for stream insects. Moreover, wetlands in this landscape setting serve an important role in the integrity of downstream waters because they also act as sinks by retaining floodwaters, sediment, nutrients, and contaminants that could otherwise negatively impact the condition or function of downstream waters.

Key Findings:

a. Riparian areas act as buffers that are among the most effective tools for mitigating nonpoint source pollution. The wetland literature shows that collectively, riparian wetlands improve water quality through assimilation, transformation, or sequestration of nutrients, sediment, and other pollutants—such as pesticides and metals—that can affect downstream water quality. These pollutants enter wetlands via various pathways that include various sources such as dry and wet atmospheric deposition, some runoff from upland agricultural and urban areas, spray drift, and subsurface water flows, as well as point sources such as outfalls, pipes, and ditches.

b. Riparian and floodplain areas connect upland and aquatic environments through both surface and subsurface hydrologic flow paths. These areas are therefore uniquely situated in watersheds to receive and process waters that pass over densely vegetated areas and through subsurface zones before reaching streams and rivers. When contaminants reach a riparian or floodplain area, they can be sequestered in sediments, assimilated into the wetland plants and animals, transformed into less harmful forms or compounds, or lost to the atmosphere. Wetland potential for biogeochemical transformations (e.g., denitrification) that can improve the quality of water entering streams and rivers is influenced by factors present in riparian areas and floodplains, including anoxic conditions, shallow water tables, slow organic matter decomposition, wetland plant communities, permeable soils, and complex topography.

c. Riparian and floodplain areas can reduce flood peaks by storing and desynchronizing floodwaters. They also can contribute to maintenance of flow by recharging alluvial aquifers. Many studies have documented the ability of riparian and floodplain areas to reduce flood pulses by storing excess water from streams and rivers. One review of wetland studies reported that riparian wetlands reduced or delayed floods in 23 of 28 studies. For example, peak discharges between upstream and downstream gaging stations on the Cache River in Arkansas were reduced 10−20% primarily due to floodplain water storage.

d. Riparian and floodplain areas store large amounts of sediment and organic matter from upland areas before those sediments enter the stream. For example, riparian areas have been shown to filter 80−90% of sediments leaving agricultural fields in North Carolina.

e. Ecosystem function within a river system is driven by interactions between the physical environment and the diverse biological communities living within the river system. Movements of organisms connect aquatic habitats and populations in different locations—even across different watersheds—through several processes important for the survival of individuals, populations, and species, and for the functioning of the river ecosystem. For example, lateral expansion and contraction of the river in its floodplain results in an exchange of matter and organisms, including fish populations that are adapted to use floodplain habitat for feeding and spawning during high water. Refuge populations of aquatic plants in floodplains can become important seed sources for the river network, especially if catastrophic flooding scours vegetation and seed banks in other parts of the channel. Many invertebrates exploit temporary hydrologic connections between rivers and floodplain wetland habitats, moving into these wetlands to feed, reproduce, or avoid harsh environmental conditions and then returning to the river network. Amphibians and aquatic reptiles in many parts of the country commonly use both streams and wetlands, including wetlands in riparian and floodplain areas, to hunt, forage, overwinter, rest, or hide from predators.

1.4.3. Conclusion (3): Unidirectional Wetlands

Wetlands in landscape settings that lack bidirectional hydrologic exchanges with downstream waters (e.g., many prairie potholes, vernal pools, and playa lakes) provide numerous functions that can benefit downstream water quality and integrity. These functions include storage of floodwater; retention, and transformation of nutrients, metals, and pesticides; and recharge of groundwater sources of river baseflow. The functions and effects of this diverse group of wetlands, which we refer to as “unidirectional wetlands,” affect the condition of downstream waters if a surface or shallow subsurface water connection to the river network is present. In unidirectional wetlands that are not connected to the river network through surface or shallow subsurface water, the type and degree of connectivity varies geographically within a watershed and over time. Because such wetlands occur on a gradient of connectivity, it is difficult to generalize about their effects on downstream waters from the currently available literature. This evaluation is further complicated by the fact that, for certain functions (e.g., sediment removal and water storage), downstream effects arise from wetland isolation rather than connectivity. The literature we reviewed does not provide sufficient information to evaluate or generalize about the degree of connectivity (absolute or relative) or the downstream effects of wetlands in unidirectional landscape settings. However, evaluations of individual wetlands or groups of wetlands could be possible through case-by-case analysis. Further, while our review did not specifically address other unidirectional water bodies, our conclusions apply to these water bodies (e.g., ponds and lakes that lack surface water inlets) as well, since the same principles govern hydrologic connectivity between these water bodies and downstream waters.

Key Findings:

a. Water storage by wetlands well outside of riparian or floodplain areas can affect streamflow. Hydrologic models of prairie potholes in the Starkweather Coulee subbasin (North Dakota) that drains to Devils Lake indicate that increasing the volume of pothole storage across the subbasin by approximately 60% caused simulated total annual streamflow to decrease 50% during a series of dry years and 20% during wet years. Similar simulation studies of watersheds that feed the Red River of the North in North Dakota and Minnesota demonstrated qualitatively comparable results, suggesting that the ability of potholes to modulate streamflow may be widespread across portions of the prairie pothole region (PPR). This work also indicates that reducing wetland water storage capacity by connecting formerly isolated potholes through ditching or drainage to the Devils Lake and Red River basins could enhance stormflow and contribute to downstream flooding. In many agricultural areas already crisscrossed by extensive drainage systems, total streamflow and baseflow are enhanced by directly connecting potholes to stream networks. The impacts of changing streamflow are numerous, including altered flow regime, stream geomorphology, habitat, and ecology. The presence or absence of an effect of prairie pothole water storage on streamflow depends on many factors, including patterns of precipitation, topography, and degree of human alteration. For examples, in parts of the prairie pothole region with low precipitation, low stream density, and little human alteration, hydrologic connectivity between prairie potholes and streams or rivers is likely to be low.

b. Unidirectional wetlands act as sinks and transformers for various pollutants, especially nutrients, which pose a serious pollution problem in the United States. In one study, sewage wastewaters were applied to forested unidirectional wetlands in Florida for a period of 4.5 years. More than 95% of the phosphorus, nitrate (NO_3), ammonium, and total nitrogen were removed by the wetland during the study period, and 66−86% of the nitrate removed was attributed to the process of denitrification. In another study, sizeable phosphorus retention occurred in unidirectional marshes that comprised only 7% of the lower Lake Okeechobee basin area in Florida. A unidirectional bog in Massachusetts was reported to sequester nearly 80% of nitrogen inputs from various sources, including atmospheric deposition, and prairie pothole wetlands in the upper Midwest were found to remove >80% of the nitrate load via denitrification. A large unidirectional prairie marsh was found to remove 86% of nitrate, 78% of ammonium, and 20% of phosphate through assimilation and sedimentation, sorption, and other mechanisms. Together, these and other studies indicate that on-site removal of nutrients by unidirectional wetlands is significant and geographically widespread. The effects of this removal on rivers are generally not reported in the literature.

c. Biological connectivity can occur between unidirectional wetlands and downstream waters through movement of amphibians, aquatic seeds, macroinvertebrates, reptiles, and mammals, including colonization by invasive species. Many species in those groups that use both stream and wetland habitats are capable of dispersal distances equal to or greater than distances between many unidirectional wetlands and river networks. Migratory birds can be an important vector of long-distance dispersal of plants and invertebrates between unidirectional waters and the river network, although their influence has not been quantified.

d. Unidirectional wetlands can be hydrologically connected directly to river networks through channels, nonchannelized surface flow, or subsurface flows. A wetland surrounded by uplands is defined as "geographically isolated." Our review found that in some cases, wetland types such as vernal pools and coastal depressional wetlands are collectively, and incorrectly, referred to as geographically isolated. Technically, the term "geographically isolated" should be applied only to the particular wetlands within a type or class that are completely surrounded by uplands. Furthermore, "geographic isolation" should not be confused with functional isolation, because geographically isolated wetlands can still have hydrological and biological connections to downstream waters.

e. Unidirectional wetlands occur along a gradient of hydrologic connectivity-isolation with respect to river networks, lakes, or marine/estuarine water bodies. This gradient includes, for example, wetlands that serve as origins for stream channels that have permanent surface water connections to the river network; wetlands with outlets to stream channels that discharge to deep groundwater aquifers; geographically isolated wetlands that have local groundwater or occasional surface water connections to downstream waters; and isolated wetlands that have minimal hydrologic connection to other water bodies (but which could include surface and subsurface connections to other wetlands). The existence of this gradient among wetlands of the same type or in the same geographic region can make it difficult to determine or generalize, from the literature alone, the degree to which particular wetlands (individually or as classes), including geographically isolated wetlands, are hydrologically connected.

f. A related issue is that spatial scale must be considered when determining geographic isolation. Individual wetlands that are geographically isolated could be connected to downstream waters when considered as a complex (a group of interacting wetlands). This principle was demonstrated in a recent study that examined a depressional wetland complex on the Texas coastal plain. These wetlands have been considered as a type of geographically isolated wetlands. Collectively, however, they are geographically and hydrologically connected to downstream waters in the area. During an almost 4-year study period, nearly 20% of the precipitation that fell on the wetland complex flowed as surface runoff through an intermittent stream to a nearby waterway, the Armand Bayou. Thus, wetland complexes could have connections to downstream waters through stream channels even when the individual wetland components are geographically isolated.

1.5. CLOSING COMMENTS

The strong hydrologic connectivity of river networks is apparent in the existence of stream channels that form the physical structure of the network itself. Given the discussion above, it is clear that streams and rivers are much more than a system of physical channels for conveying water and other materials downstream, but the presence of physical channels is one strong line of evidence for surface water connections from tributaries, or water bodies of other types, to downstream waters. Physical channels are defined by continuous bed-and-bank structures, which may include apparent disruptions (such as by bedrock outcrops, braided channels, flow-through wetlands) associated with changes in the material and gradient over and through which water flows. The continuation of bed and banks down gradient from such disruptions is evidence of the surface connection with the channel that is up gradient of the perceived disruption.

The structure and function of rivers are highly dependent on the constituent materials that are stored in and transported through them. Most of these materials, broadly defined here as any physical, chemical, or biological entity, including but not limited to water, heat energy, sediment, wood, organic matter, nutrients, chemical contaminants, and organisms, originate outside of the river. They originate from either the upstream river network or other components of the river system, and then are transported to the river by water movement or other mechanisms. Thus, the fundamental way in which streams and wetlands affect river structure and function is by altering fluxes of materials to the river. This alteration of material fluxes depends on two key factors: (1) functions within streams and wetlands that affect material fluxes, and (2) connectivity (or isolation) between streams and wetlands and rivers that allows (or prevents) transport of materials between the systems.

Absence of channels does not, however, mean that a wetland or open-water is isolated or only infrequently connected to downstream waters. Areas that are infrequently flooded by surface water can be connected more regularly through shallow groundwater or through dispersal among biological populations and communities. Such wetlands and open-waters also can reduce flood peaks by storing flood waters, filter large amounts of sediment and nutrients from upland areas, influence stream geomorphology by providing woody debris and sediment, and regulate stream temperature. They also serve as sources of food for river biota and sources of genetic diversity for populations of stream invertebrates.

Unidirectional wetlands can reduce and attenuate floods through water storage, and can recharge groundwater, thereby contributing to stream and river baseflow. These wetlands also affect nutrient delivery and improve water quality by functioning as sources of food and as sinks for metals, pesticides, and excess nutrients. Biological connectivity can also occur between unidirectional wetlands and downstream waters, through movement of amphibians, aquatic insects, aquatic reptiles, migratory birds, and riverine mammals that require or opportunistically use both river and wetland or open-water habitats. However, for a geographically isolated wetland for which a surface water connection cannot be observed, it is difficult to assess its degree of connectivity with the river network without site-specific data.

Additionally, caution should be used in interpreting connectivity for wetlands based on their being designated as "geographically isolated" since (a) the term can be mistakenly applied to a heterogeneous group of wetlands that can include wetlands that are not geographically isolated, (b) wetlands with permanent channels could be miscategorized as geographically isolated if the designation is based on maps or imagery with inadequate spatial resolution, obscured views, etc., and (c) wetland complexes could have connections to downstream waters through stream channels even if individual wetlands within the complex are geographically isolated. Thus, the term "geographically isolated" should only be applied to groups of wetlands if they fit the technical definition (i.e., they are surrounded by uplands). Further, geographically isolated wetlands can be connected to the river network via nonchannelized surface flow (e.g., swales or overland flow), groundwater, or biological dispersal. Thus, the term "geographically isolated" should not be used to infer lack of hydrologic, chemical, or biological connectivity.

Lastly, to understand the health, behavior, and sustainability of downstream waters, the effects of small water bodies in a watershed need to be considered in aggregate. The contribution of material by a particular stream and wetland might be small, but the aggregate contribution by an entire class of streams and wetlands (e.g., all ephemeral streams in the river network) might be substantial. For example, western vernal pools typically occur within "vernal pool landscapes" or complexes of pools in which swales connect pools to each other and to seasonal streams, and in which the hydrology and ecology are tightly coupled with the local and regional geological processes that formed them. The vernal pool basins, swales, and seasonal streams are part of a single surface water and shallow groundwater system connected to the river network when seasonal precipitation exceeds storage capacity of the wetlands. Since rivers develop and respond over time and are functions of the whole watershed, understanding the integration of contributions and effects over time is also necessary to have an accurate understanding of the system, taking into account the duration and frequency of material export and delivery to downstream waters. In addition, when considering the effect of an individual stream or wetland, it is important to include the cumulative effect of all materials that originate from it, rather than each material individually, to understand that water body's influence on downstream waters.

2. INTRODUCTION

2.1. PURPOSE AND SCOPE

The purpose of this document is to review and synthesize available evidence in the peer-reviewed scientific literature pertaining to three questions:

1. What are the physical, chemical, and biological connections to and effects of ephemeral, intermittent, and perennial streams on downstream waters?
2. What are the physical, chemical, and biological connections to and effects of riparian or floodplain wetlands and open-waters (e.g., riverine wetlands, oxbow lakes) on downstream waters?
3. What are the physical, chemical, and biological connections to and effects of wetlands and certain open-waters that lack bidirectional hydrologic exchanges with downstream waters (e.g., most prairie potholes, vernal pools), hereafter referred to as unidirectional wetlands, on downstream waters?

We focus on peer-reviewed sources of information about surface and subsurface (particularly shallow subsurface) connections and interactions that influence the function and condition of surface waters, because these waters often fall within the purview of the Clean Water Act (CWA). As a scientific review, however, this report does not consider or make judgments regarding legal standards for CWA jurisdiction. Information about connections among water bodies of the same type (e.g., wetland-wetland, headwater stream-headwater stream) that do not influence the condition of downstream waters, are considered out of scope, as are non-peer-reviewed sources. Our review of subsurface flows emphasizes shallow (local) groundwater, because flows in this category have the greatest interchange with surface waters (Winter et al., 1998). Relevant surface-subsurface exchanges occur at depths ranging from centimeters to tens of meters, depending on geographic location, stream channel geometry, and other factors (Woessner, 2000). Readers should refer to the cited publications for quantitative information, such as flow length, depth, duration, timing, and magnitude, about specific surface and groundwater connections discussed in this report.

2.2. APPROACH

We used two types of evidence from the peer-reviewed published literature to identify connections and effects of wetlands, streams, and other water bodies on downstream waters: (1) direct evidence demonstrating a connection or effect (e.g., observed transport of materials or movement of organisms from streams or wetlands to rivers) and (2) indirect evidence supporting inference of a connection or effect (e.g., presence of environmental factors known to influence connectivity, a gradient of impairment associated with cumulative loss of streams or wetlands). In some cases, an individual line of evidence demonstrated connections along the entire river network (e.g., from headwaters to large rivers). In most cases, multiple sources of evidence were gathered and conclusions drawn via logical inference—for example, when one body of evidence shows that headwaters are connected to downstream segments, another body of evidence shows those downstream segments are linked to other segments farther downstream, and so on. This approach, which borrows from weight-of-evidence approaches in causal analysis (Suter et al., 2002), is an effective way to synthesize the diversity of evidence needed to address questions at regional and national scales.

To help readers understand the evidence presented in this review, we begin with a conceptual framework (see Section 3) that presents an overview of river system components, describes the spatial and temporal dynamics of connections within and among aquatic ecosystems, and provides context for interpreting empirical evidence of connections and functions and for making reasonable inferences about effects. We then review and synthesize the evidence for streams (see Section 4) and wetlands and certain open-waters (see Section 5), with illustrative examples for physical, chemical, and biological connections to downstream waters. Sections 4 and 5 include case studies of two lotic systems (prairie streams, southwestern intermittent and ephemeral streams) and four lentic systems (Carolina bays, oxbow lakes, prairie potholes, vernal pools) with more in-depth review of the literature on these types and locales. Prairie streams and arid streams of the Southwest were selected for case studies in part because a high proportion of these river networks are composed of intermittent and ephemeral streams. The four lentic systems case studies were selected as examples of water bodies having variable surface connectivity to downstream waters that is influenced by a range of local, regional, and global (e.g., climatic) factors. Section 6 presents a summary of major conclusions from the review.

As with any literature review, readers should refer to the cited publications for details and additional information about the systems and studies discussed in this report.

3. EFFECTS OF STREAMS AND WETLANDS ON DOWNSTREAM WATERS: A CONCEPTUAL FRAMEWORK

3.1. INTRODUCTION

A river is the time-integrated result of all waters contributing to it, and connectivity is the property that spatially integrates individual components. In a discussion of connectivity, the watershed scale is the appropriate context for interpreting technical evidence about individual watershed components (Newbold et al., 1982b; Stanford and Ward, 1993; Bunn and Arthington, 2002; Power and Dietrich, 2002; Benda et al., 2004; Naiman et al., 2005; Nadeau and Rains, 2007a; Rodriguez-Iturbe et al., 2009). This requires that freshwater resources be viewed within a landscape, or systems context (Baron et al., 2002). Addressing the questions asked in this report (see Section 2.1), therefore, requires an integrated systems perspective that considers both the components contributing to the river and the connections between those components and the river. This chapter provides a conceptual framework that describes this integrated systems perspective. Section 3.2 outlines the basic hydrologic foundation of river systems. Section 3.3 provides a general overview of how streams and wetlands affect downstream waters, focusing on functions within streams and wetlands and how they are connected to downstream waters. Finally, Section 3.4 examines key factors that affect connectivity between streams and wetlands and rivers. Although we focus our discussion here on interactions between streams, wetlands, and rivers, it should be noted that similar exchanges of water, influenced by many of the same factors, also occur between rivers, lakes, estuaries, and marine waters.

3.2. AN INTRODUCTION TO RIVER SYSTEMS

3.2.1. River System Components

In this report, the term **river** refers to a relatively large volume of flowing water within a visible channel, including subsurface water moving in the same direction as the surface water, and lateral flows exchanged with associated floodplain and riparian areas (Naiman and Bilby, 1998). **Channels** are natural or constructed passageways or depressions of perceptible linear extent that convey water and associated materials downgradient. They are defined by the presence of continuous bed and bank structures, or uninterrupted (though not impermeable) bottom and lateral boundaries. While bed and bank structures may in places be perceived as being disrupted (e.g., bedrock outcrops, braided channels, flow-through wetlands), the continuation of bed and banks down gradient from such disruptions is evidence of the surface connection with the channel that is up gradient of the perceived disruption. Such disruptions are associated with changes in the material and gradient over and through which water flows. If a disruption in the bed and bank structure prevented connection, then the area down gradient would lack a bed and banks, be colonized with terrestrial vegetation, and would not be discernible from the adjacent land. The concentrated longitudinal movement of water and sediment through these channels lowers local elevation, prevents soil development, selectively transports and stores sediment, and hampers the colonization and persistence of terrestrial vegetation. **Streams** are defined in a similar manner as rivers: a relatively small volume of flowing water within a visible channel, including subsurface water moving in the same direction as the surface water, and lateral flows exchanged with associated floodplain and riparian areas (Naiman and Bilby, 1998).

A **river network** is a hierarchical, interconnected population of channels that drains surface and subsurface water (see Sections 3.2.2 and 3.2.3) from a drainage basin to a river and includes the river itself. Drainage basin boundaries are traditionally topographically defined, such as by ridges, but groundwater sources and losses may occur outside of topographic boundaries (Winter et al., 2003). These channels can convey water year-round, weekly to seasonally, or only in direct response to rainfall and snowmelt (Frissell et al., 1986; Benda et al., 2004). The smallest of these channels, where stream flows begin, are considered **headwater streams**. Headwater streams are first to third-order streams (Vannote et al., 1980; Meyer and Wallace, 2001; Gomi et al., 2002; Fritz et al., 2006; Nadeau and Rains, 2007b), where stream order is a classification system based on the position of the stream in the river network (see Figure 3-1; Strahler, 1957). The point at which stream or river channels intersect within a river network is called a **confluence** (see Figure 3-1). The confluence of two streams with the same order results in an increase of stream order (i.e., two first-order streams join to form a second-order stream, two second-order streams join to form a third-order stream, and so on); when streams of different order join, the order of the larger stream is retained.

Mock (1971) presented a classification of the streams comprising stream or river networks. First order streams that intersect other first-order streams were designated as sources. We refer to these as **terminal source streams.** Mock defined first order streams that flow into higher order streams as tributary sources, and we refer to this class of streams as **lateral source streams.**

One weakness of stream order is that it disregards the contributions of lower-order streams where they join a higher-order stream. Link magnitude is an alternative method for classifying streams that resolves this issue. Link magnitude is the sum of all source streams draining into a given stream segment (Scheidegger, 1965; Shreve, 1967). Therefore, unlike stream order, the link magnitude of a segment accounts for all contributing lower-order streams regardless of their position in river networks. For some properties, link magnitude may better reflect the aggregate upstream contributions to downstream waters.

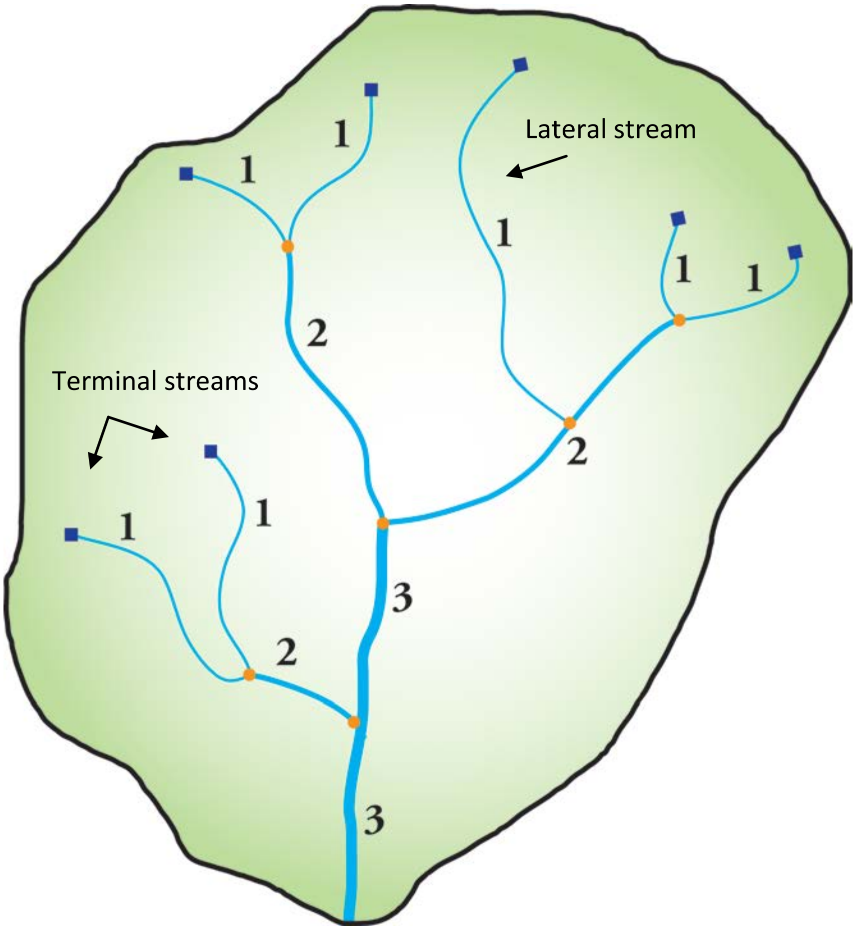


Figure 3-1. A generalized example of a river network within its drainage basin. Blue lines illustrate the river network, within the light green area of its drainage basin. Numbers represent Strahler stream order, with streams increasing in order when two streams of equal order join. Channel heads (blue squares) and confluences (orange dots) are also shown.

Terminal and lateral source streams typically originate at channel heads (Dietrich and Dunne, 1993), which occur where surface water runoff is sufficient to erode a definable channel. The channel head denotes the upstream extent of a stream’s continuous bed and bank structure (see Figure 3-1).

Channel heads are relatively dynamic zones in river networks, as their position can advance upslope by overland or subsurface flow-driven erosion, or retreat downslope by colluvial infilling. Source streams can also originate at seeps or springs and associated wetlands.

When two streams join at a confluence, the smaller stream (i.e., that with the smaller drainage area, or lower mean annual discharge) is called a **tributary** of the larger stream, which is referred to as the **mainstem**. A basic way of classifying tributary contributions to a mainstem is the **symmetry ratio**, which describes the size of a tributary relative to the mainstem at their confluence, in terms of their respective discharges, drainage areas, or channel widths (Roy and Woldenberg, 1986; Rhoads, 1987; Benda, 2008).

Surface water hydrologic connectivity within river network channels occurs through the unidirectional movement of water from channels at higher elevations to ones at lower elevations—that is, hydrologic connectivity exists because water flows downhill. In essence, the river network represents the above ground flow route and associated subsurface water interactions, transporting water, energy, and materials from the surrounding drainage basin (i.e., the watershed) to downstream rivers, lakes, estuaries, and oceans (The River Continuum Concept; Vannote et al., 1980).

A **river system** (see Figure 3-2) consists of a river network and its entire drainage basin, including all connected or isolated surface water bodies (e.g., lakes and wetlands), any groundwater flow systems connecting the drainage basin with the river network and surface water bodies, and terrestrial ecosystems (Stanford and Ward, 1993; Naiman et al., 2005).

Riparian areas and floodplains are important components of river systems (see Figure 3-3). **Riparian areas** are transition zones between terrestrial and aquatic ecosystems that are distinguished by gradients in biophysical conditions, ecological processes, and biota. They are areas through which surface and subsurface hydrology connect water bodies with their adjacent uplands, and they include those portions of terrestrial ecosystems that significantly influence exchanges of energy and matter with aquatic ecosystems (National Research Council, 2002). Riparian areas often are locations with high biodiversity (Naiman et al., 2005).

They occur adjacent to lakes and estuarine-marine shorelines and along river networks, where their width can vary from narrow bands along headwater streams (see Figure 3-3A) to broad zones that encompass the floodplains of large rivers (see Figure 3-3B).

Floodplains are level areas bordering stream or river channels that are formed by sediment deposition from those channels under present climatic conditions. These natural geomorphic features are inundated during moderate to high water events (Leopold, 1994; Osterkamp, 2008). **Terraces** are historical floodplains formed under different climatic conditions and are no longer connected to the river or stream channel that formed them (see Figure 3-3B).

Floodplains are also considered riparian areas, but not all riparian areas have floodplains. All rivers and streams within river networks have riparian areas, but small streams in constrained valleys are less likely to have floodplains than larger streams and rivers in unconstrained valleys (see Figures 3-2 and 3-3). The Federal Emergency Management Agency defines the area that will be inundated by the flood event having a 1% chance of being equaled or exceeded in any given year as the “Special Flood Hazard Area,” also referred to as the “100-year floodplain.” The 100-year floodplain may or may not coincide with the geomorphic floodplain.

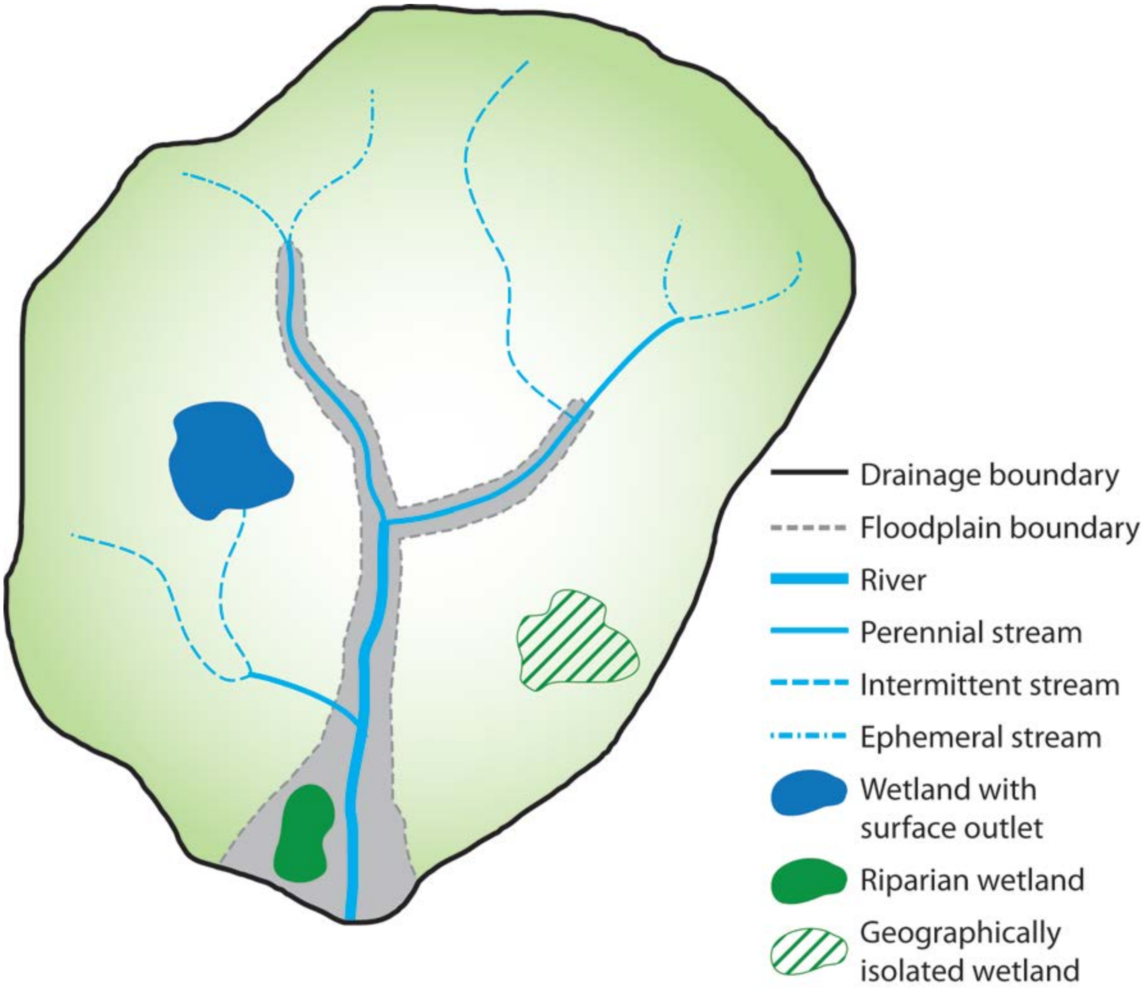


Figure 3-2. Elements of a river system. These elements include: the drainage basin (light green area), river network (rivers and streams), and other water bodies (riparian and floodplain wetlands, lakes, and unidirectional wetlands). Note that the unidirectional wetland that lacks a stream outlet would also be considered geographically isolated.

Like riparian areas, wetlands are transitional areas between terrestrial and aquatic ecosystems. According to Cowardin et al. (1979), an area is classified as a wetland if it has one or more of the following three attributes: (1) the area supports predominantly hydrophytes (i.e., water-loving plants) at least periodically; (2) the land has substrate that is predominantly undrained hydric soil; or (3) the land has nonsoil substrate that is saturated with water or covered by shallow water at some time during the growing season of each year. Note that the Cowardin et al. (1979) definition requires only one of these characteristics, in contrast to the Federal regulatory definition, which requires all three (33 CFR 328.3(b); see also USACE, 1987). Thus,

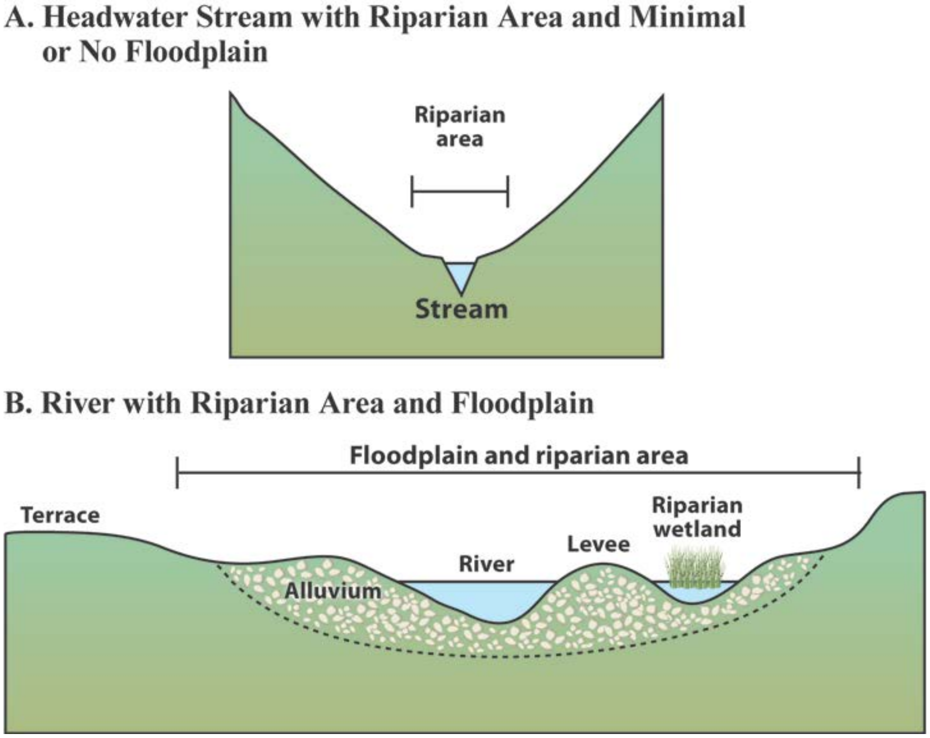


Figure 3-3. Hypothetical cross-sections of (A) a headwater stream and (B) a large river within a river network. Each cross-section shows the width of the riparian and floodplain area. The headwater stream (A) is a constrained reach with a narrow riparian area but no floodplain; the river (B) has both a riparian area and a floodplain with the same spatial extent. Examples of other common natural floodplain features are shown in (B). The lateral extent of riparian areas may vary depending on the criteria used for delineation.

as used in this report, a wetland need not meet the Federal regulatory definition. Wetlands include areas such as swamps, bogs, fens, marshes, ponds, and pools (Mitsch et al., 2009).

Many different classification systems have been developed for wetlands (Mitsch and Gosselink, 2007). These classifications can focus on vegetation, hydrology, hydrogeomorphic characteristics, or other factors (Cowardin et al., 1979; Brinson, 1993; Tiner, 2003a; Comer et al., 2005). Because the focus of this report is on downstream connectivity, here we consider two landscape settings in which wetlands occur based on directionality of hydrologic flows. Directionality of flow is also included as a component of hydrodynamic setting in the hydrogeomorphic approach (Brinson, 1993; Smith et al., 1995), and as an element of water flow path in an enhancement of National Wetlands Inventory data (Tiner, 2011). This emphasis on directionality of flow is necessary because hydrologic connectivity plays a dominant role in determining the types of effects wetlands have on downstream waters (see Section 3.3.2).

A **unidirectional wetland setting** is a landscape setting where there is a potential for unidirectional hydrologic flows from wetlands to the river network through surface water or groundwater. This would include upgradient areas such as hillslopes or upland areas outside of the floodplain. Any wetland setting where water could only flow from the wetland to a river network would be considered unidirectional, regardless of the magnitude and duration of flows and of travel times. Wetlands that occur in unidirectional settings are henceforth referred to as unidirectional wetlands.

A **bidirectional wetland setting** is a landscape setting (e.g., floodplains, most riparian areas, lake and estuarine fringes, etc.) that is subject to bidirectional hydrologic flows. Wetlands in bidirectional settings can have some of the same types of hydrologic connections as those in unidirectional settings. In addition, wetlands in these settings (henceforth referred to as bidirectional wetlands) also have bidirectional flows. For example, wetlands within a riparian area are connected to the river network through lateral movement of water between the channel and riparian area (e.g., through overbank flooding, hyporheic flow, etc.). Given our interest in addressing the effects of wetlands on downstream waters (see Section 2.1), we have focused in particular on the subset of bidirectional wetlands that occur in riparian areas and floodplains (referred to hereafter as **riparian/floodplain wetlands**); bidirectional wetlands at lake and estuarine fringes are mostly not addressed. Riparian wetlands are portions of riparian areas that meet the Cowardin et al. (1979) three-attribute wetland criteria (i.e., having wetland hydrology, hydrophytic vegetation, or hydric soils); floodplain wetlands are portions of the floodplain that meet these same criteria.

Our usage of landscape setting to define unidirectional and bidirectional wetlands is similar to Tiner's (2011) use of landscape position to supplement the Cowardin et al. (1979) classification. Our bidirectional setting is generally comprised of his estuarine, lotic, and lentic landscape positions, while our unidirectional setting is similar to his terrene category (Tiner, 2011). One important difference is that Tiner (2011) would consider a wetland terrene if it were located along a river but not subject to frequent overflow. Given that even infrequent flooding can have profound effects on wetland development and function, we would consider such a wetland bidirectional.

The terms unidirectional and bidirectional are meant to describe the landscape setting in which wetlands occur, and do not refer to wetland type or class. Many wetland types occur in both unidirectional and bidirectional settings. For example, a palustrine emergent wetland (Cowardin et al., 1979) could be located outside of a floodplain, in which case it would be considered unidirectional, or it could be located within a floodplain and subject to bidirectional flows. A wetland that is classified as depressional in the hydrogeomorphic approach could have any combination of inlets and outlets or none at all (Smith et al., 1995). The setting for such a wetland would be bidirectional if it had both an input and output channel, since water from the stream flows into and affects the wetland. However, a depressional wetland with a surface outlet and no inlet, or with no outlets and inlets, would be considered unidirectional, since water could only flow downgradient from the wetland to the river network, and not from a stream to the wetland. Similarly, a riverine wetland (Smith et al., 1995) that serves as the origin for a stream would be considered unidirectional if it had no input channel, even though it occurs in a riparian area. In most cases, however, riverine wetlands would be considered bidirectional. Thus, directionality of hydrologic flow is a function of landscape setting and cannot necessarily be determined from wetland class.

A major consequence of the two different landscape settings is that water-borne materials can only be transported from the wetland to the river network for a unidirectional wetland, whereas water-borne materials can also be transported from the river network to the wetland for a riparian/floodplain wetland. In the latter case, there is a mutual, interacting effect on the function and development of both the wetland and river network. In contrast, water-borne transport of materials from a unidirectional wetland can affect a river, but the opposite is not true. Note that our usage of unidirectional and bidirectional is limited to the direction of hydrologic flow, and should not be construed as suggesting directionality of geochemical or biological flows. For example, mobile organisms can move from a stream to a unidirectional wetland (e.g., Subalusky et al., 2009a; Subalusky et al., 2009b). In Alaska, transport of live salmon or their carcasses from stream to riparian area by brown bears (*Ursus arctos*) may account for over 20% of riparian nitrogen budgets (Helfield and Naiman, 2006). While this occurs within a bidirectional setting, it serves as an example of how geochemical fluxes can be decoupled from hydrologic flows.

Both unidirectional and bidirectional wetlands can include **geographically isolated wetlands**, or wetlands completely surrounded by uplands (Tiner, 2003b). Here, we define an **upland** as any area not meeting the Cowardin et al. (1979) three-attribute wetland criteria, meaning that uplands can occur in both terrestrial and riparian areas. Thus, a wetland that is located on a floodplain but is surrounded by upland would be considered a geographically isolated bidirectional wetland that is subject to periodic inundation from the river network. Given our concern with connectivity, it is important to discuss geographically isolated wetlands since hydrologic connectivity is generally difficult to characterize for these wetlands. This is because there are no apparent surface water outlets and because hydrologic monitoring or additional information and analyses would be necessary to determine whether connections through spillage or groundwater occur (see also Section 5.4.5).

3.2.2. River System Hydrology

Water moves from drainage basins to river networks, within river networks, and from river networks to drainage basins via numerous hydrologic flowpaths, both above and below ground. Similar flowpaths also occur between riparian/floodplain wetlands, unidirectional wetlands, and other components of river systems. This water movement shapes the development and function of river systems and is critical to maintaining their long-term health (Montgomery, 1999; Church, 2002).

Because groundwater-surface water interactions are essential processes in rivers, knowledge of basic groundwater hydrology is necessary to understand the interaction between surface and subsurface water and its relationship to connectivity within river systems. Subsurface water occurs in two principal zones: the unsaturated zone and the saturated zone (see Figure 3-4; Winter et al., 1998). In the **unsaturated zone**, the spaces between soil, gravel, and other particles contain both air and water. In the **saturated zone**, these spaces are completely filled with water. **Groundwater** refers to any water that occurs and flows in the saturated zone beneath a watershed surface (Winter et al., 1998).

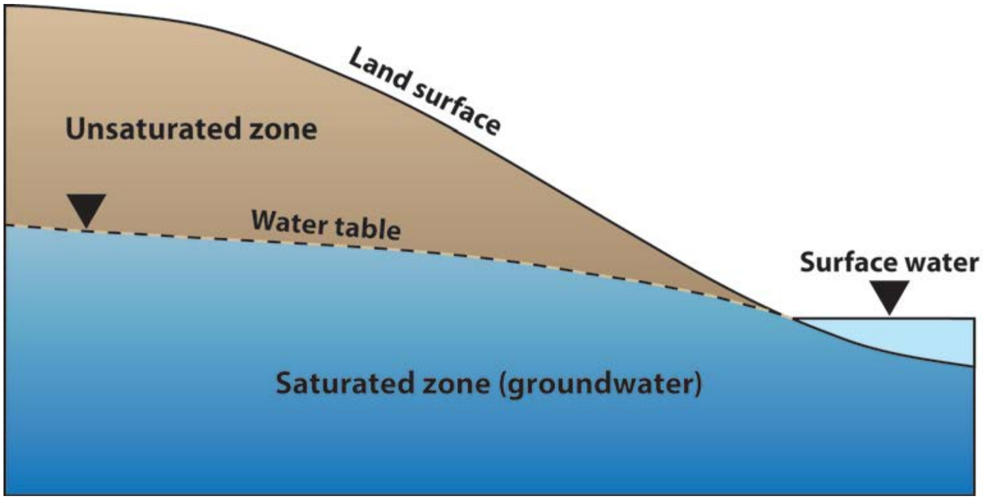


Figure 3-4. Water below the land surface occurs in either the unsaturated or the saturated zone. The upper surface of the saturated zone is the water table. Groundwater and groundwater flow occur in the saturated zone. If a surface water body is connected to the groundwater system, the water table intersects the water body at or near the surface of its shoreline.

Modified from Winter et al. (1998).

Traditionally, geologic formations in which groundwater occurs is commonly divided into two major categories: (1) **aquifers** are saturated geologic units capable of transmitting significant amounts of water under ordinary hydraulic gradients; and (2) **aquicludes** are saturated geologic units that are *not* capable of transmitting significant quantities of water and are also referred to as confining layers or confining units (Freeze and Cherry, 1979). Water flow in an aquifer can take various forms: water can flow in small voids and pores between the aquifer strata (porous media aquifers), in large voids (karst), or in fractures and cracks within the aquifer formation (fractured flow aquifers). Flow differs in its characteristics between the various aquifer types mentioned, yet follows the same basic rule, by which flow occurs from regions of high hydraulic pressure to regions of lower hydraulic pressure, down the pressure gradient (Jones and Mulholland, 2000).

There are two main types of aquifers (Freeze and Cherry, 1979). **Unconfined aquifers** are underlain by a confining unit but remain open to the atmosphere at their top and exchange gases with the environment. The upper saturated horizon in unconfined aquifers is known as the **water table** (see Figure 3-5). Complex geologic conditions can lead to more complex distributions of saturated and unsaturated zones. Discontinuous saturated lenses creating **perched water tables** can occur where low-permeability layers (e.g., clay) occur in the midst of highly permeable materials such as sand (Freeze, 1971). **Confined aquifers** are bounded by an underlying and an overlying confining unit and typically lack a direct connection with current surface and atmospheric conditions (see Figure 3-5). Water in confined aquifers is often pressurized and water levels in wells penetrating confined aquifers occur at elevations above the upper confining unit. The surface representing water levels in wells penetrating a confined aquifer is called the **potentiometric surface**. Confined aquifers typically occur deeper below the land surface than unconfined aquifers and generally have less frequent influence on surface waters than unconfined aquifers.

Traditionally, identification of aquifers was based solely on their ability to support water production wells, but in recent years hydrologists studying groundwater-surface water interactions have recognized the need for a broader definition that recognized the importance of low-flow geologic formations to aquatic ecosystems. Payne and Woessner (2010) recognized the importance of aquifers with varying flow rates on streams and proposed a classification of aquifer flow systems that ranged from high flow to low flow, with low flow aquifers having limited groundwater discharge potential except for small streams and wetlands. Winter et al. (1998) simply defined aquifers as the permeable materials (e.g., soil, rock) through which groundwater flows. In this report, we have adopted the Winter et al. (1998) aquifer definition.

Unless otherwise noted, our discussion of groundwater and aquifers is limited to unconfined systems.

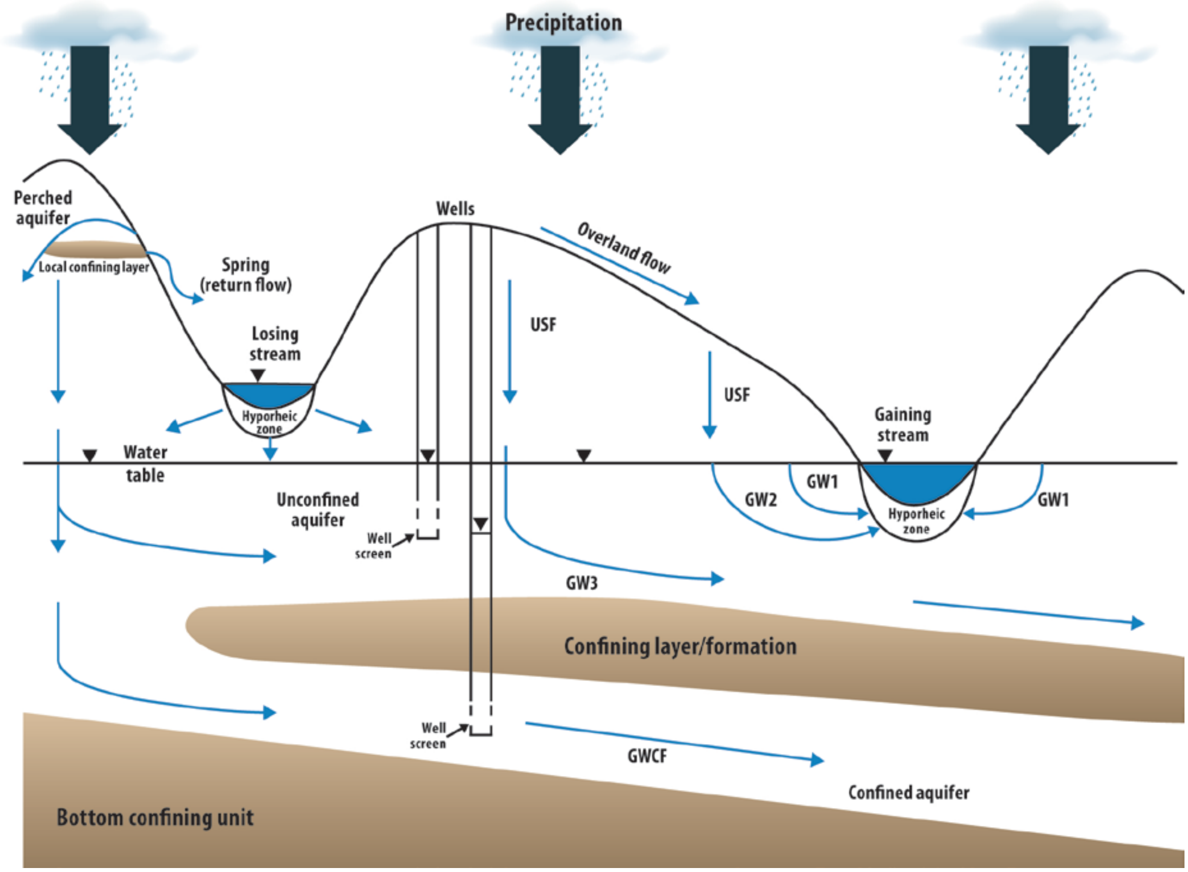


Figure 3-5. Cross-section showing major hydrologic flowpaths in a stream-watershed system regional in scale. USF = unsaturated flow, GW = groundwater flowpath (saturated flow); GW1, GW2, and GW3 = groundwater flowpaths on varying depth and length. GW1 represents local groundwater and GW3 represents regional groundwater. GWCF = groundwater flowpath in confined aquifer.

Groundwater **recharge area** occurs where water from land surfaces or surface water bodies infiltrates and moves into the saturated zone. A **discharge area** occurs where water flows from the saturated zone into a river network or other water body, or onto the land surface. River networks and other surface water bodies can gain water from or lose water to groundwater sources with great spatial and temporal variability (Harrington et al., 2002; Wilson and Guan, 2004; Scanlon et al., 2006; Vivoni et al., 2006; Larned et al., 2008).

A **gaining stream** within a river network receives inflow of groundwater. In this situation, the elevation of the water table in the vicinity of the stream must be greater than the elevation of the stream water surface. In a **losing stream** water flows from the stream to groundwater. In this situation, the water table elevation in the vicinity of the stream or wetland is lower than the stream or wetland water surface. Conditions conducive to losing or gaining streams and wetlands can change over short distances within river networks and river basins (Winter et al., 1998). Overall, the volume and sustainability of streamflow within river networks, however, typically depend on contributions from groundwater (Winter, 2007), especially in areas with shallow groundwater tables and pervious subsurfaces (de Vries, 1995; Kish et al., 2010).

Groundwater flow systems within river basins can be complex with varying sizes and depths that overlie one another (Toth, 1963; Winter et al., 1998; Haitjema and Mitchell-Bruker, 2005). Although in reality there is a continuum of flowpath lengths that occur within river basins (Bencala et al., 2011), they are commonly grouped into three categories (see Figure 3-5).

In a **local groundwater** flow system (also referred to as shallow groundwater), groundwater flows from a water table high to an adjacent lowland or surface water (Winter and LaBaugh, 2003). An intermediate groundwater flow system is one in which groundwater flows from a water table high to a lowland that is not immediately adjacent to the water table high. If the depth-to-width ratio of the aquifer is sufficiently large, a regional flow system (deepest groundwater flowpaths) may also be present. Local groundwater flow is the most dynamic of groundwater flow systems, so local groundwater has the greatest interchange with surface waters. **Regional groundwater** (also referred to as deep groundwater) originates from precipitation in distant upland recharge areas and moves over long distances, through deep regional-scale aquifers, to river networks (see Figure 3-5). These deep and long flow systems result in longer contact times between groundwater and subsurface materials than do local systems. Eventually, deep regional flow systems also discharge to surface waters in the lower portions of river networks where they influence surface water conditions. **Intermediate groundwater** flow systems are representative of the wide range of flowpath lengths and depths that occur between local and regional groundwater systems.

Other hydrologic flowpaths are also important to river systems. The most obvious flowpath is the downstream water movement within stream or river channels, or **open channel flow**. Water can reach riparian areas and floodplains via **overbank flow** (see Figure 3-6A), which occurs when floodwaters overflow stream and river channels (Mertes, 1997). Precipitation either infiltrates or flows over the surface when it falls on a watershed surface.

Overland flow is the portion of streamflow derived from net precipitation that fails to infiltrate the land surface and runs over the surface to the nearest stream channel without infiltrating at any point (see Figure 3-6A; Hewlett, 1982). **Return flow** occurs when water infiltrates, percolates through the unsaturated zone, enters the saturated zone, and then returns to and flows over watershed surfaces, commonly at hillslope-floodplain transitions.

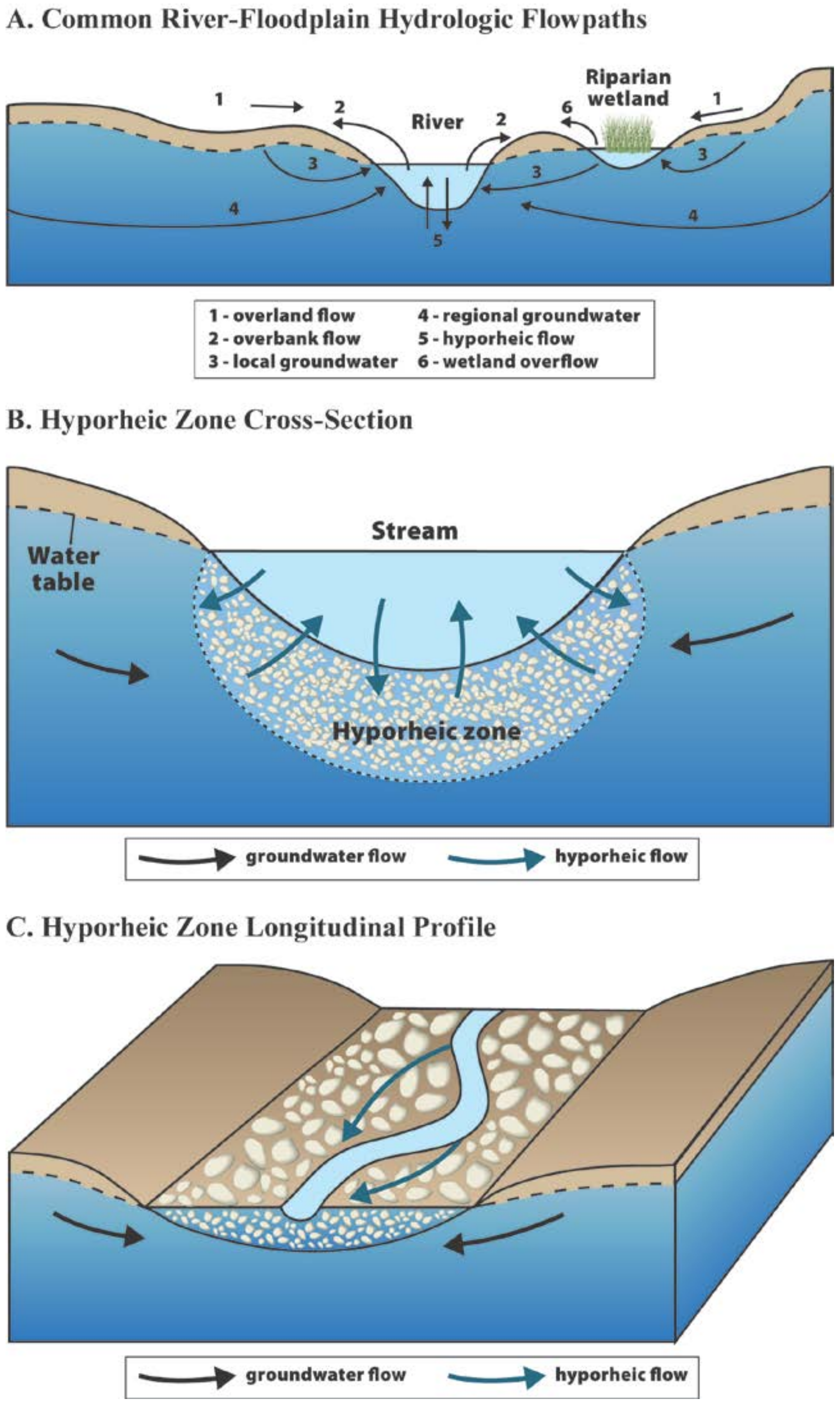


Figure 3-6. Hyporheic zone flows. (A) Common hydrologic flowpaths by which water flows between drainage basins and river networks. (B) and (C) The three-dimensional process of hyporheic flow, or the movement of water from a river or stream to adjacent alluvium and then back to the river or stream.

Modified from Winter et al. (1998).

Riparian areas have diverse hydrologic inputs and outputs that influence riparian/floodplain wetlands. These areas receive water from precipitation; overland flow from upland areas; and local, intermediate, and regional groundwater flows (see Figure 3-6A; National Research Council, 2002; Richardson et al., 2005; Vidon et al., 2010). Water flowing over the land surface can infiltrate vegetated or backwater riparian areas having low permeability soils or impervious clay layers. This infiltration increases water contact with the plant rooting zone, where ecological functions such as denitrification filter water before it reaches the stream channel (see Section 5.3.2; National Research Council, 2002; Naiman et al., 2005; Vidon et al., 2010).

Both bidirectional wetlands and unidirectional wetlands can be connected directly to river networks through channelized flow. Geographically isolated wetlands (bidirectional or unidirectional) also can be hydrologically connected to the river network via nonchannelized surface flow (e.g., swales or overland flow) or groundwater. In all cases, the hydrologic connections that exist between wetlands and the river network can be permanent or temporary.

Alluvium (see Figure 3-3) comprises deposits of clay, silt, sand, gravel, or other particulate materials that have been deposited by running water in a streambed, on a floodplain, on a delta, or in a fan at the base of a mountain. These deposits are found near active river systems but can also be found in buried river valleys, the remnants of relic river systems (Lloyd and Lyke, 1995). In this report, we are concerned primarily with alluvium deposited along active river networks. Commonly, alluvium is highly permeable, creating a preferential environment for groundwater flow. **Alluvial groundwater** (typically a mixture of river water and local, intermediate, and regional groundwater) moves through the alluvium. Together the alluvium and alluvial groundwater make up **alluvial aquifers.** Alluvial aquifers are closely associated with floodplains and have high levels of **hyporheic exchange** (Stanford and Ward, 1993; Amoros and Bornette, 2002; Poole et al., 2006), which occurs when water moves from stream or river channels into alluvial deposits and then returns to the channels (see Figure 3-6B and 3-6C; Bencala, 2005; Leibowitz et al., 2008).

Hyporheic exchange allows for the mixing of surface water and groundwater, can occur during both high- and low-flow periods, and typically has relatively horizontal flowpaths at scales of m to tens of m (Bencala, 2005) and vertical flowpaths with depths ranging from cm to tens of m (Stanford and Ward, 1988; Woessner, 2000 and references therein).

The relative importance of these different hydrologic flowpaths among river systems varies, creating streams and rivers with different flow duration (or hydrologic permanence) classes (see Figure 3-7). **Perennial streams** or stream reaches (see Figure 3-7a) typically flow year-round, and are maintained by local or regional groundwater discharge or streamflow from higher in the stream or river network. **Intermittent streams** or stream reaches (see Figure 3-7b) flow continuously, but only at certain times of the year (e.g., during certain seasons such as spring snowmelt); drying occurs when the water table drops lower than the channel bed elevation. **Ephemeral streams** or stream reaches (see Figure 3-7c) flow briefly (typically hours to days) during and immediately following precipitation; these channels are above the

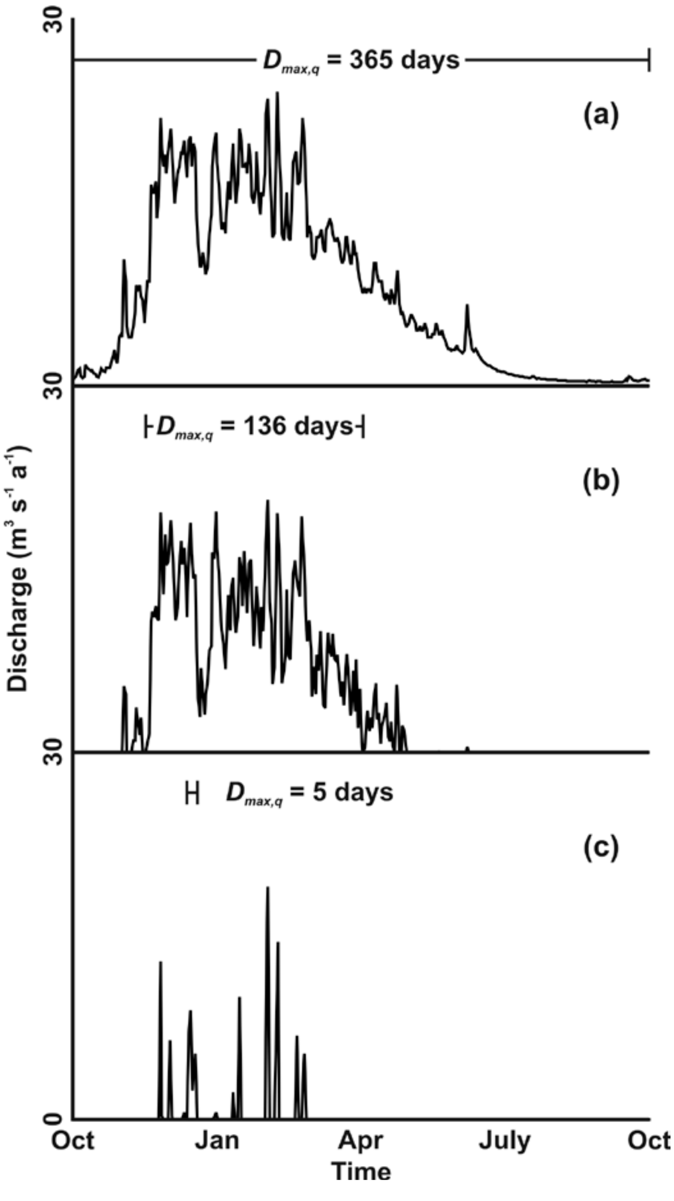


Figure 3-7. Hypothetical hydrographs illustrating maximum duration of flow ($D_{max,\ q}$) for (a) perennial, (b) intermittent, and (c) ephemeral streams.

From Leibowitz et al. (2008).

water table at all times. Streams in these flow duration classes often transition longitudinally, from ephemeral to intermittent to perennial, as drainage area increases and elevation decreases along river networks. Many headwater streams, however, originate from permanent springs and flow into intermittent downstream reaches, and at low flows, intermittent streams can contain dry segments alternating with flowing segments. Transitions between flow duration classes can coincide with confluences or with geomorphic discontinuities within the network (May and Lee, 2004; Hunter et al., 2005).

Similarly, the occurrence and persistence of riparian/floodplain wetland and unidirectional wetland hydrologic connections with river networks, via surface water or groundwater, can be continuous, seasonal, or ephemeral, depending on the overall hydrologic conditions in the drainage basin. For example, a unidirectional wetland might have a direct groundwater connection with a river network during wet conditions but have an indirect regional groundwater connection (via groundwater recharge) under dry conditions.

Variation of streamflow within river systems occurs in response to **hydrologic events** resulting from rainfall or snowmelt. **Stormflow** is streamflow that occurs in direct response to rainfall or snowmelt (see Figure 3-8A), which might stem from multiple groundwater and surface water sources (Dunne and Leopold, 1978). **Baseflow** is streamflow originating from groundwater discharge or seepage (locally or from higher in the river network), which sustains water flow through the channel between hydrologic events (see Figure 3-8A). Perennial streams have baseflow year-round; intermittent streams have baseflow seasonally; ephemeral streams do not have baseflow. All three stream types convey stormflow. Thus, perennial streams are more common in areas receiving high precipitation, whereas intermittent and ephemeral streams are more common in the more arid portions of the United States (see Figure 3-9; NHD, 2008). The distribution of headwater streams (perennial, intermittent, or ephemeral) as a proportion of total stream length is similar across geographic regions and climates (see Figure 3-9C).

3.2.3. River Network Expansion and Contraction

River networks expand and contract longitudinally (in an upstream-downstream direction) and laterally (in a stream channel-floodplain direction) in response to seasonal environmental conditions and precipitation events (Hewlett and Hibbert, 1967; Gregory and Walling, 1968; Day, 1978; Wigington et al., 2005). Figure 3-10 shows the expansion of the flowing portion of two stream networks in western Oregon during a wet, winter season. Intermittent and perennial streams flow during wet seasons, whereas ephemeral streams flow only in response to rainfall or snowmelt. During dry periods, flowing portions of river networks are limited to perennial streams; these perennial portions of the river network can be discontinuous (Stanley et al., 1997; Hunter et al., 2005; Larned et al., 2010) or interspersed with intermittently flowing stream reaches.

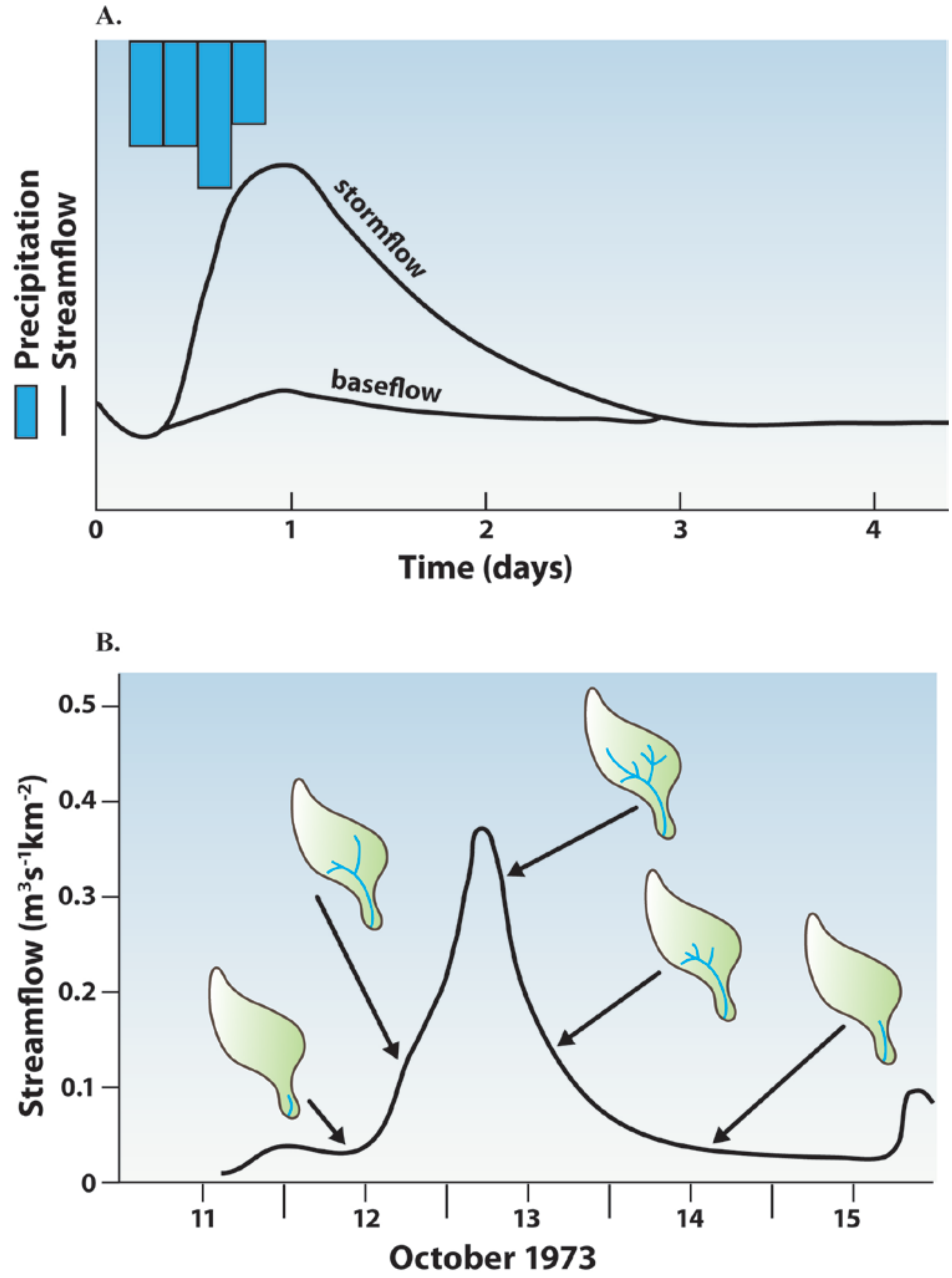


Figure 3-8. (A) Hypothetical hydrograph showing stormflow and baseflow responses to a rainfall event. (B) Expansion and contraction of flowing water in a stream network following a rainfall event.

Modified from NRCS (2007) (A) and Cheng et al. (1988) (B).

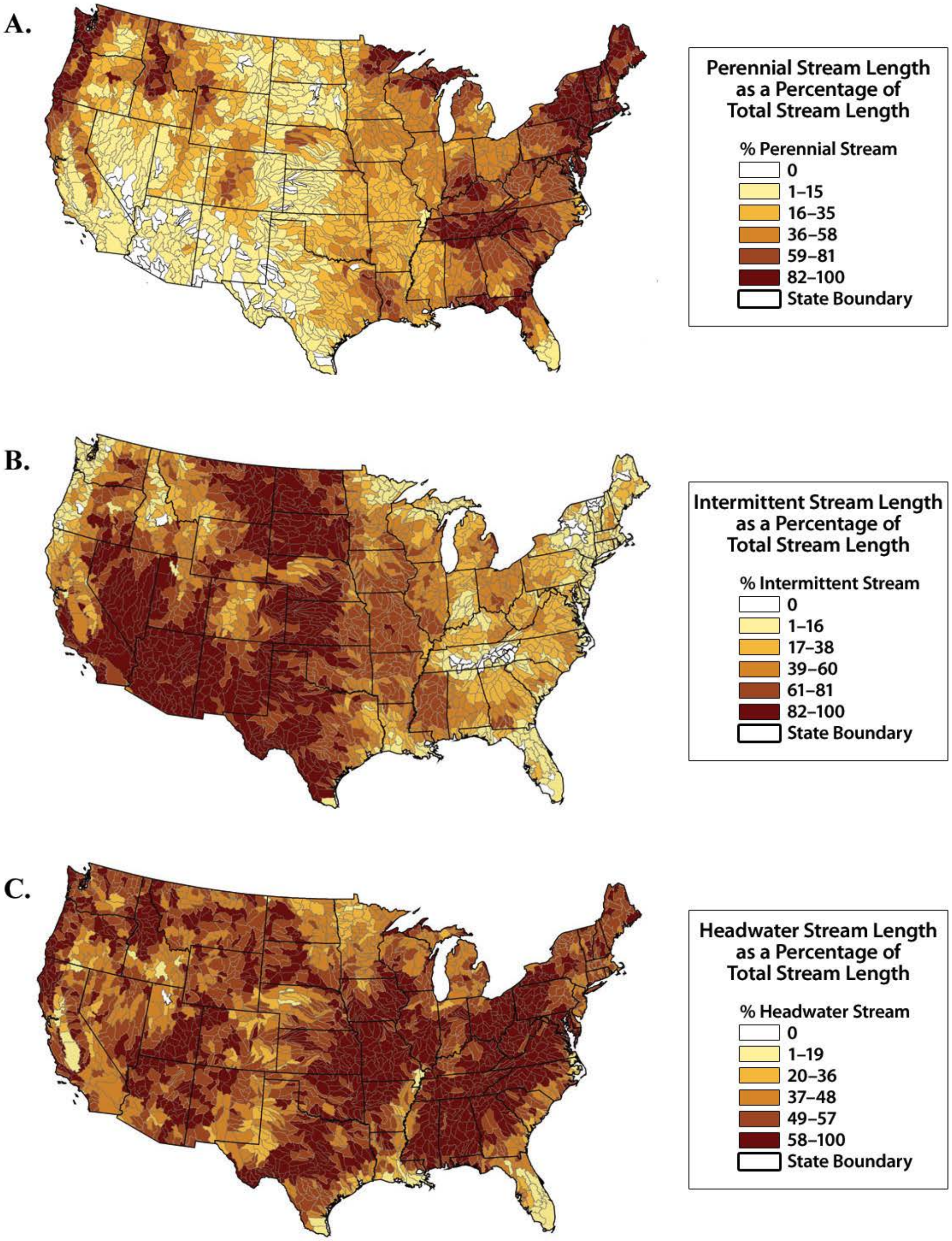


Figure 3-9. Characteristics of U.S. streams by watershed, in terms of percent of total stream length as (A) perennial, (B) intermittent, and (C) headwater streams. Data from the National Hydrographic Dataset (NHD) Reach Address Database (RAD) v2.0 at 1:100,000 scale using 8-digit HUC watersheds. Here, "intermittent" includes streams having intermittent or ephemeral flow. Note that NHD data generally do not capture streams <1.6 km, and ranges of color categories are not consistent across maps.

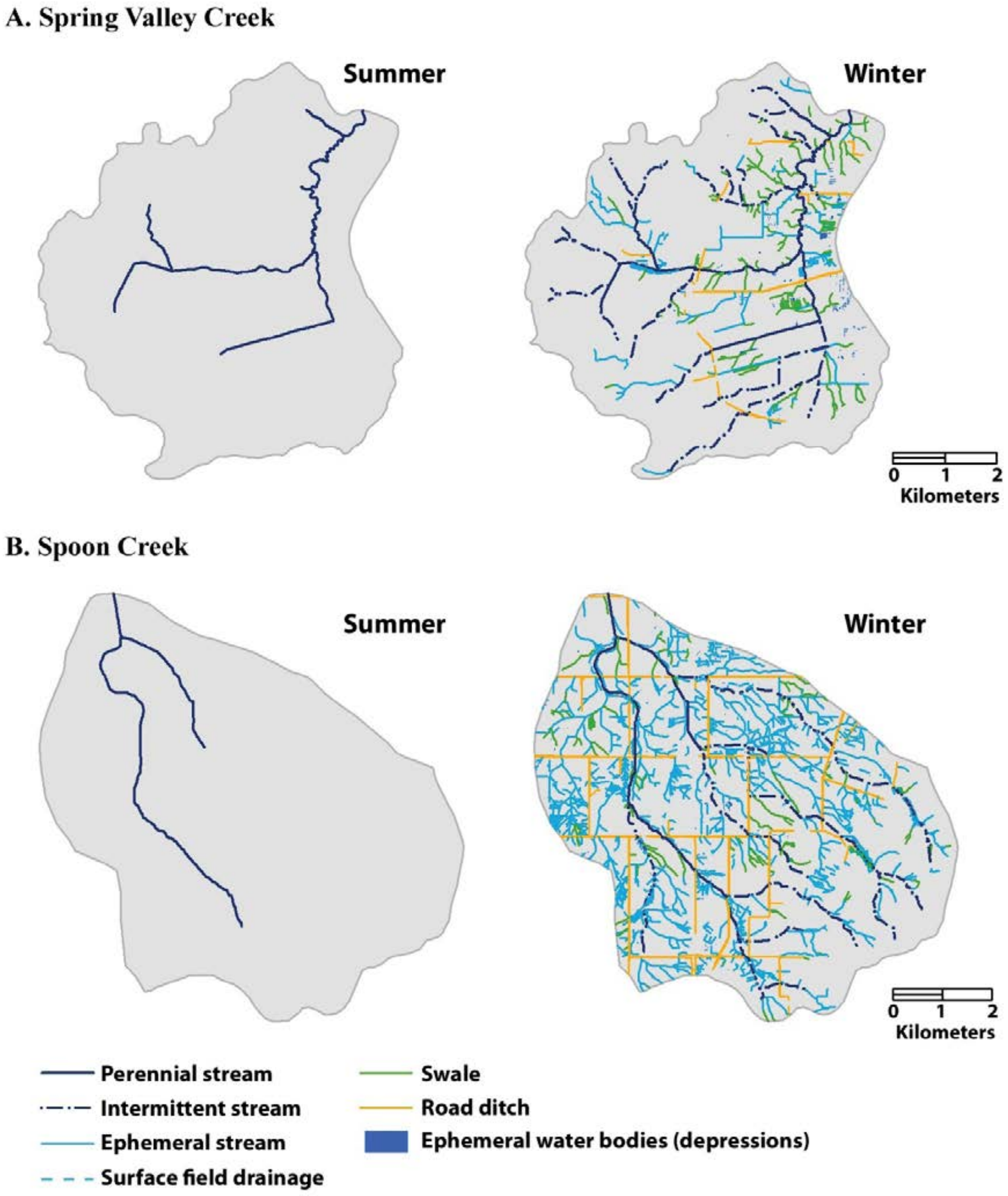


Figure 3-10. Extent and connectivity of streams with flowing water, wetlands, and other water bodies in (A) Spring Valley Creek, OR, and (B) Spoon Creek, OR during dry summer (left) and wet winter (right) conditions.

Modified from Wigington et al. (2005).

The dominant sources of water to a stream can shift during river network expansion and contraction (Malard et al., 1999; McGlynn and McDonnell, 2003; McGlynn et al., 2004; Malard et al., 2006). Rainfall and snowmelt cause an expansion of the river network in two ways. First, local aquifers expand and water moves into dry channels, which increases the total length of wet channel (Winter et al., 1998); these intermittent streams will contain water during the entire wet season. Second, stormflow can cause water to enter ephemeral and intermittent streams (see Figure 3-8). The larger the rainfall or snowmelt event, the greater the number of ephemeral streams and total length of flowing channels within the river network. Ephemeral flows cease within days after rainfall or snowmelt ends (see Figure 3-8B), causing the length of wet channels to decrease and river networks to contract. The flowing portion of river networks shrinks further as the spatial extent of the aquifer with groundwater in contact with streams contract and intermittent streams dry. In many river systems across the United States, stormflow comprises a major portion of annual streamflow (Hewlett et al., 1977; Miller et al., 1988; Turton et al., 1992; Goodrich et al., 1997; Vivoni et al., 2006). In these systems, intermittent and ephemeral streams are major sources of river water (see Section 4.8). When rainfall or snowmelt induces stormflow in headwater streams or other portions of the river network, water flows downgradient through the network to its lower reaches. As water moves downstream through the river network, the hydrograph for a given event typically changes (see Figure 3-11). The broadening of the hydrograph shape from upstream to downstream (see Figure 3-11A), representing a longer total time for the hydrologic event to pass, results from transient storage of water in river network channels and nearby alluvial aquifers (Fernald et al., 2001).

Floodplains and riparian areas can be locations with significant groundwater recharge and discharge (National Research Council, 2002; Naiman et al., 2005). During very large hydrologic events, aggregate flows from headwaters and other tributary streams can result in overbank flooding in river reaches with floodplains; this occurrence represents lateral expansion (see Figure 3-12) of the river network (Mertes, 1997). Water from overbank flows can recharge alluvial aquifers, supply water to floodplain wetlands, surficially connect floodplain wetlands to rivers, and shape the geomorphic features of the floodplain (Wolman and Miller, 1960; Hammersmark et al., 2008). Depending on the nature of the hydraulic gradients, groundwater within floodplain alluvium can move both parallel and perpendicular to streams or rivers (National Research Council, 2002) and enter river networks at various discharge points. Bidirectional exchanges of water between groundwater and river networks, including hyporheic flow, can happen under a wide range of streamflows, ranging from flood flows to low flows (National Research Council, 2002; Naiman et al., 2005; Vivoni et al., 2006).

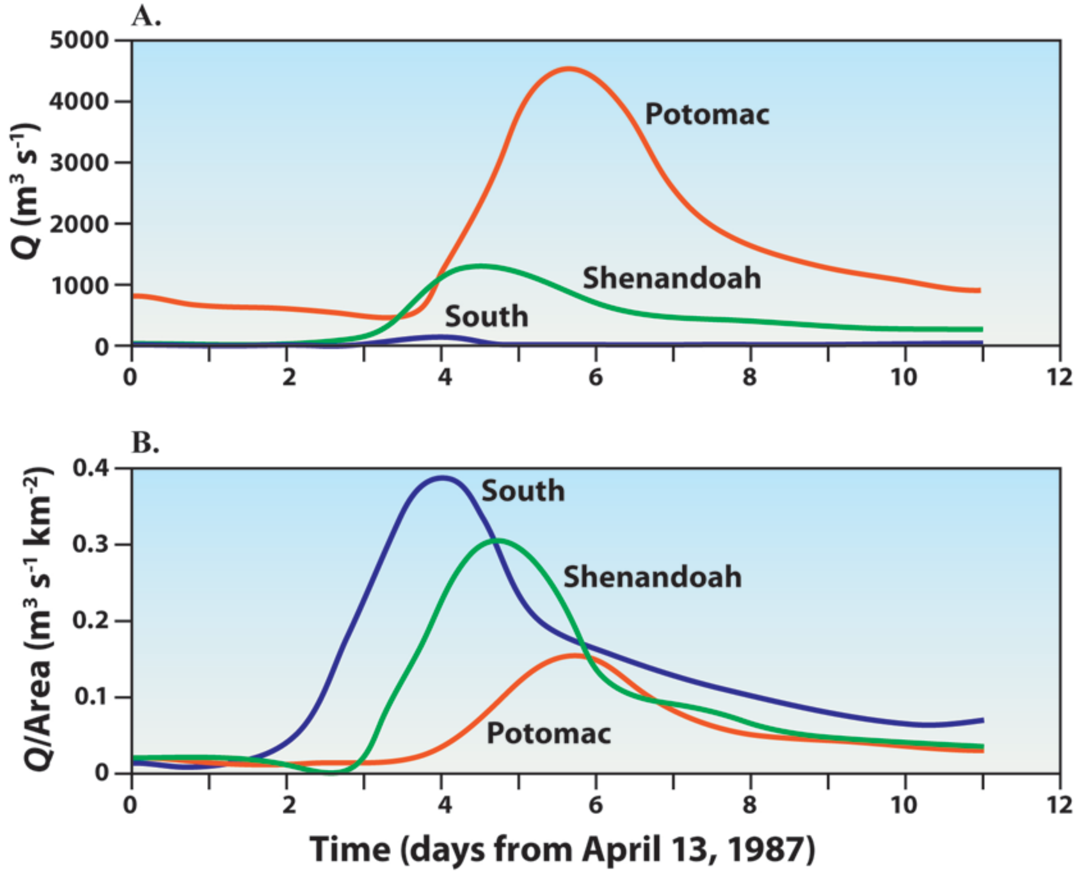


Figure 3-11. Stormflow moves downstream through the river network and interacts with lower stream reaches, floodplains, and alluvial aquifers. (A) Hydrographs for three nested rivers in the Potomac River drainage (drainage area Potomac > Shenandoah > South). (B) Hydrographs for the same three rivers with streamflow normalized by drainage area.

Modified from Hornberger et al. (1998).

The hydrologic connections with river networks fundamentally differ for riparian/floodplain wetlands and unidirectional wetlands. Riparian/floodplain wetlands can have bidirectional, lateral hydrologic connections to the river network, either through overbank flooding (i.e., lateral expansion of the network) or hyporheic flow, in addition to unidirectional flows from upland and groundwater sources (see Figure 3-6A). In contrast, hydrologic connections between unidirectional wetlands and river networks originate via surface water spillage or groundwater flow when water inputs exceed evapotranspiration and available storage. Although riverine wetlands that serve as origins for streams are riparian, we group them with unidirectional wetlands because they also have unidirectional flow through their outlet streams. In both cases, the degree of hydrologic connectivity between riparian/floodplain and

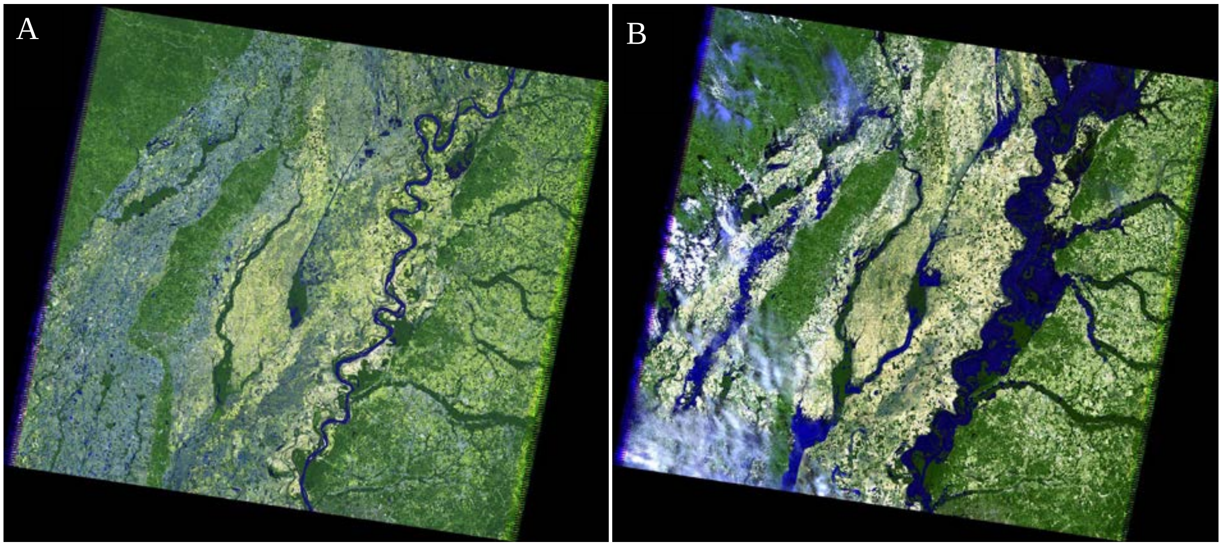


Figure 3-12. Landsat 5 satellite images of the Mississippi River along the borders of Tennessee, Kentucky, Missouri, and Arkansas on (A) May 12, 2006 and (B) May 10, 2011.

Images courtesy of USGS/NASA.

unidirectional wetlands and the river network varies with lateral expansion and subsequent contraction.

One factor affecting the lateral distance that overbank flow spreads is preexisting moisture conditions on the floodplain (Mertes, 1997; Naiman et al., 2005). River overbank flow that enters a dry floodplain will spread and then infiltrate the soil (Naiman et al., 2005). If inflows from streams, rainfall, or groundwater have water tables elevated to the floodplain surface, water entering the riparian area from overbank flow cannot infiltrate soils. The result is standing water on the floodplain and subsequent movement of water to lower elevations of the floodplain. This water can alter the geomorphology of the floodplain (Hupp and Osterkamp, 1996), be biogeochemically transformed (see Section 5.3.2; Naiman et al., 2005), be lost by evaporation, or be transpired by vegetation (Meyboom, 1964). As the river and floodplain water table elevations decrease, surface water on the floodplain can flow back into the river or infiltrate floodplain soils.

Many studies have documented the ability of riparian/floodplain wetlands to attenuate flood pulses of streams and rivers by storing excess water from streams and rivers. Bullock and Acreman (2003) reviewed wetland studies and reported that wetlands reduced or delayed floods in 23 of 28 studies. For example, Walton et al. (1996) found that peak discharges between upstream and downstream gaging stations on the Cache River in Arkansas were reduced 10−20%

primarily due to floodplain water storage. Locations within floodplains and riparian areas with higher elevations likely provide flood storage on a less frequent basis than lower elevation areas.

The interaction of high flows with floodplains and associated alluvial aquifers of river networks are important determinants of hydrologic and biogeochemical conditions of rivers (Ward, 1989; Stanford and Ward, 1993; Boulton et al., 1998; Burkart et al., 1999; Malard et al., 1999; Amoros and Bornette, 2002; Malard et al., 2006; Poole, 2010). Bencala (1993; 2011) noted that streams and rivers are not pipes: they interact with the alluvium and geologic materials adjacent to and under channels. In stream or river reaches constrained by topography, significant floodplain and near-channel alluvial aquifer interactions are limited (see Figure 3-3A). In reaches with floodplains, however, stormflow commonly supplies water to alluvial aquifers during high flow periods through the process of **bank storage** (see Figure 3-13; Whiting and Pomeranets, 1997; Winter et al., 1998; Chen and Chen, 2003). As streamflow decreases after hydrologic events, the water stored in these alluvial aquifers can serve as another source of baseflow in rivers (see Figure 3-13C).

In summary, the extent of wetted channels is dynamic because open channel flow is determined by interactions between surface water in the channel and alluvial groundwater, via hyporheic exchange. The flowing portion of river networks expands and contracts in two primary dimensions: longitudinally, as intermittent and ephemeral streams wet-up and dry, and laterally, as floodplains and associated alluvial aquifers receive (via overbank flooding, bank storage, and hyporheic exchange) and lose (via draining of alluvial aquifers and evapotranspiration) water. Vertical groundwater exchanges between streams and rivers and underlying alluvium are also important connections, and variations in these vertical exchanges contribute to the expansion and contraction of the portions of river networks with open channel flow. Numerous studies have documented expansion and contraction of river systems (e.g., Gregory and Walling, 1968); the temporal and spatial pattern of this expansion and contraction varies in response to many factors, including interannual and long-term dry cycles, climatic conditions, and watershed characteristics (Cayan and Peterson, 1989; Fleming et al., 2007).

3.3. INFLUENCE OF STREAMS AND WETLANDS ON DOWNSTREAM WATERS

The previous section provided background on river system hydrology. In this section, we provide a general overview of how streams and wetlands affect downstream waters, focusing on functions within streams and wetlands and their connectivity to rivers.

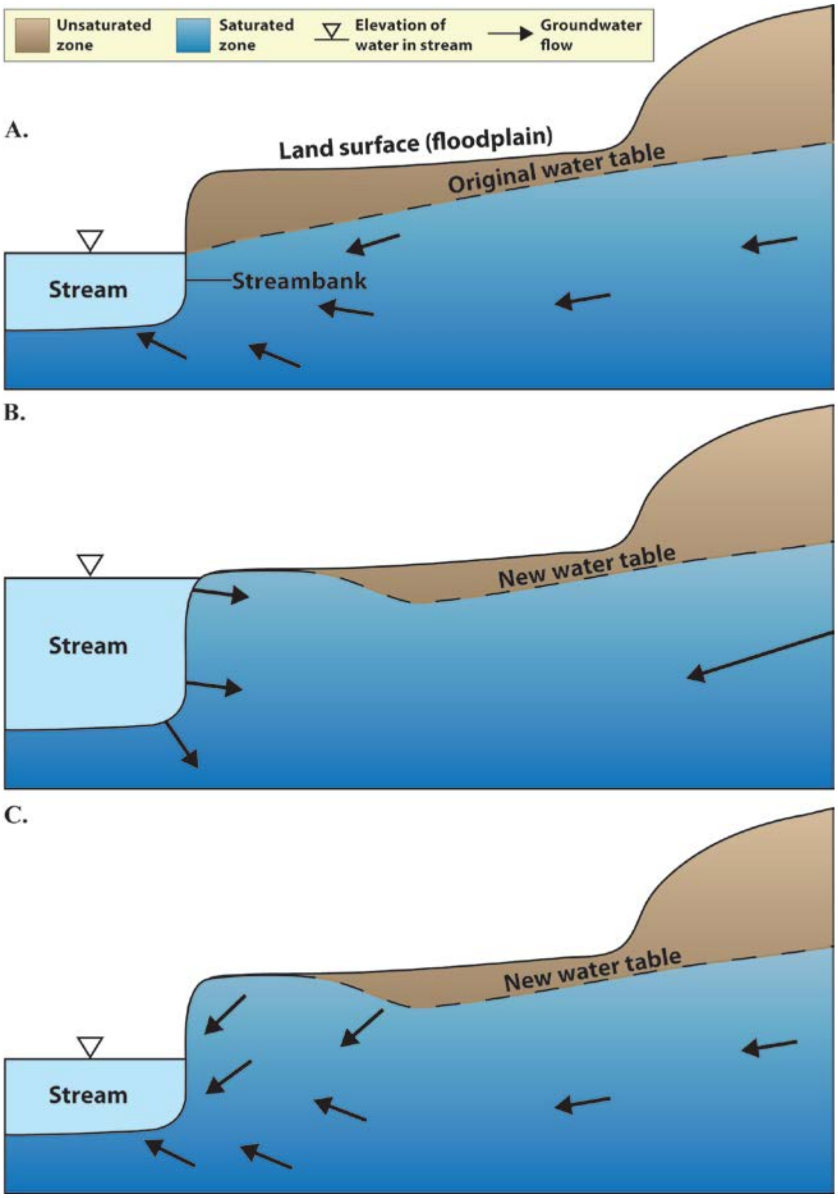


Figure 3-13. The direction and magnitude of surface water-groundwater interactions can dramatically change during large hydrological events, including floods. (A) In a hypothetical stream-floodplain cross-section, groundwater flows from the alluvial aquifer to the stream prior to a major hydrological event. (B) During the bank-full hydrologic event, surface water moves from the stream and becomes groundwater in the alluvial aquifer. (C) After recession of the event water in the stream channel, groundwater that was stored in the alluvial aquifer during the hydrologic event flows back to the stream. This process is called bank storage and can sustain baseflow in streams and rivers after the hydrologic event has ended.

Modified from Winter et al. (1998).

The structure and function of rivers are highly dependent on the constituent materials that are stored in and transported through them. Most of these materials, broadly defined here as any physical, chemical, or biological entity, including water, heat energy, sediment, wood, organic matter, nutrients, chemical contaminants, and organisms, originate outside of the river: they originate from either the upstream river network or other components of the river system, and then are transported to the river by water movement or other mechanisms. Thus, the fundamental way in which streams and wetlands affect river structure and function is by altering fluxes of materials to the river. This alteration of material fluxes depends on two key factors: functions within streams and wetlands that affect material fluxes, and connectivity (or isolation) between streams and wetlands and rivers that allows (or prevents) transport of materials between the systems.

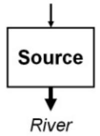
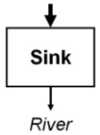
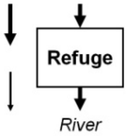
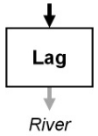
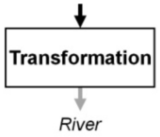
3.3.1. Effects of Streams and Wetlands on Material Fluxes

Streams and wetlands affect the amounts and types of materials that are or are not delivered to downstream waters, ultimately contributing to the structure and function of those waters. Leibowitz et al. (2008) identified three functions, or general mechanisms of action, by which streams and wetlands influence material fluxes into downstream waters: **source**, **sink**, and **refuge**. We have expanded on this framework to include two additional functions: **lag** and **transformation**. These five functions (summarized in Table 3-1) provide a framework for understanding how physical, chemical, and biological connections between streams and wetlands and downstream waters influence river systems.

These five functions (see Table 3-1) are neither static nor mutually exclusive, and often the distinctions between them are not sharp. A stream or wetland can provide different functions at the same time, and these functions can vary with the material considered (e.g., acting as a source of organic matter and a sink for nitrogen) and can change over time (e.g., acting as a water sink when evapotranspiration is high and a water source when evapotranspiration is low). The magnitude of a given function also is likely to vary temporally: For example, streams generally are greater sources of organic matter and contaminants during high flows.

Leibowitz et al. (2008) explicitly focused on functions that benefit downstream waters, but these functions can also have negative effects—for example, when streams and wetlands serve as sources of chemical contamination (see Table 3-1 and Sections 4.4.3, 5.3.2.6, 5.3.2.5, and 5.4.3.1). In fact, benefits need not be linear with respect to concentration; a beneficial material could be harmful at higher concentrations due to nonlinear and threshold effects. For example, nitrogen can be beneficial at lower concentrations but can reduce water quality at

Table 3-1. Functions by which streams and wetlands affect material fluxes to downstream waters

Function	Definition	Examples
	Net increase in a material flux (exports > imports)	*Streams*: invertebrate production (Wipfli and Gregovich, 2002) *Wetlands*: phytoplankton production from floodplain (Schemel et al., 2004; Lehman et al., 2008)
	Net decrease in a material flux (exports < imports)	*Streams*: upstream fish populations that are not sustainable without net immigration from downstream areas (Woodford and McIntosh, 2010) *Wetlands*: sediment deposition, denitrification (Johnston, 1991)
	Avoidance of a nearby sink function, thereby preventing a net decrease in material flux (exports = imports)	*Streams*: headwaters as summer coldwater refuges (Curry et al., 1997) *Wetlands*: riparian wetlands as aquatic refuges in dryland rivers (Leigh et al., 2010)
	Temporary storage and subsequent release of materials without affecting cumulative flux (exports = imports); delivery is delayed and can be stretched out	*Streams*: delay of downstream peak flows due to bank storage (Burt, 1997); temporary heat storage within the alluvial aquifer (Arrigoni et al., 2008) *Wetlands*: flood attenuation (Bullock and Acreman, 2003)
	Conversion of a material into a different form; the amount of the base material is unchanged (base exports = base imports), but its composition (i.e., mass of the different forms) can vary	*Streams*: conversion of coarse to fine particulate organic matter (Wallace et al., 1995) *Wetlands*: mercury methylation (Galloway and Branfireun, 2004; Selvendiran et al., 2008)

Notes: Arrows indicate material imports to and exports from a stream or wetland, in terms of mass; arrow widths represent relative material mass and differences in arrow shades represent timing (lag) or composition (transformation) changes. Imports into streams and wetlands can come from upland terrestrial areas, other streams and wetlands, or from the river itself. Arrows are meant to be illustrative, and do not necessarily represent upstream/downstream relationships. For example, materials can move downstream, upstream, or laterally into streams and wetlands. Examples of commonly exchanged materials include water, heat energy, nutrients, contaminants, sediment, particulate organic matter, organisms, and reproductive propagules; note that exchange of materials between streams and wetlands and downstream systems can result in positive or negative effects on downstream waters.

higher concentrations. Although here we focus primarily on the effects of streams and wetlands on downstream waters, these same functions can describe effects of downstream waters on streams and wetlands (e.g., downstream rivers as sources of colonists for upstream tributaries).

Because many of these functions depend on import of materials into streams and wetlands, distinguishing between *actual function* and *potential function* is instructive. For example, a wetland with appropriate conditions (e.g., a reducing environment and denitrifying bacteria) is a potential sink for nitrogen (see Sections 5.3.2.2 and 5.4.3.2): if nitrogen is imported into the wetland, the wetland has the capacity to remove it by denitrification. The wetland will not serve this function, however, if nitrogen is not imported. Thus, even if a stream and wetland is not currently serving a function, it has the potential to provide the function under appropriate conditions (e.g., when material imports or environmental conditions change). Although potential functions do not actively affect downstream waters, they can play a critical role in protecting those waters from future impacts. Ignoring potential function can also lead to the paradox that degraded streams and wetlands (e.g., those receiving nonpoint-source nitrogen inputs) receive more protection than less impacted systems (Leibowitz et al., 2008).

The effect that material fluxes from streams and wetlands have on downstream waters is influenced by three factors: (1) proportion of the material originating from (or reduced by) streams and wetlands relative to the importance of other system components, such as the river itself; (2) residence time of the material in the downstream water; and (3) relative importance of the material. In many cases, the effects on downstream waters need to be considered in aggregate. For example, the contribution of material by a particular stream and wetland (e.g., a specific ephemeral stream) might be small, but the aggregate contribution by an entire class of streams and wetlands (e.g., all ephemeral streams in the river network) might be substantial. Integrating contributions over time also might be necessary, taking into account duration and frequency of material export and delivery. Considering the cumulative material fluxes, rather than the individual materials separately, that originate from a specific stream and wetland is also important in understanding the effects of material fluxes on downstream waters.

In general, the more frequently a material is delivered to the river, the greater its effect. The effect of an infrequently supplied material, however, can be large if the material has a long residence time in the river (Leibowitz et al., 2008). For example, woody debris might be exported to downstream waters infrequently, but it can persist in downstream channels. Also, some materials are more important than others in defining the structure and function of a river. For example, woody debris can have a large effect on river structure and function because it affects water flow, sediment and organic matter transport, and habitat (Harmon et al., 1986; Gurnell et al., 1995), or salmon migrating to a river can serve as a keystone species that regulates other populations and serves as a source of marine-derived nutrients (Schindler et al., 2005).

3.3.2. Connectivity and Transport of Materials to and from Streams and Wetlands

3.3.2.1. *Connectivity and Isolation*

The functions discussed above represent general mechanisms by which streams and wetlands influence downstream waters. For these altered material fluxes to affect a river, however, transport mechanisms that deliver (or could deliver) these materials to the river are necessary. **Connectivity** describes the degree to which components of a system are connected and interact through various transport mechanisms; connectivity is determined by the characteristics of both the physical landscape and the biota of the specific system. This definition is related to, but is distinct from, definitions of connectivity based on the actual flow of materials between system components (e.g., Pringle, 2001). The concept that connectivity among river system components, including streams and wetlands, plays a significant role in the structure and function of these systems is not new. In fact, much of the theory developed to explain how these systems work has focused on connectivity and linkages between system components (e.g., Vannote et al., 1980; Newbold et al., 1982a; Newbold et al., 1982b; Junk et al., 1989; Ward, 1989; Benda et al., 2004; Thorp et al., 2006).

In addition to its central role in defining river systems (see Section 3.2.1), water movement through the river system (see Figure 3-6) is the primary mechanism providing physical connectivity both within river networks and between those networks and the surrounding landscape (Fullerton et al., 2010). Hydrologic connectivity results from the flow of water, which provides a “hydraulic highway” (Fausch et al., 2002) along which physical, chemical, and biological materials associated with the water are transported (e.g., sediment, woody debris, contaminants, organisms).

Ecosystem function within a river system is driven by interactions between its physical environment and the diverse biological communities living within it (Wiens, 2002; Schroder, 2006). Thus, river system structure and function also depend on biological connectivity among the system’s populations of aquatic and semiaquatic organisms. Biological connectivity refers to the movement of biota, either in terms of entire organisms or reproductive materials (e.g., seeds, eggs, genes), through river systems. These movements link aquatic habitats and populations in different locations through several processes important for the survival of individuals, populations, and species (see Sections 4.5, 5.3.3, and 5.4.4). Movements include dispersal, or movement away from an existing population or parent organism; migration, or long-distance movements undertaken on a seasonal basis; localized movement over an organism’s home range to find food, mates, or refuge from predators or adverse conditions; and movement to different habitats to complete life-cycle requirements. At the population and species levels, dispersal and migration contribute to persistence at local and regional scales via colonization of new habitats (e.g., Hecnar and McLoskey, 1996; Tronstad et al., 2007), location of mates and breeding habitats (Semlitsch, 2008), rescue of small populations threatened with local extinction (Brown and Kodric-Brown, 1977), and maintenance of genetic diversity (e.g., Waples, 2010). These movements can result from passive transport by water, wind, or other organisms (e.g., birds, terrestrial mammals), from active movement with or against water flow (e.g., upstream fish migration), or from active movement over land (for biota capable of terrestrial dispersal) or through the air (for birds or insects capable of flight). Thus, biological connectivity can occur within aquatic ecosystems or across ecosystem or watershed boundaries, and it can be multidirectional. For example, biota can move downstream from perennial, intermittent, and ephemeral headwaters to rivers, upstream from estuaries to rivers to headwaters, or laterally between floodplain wetlands, geographically isolated wetlands, rivers, lakes, or other water bodies. Significant biological connectivity can also exist between aquatic and terrestrial habitats (Nakano et al., 1999; Gibbons, 2003; Baxter et al., 2004), but here we focus on connections among components of aquatic systems.

As noted in Section 3.2.3, streams and rivers are not pipes (Bencala, 1993; Bencala et al., 2011); they provide opportunities for water to interact with internal components (e.g., alluvium, organisms) through the five functions by which streams and wetlands alter material fluxes (see Table 3-1). Connectivity between streams and wetlands provides opportunities for material fluxes to be sequentially altered by multiple streams and wetlands as the materials are transported downstream. The proportion of a material that ultimately reaches the river is determined by the aggregate effect of these sequential fluxes. The form of the exported material can change as it moves down the river network (see Figure 3-14), however, making quantitative assessments of the importance of individual stream and wetland resources within the entire river system difficult. For example, organic matter can be exported from headwater streams and consumed by downstream macroinvertebrates (see Figure 3-14). Those invertebrates can drift farther downstream and be eaten by juvenile fish that eventually move into the mainstem of the river, where they feed further and grow.

The assessment of stream and wetland influence on rivers is also complicated by the cumulative time lag resulting from these sequential transformations and transportations. For example, cations in stream water convert dissolved organic matter to fine particulate organic matter (FPOM, particle size <1 mm) that is taken up directly by benthic bacteria, delaying its export downstream.

The opposite of connectivity is **isolation**, or the degree to which transport mechanisms (i.e., pathways between system components) are lacking; isolation acts to reduce material fluxes between system components. Although here we primarily focus on the benefits that connectivity can have on downstream systems, isolation also can have important positive effects on the

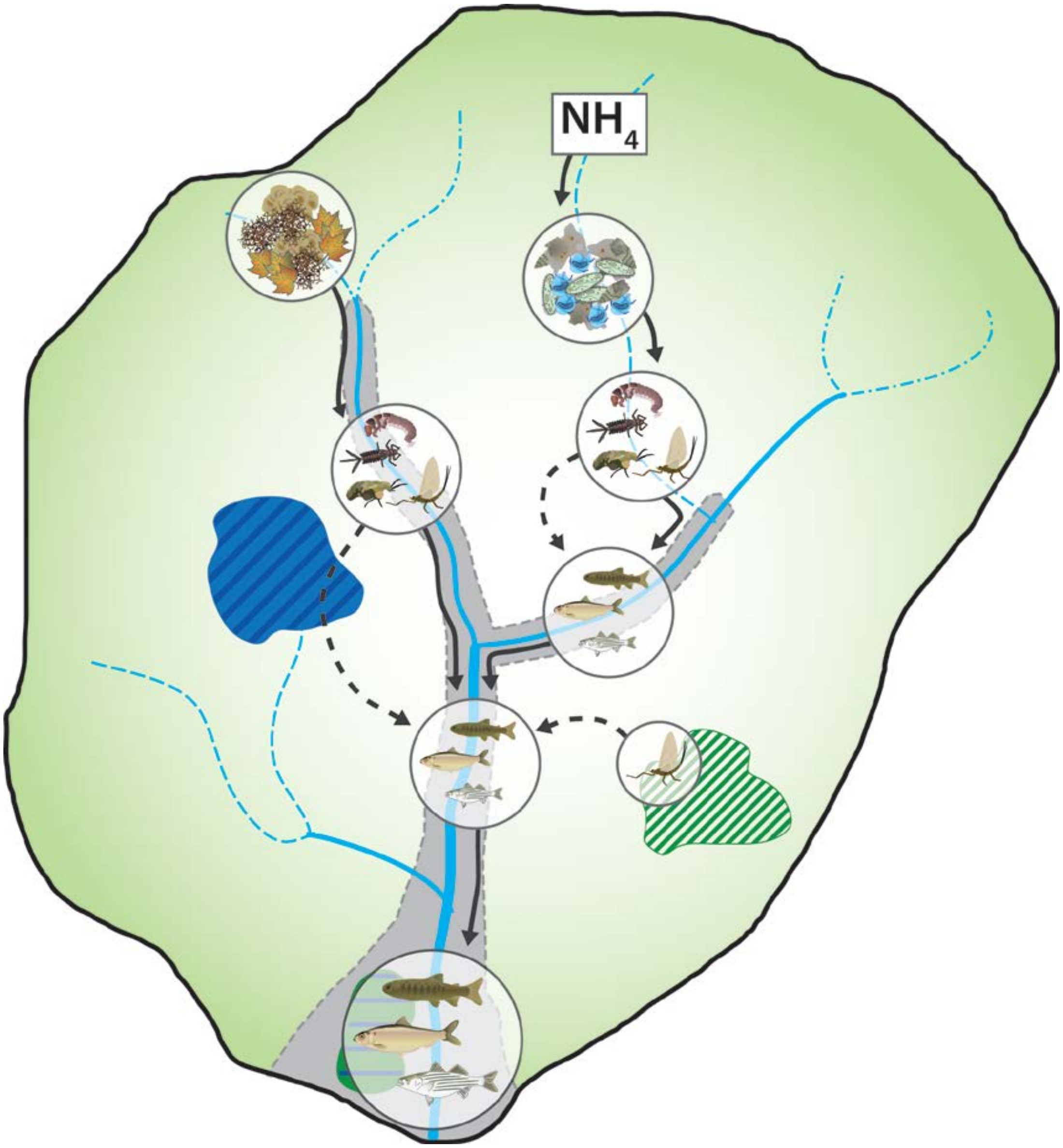


Figure 3-14. Illustration of the sequential transformation of materials as they move through the river network, via either downstream transport with water flow (solid black arrows) or via aerial or terrestrial movements (dashed black arrows). Here, an ephemeral headwater stream exports organic matter (at left) and an intermittent headwater stream exports ammonium, which is taken up and incorporated into algal biomass (at right). These basal food resources are eaten and transformed into macroinvertebrate biomass, which in turn is eaten and transformed into fish biomass in both local and downstream reaches.

condition and function of downstream waters. For example, waterborne contaminants that enter a wetland cannot be transported to a river if the wetland is hydrologically isolated from the river, except by terrestrial (overland) pathways. Increased isolation can decrease the spread of pathogens (Hess, 1996) and invasive species (e.g., Bodamer and Bossenbroek, 2008), and increase the rate of local adaptation (e.g., Fraser et al., 2011). Thus, both connectivity and isolation should be considered when examining material fluxes from streams and wetlands, and biological interactions should be viewed in light of the natural balance between these two factors.

When assessing the effects of connectivity/isolation and the five general functions (sources, sinks, refuges, lags, and transformation; see Table 3-1) on downstream waters, dimensions of time and space must be considered. Water or organisms transported from distant headwater streams or wetlands will generally require longer times for travel to a larger river than materials transported from streams or wetlands near the river (see Section 3.4.2). This can introduce a lag between the time when the function occurs and the time when the material arrives at the river. In addition, the distribution of streams and wetlands can be a function of their distance from the mainstem channel. For example, in a classic dendritic network there is an inverse geometric relationship between number of streams and stream order. In such a case, the aggregate level of function could potentially be greater for terminal source streams, compared to higher order or lateral source streams. This is one reason why terminal source stream watersheds often provide the greatest proportion of water for major rivers. However, connectivity results from many interacting factors (see Section 3.4.5). For example, the relationship between stream number and order can vary with basin shape and network configuration (see Section 3.4.2). Thus, caution must be exercised when making generalizations about these spatial and temporal relationships. Spatial and temporal variability of connectivity is discussed below, and the factors influencing them are considered in Section 3.4.

3.3.2.2. *Spatial and Temporal Variability of Connectivity*

Connectivity is not a fixed characteristic of a system, but rather varies over space and time (Leibowitz, 2003; Leibowitz and Vining, 2003). Variability in hydrologic connectivity results primarily from the longitudinal (see Figures 3-8 and 3-10) and lateral (see Figure 3-12) expansion and contraction of the river network and transient connection with other components of the river system (see Section 3.2.3).

The expansion and contraction of river networks affects the extent, magnitude, timing, and type of hydrologic connectivity. For example, intermittent and ephemeral streams (see Figure 3-7) only flow during wetter seasons (see Section 3.4) or during and immediately following precipitation events. Thus, the spatial extent of connectivity between streams and wetlands and rivers increases greatly during these high flow events because intermittent and ephemeral streams are estimated to account for 59% of the total length of streams in the contiguous United States (Nadeau and Rains, 2007b). Changes in the spatial extent of connectivity due to expansion and contraction are even more pronounced in the arid and semiarid Southwest, where more than 80% of all streams are intermittent or ephemeral (see Figure 3-9B; Levick et al., 2008). Expansion and contraction also affect the magnitude of connectivity because larger flows provide greater potential for material transport (e.g., see Section 4.3.2).

Besides affecting the spatial extent and magnitude of hydrologic connectivity, expansion, and contraction of the stream network also affect the duration and timing of flow in different portions of the network. Perennial streams have year-round connectivity with a downstream river, while intermittent streams have seasonal connectivity. The temporal characteristics of connectivity for ephemeral streams depend on the duration and timing of storm events. Similarly, connectivity between wetlands and downstream waters can range from permanent to seasonal to episodic.

The expansion and contraction of river systems also affect the type of connectivity. For example, during wet periods when input from precipitation can exceed evapotranspiration and available storage, unidirectional wetlands could have connectivity with other wetlands or streams through surface spillage (Leibowitz and Vining, 2003; Rains et al., 2008). With cessation of spillage due to drier conditions, hydrologic connectivity could only occur through groundwater (Rains et al., 2006; Rains et al., 2008).

When dispersal, migration, and other forms of biotic movement are mediated by the flow of water, biological and hydrologic connectivity can be tightly coupled. For example, seasonal flooding of riparian/floodplain wetlands creates temporary habitat that fish, aquatic insects, and other organisms use (Smock, 1994; Robinson et al., 2002; Tronstad et al., 2007). Factors other than hydrologic dynamics can also affect the temporal and spatial dynamics of biological connectivity. Such factors include movement associated with seasonal habitat use (Moll, 1990; Lamoureux and Madison, 1999) and shifts in habitat use due to life history changes (Huryn and Gibbs, 1999; Gibbons et al., 2006; Subalusky et al., 2009a), quality or quantity of food resources (Smock, 1994), presence or absence of favorable dispersal conditions (Schalk and Luhring, 2010), physical differences in aquatic habitat structure (Grant et al., 2007), or the number and size of nearby populations (Gamble et al., 2007). For a specific river system with a given spatial configuration, variability in biological connectivity also occurs due to variation in the dispersal distance of organisms and reproductive propagules (see Section 3.4.4; Semlitsch and Bodie, 2003).

Finally, just as connectivity from temporary or seasonal wetting of channels can have effects on downstream waters, temporary or seasonal drying can also affect river networks.

Riverbeds or streambeds that temporarily go dry are utilized by aquatic biota having special adaptations to wet and dry conditions, and can serve as egg and seed banks for a number of organisms, including aquatic invertebrates and plants (Steward et al., 2012). These temporary dry areas can also affect nutrient dynamics due to reduced microbial activity, increased oxygen availability, and inputs of terrestrial sources of organic matter and nutrients (Steward et al., 2012).

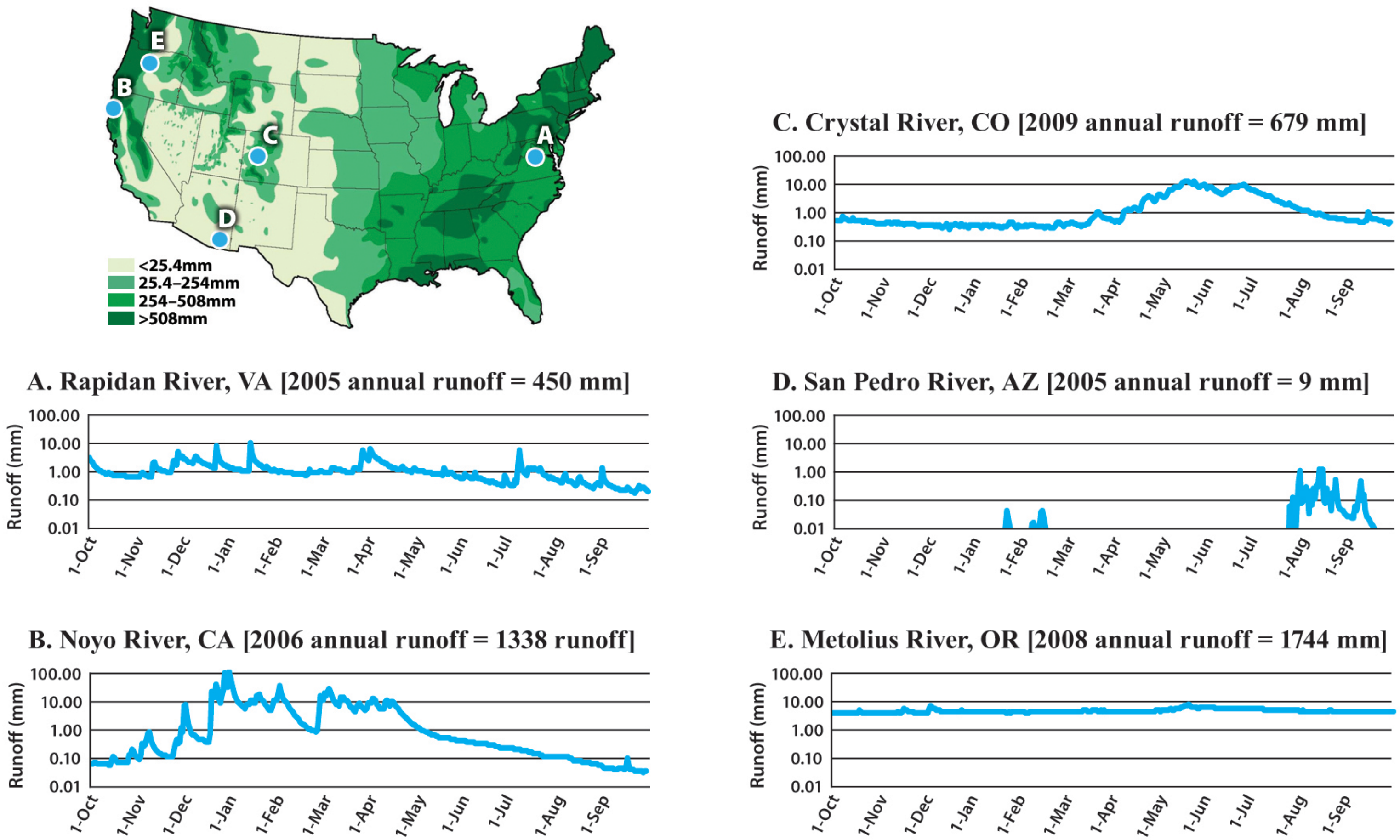
3.4. FACTORS INFLUENCING CONNECTIVITY

Numerous factors affect physical, chemical, and biological connectivity within river systems. These factors operate at multiple spatial and temporal scales, and interact with each other in complex ways to determine where components of a system fall on the connectivity-isolation gradient at a given time. In this section, we focus on five key factors: climate, watershed characteristics, spatial distribution patterns, biota, and human activities and alterations. These are by no means the only factors influencing connectivity, but they illustrate how physical, chemical, and biological connectivity are shaped by many different variables. We also examine how interactions among different factors influence connectivity, using wetlands in the prairie pothole region as a case study.

3.4.1. Climate-Watershed Characteristics

The movement and storage of water in watersheds varies with climatic, geologic, topographic, and edaphic characteristics of river systems (Winter, 2001; Wigington et al., 2012). At the largest spatial scale, climate determines the amount, timing, and duration of water available to watersheds and river basins. Key characteristics of water availability that influence connectivity include annual water surplus (precipitation minus evapotranspiration), timing (seasonality) of water surplus during the year, and rainfall intensity.

Annual runoff generally reflects water surplus and varies widely across the United States (see Figure 3-15). Seasonality of water surplus during the year determines when and for how long runoff and groundwater recharge occur. Precipitation and water surplus in the eastern United States is less seasonal than in the West (Finkelstein and Truppi, 1991). The Southwest experiences summer monsoonal rains (see Section 4.8), while the West Coast and Pacific Northwest receive most precipitation during the winter season (Wigington et al., 2012). Throughout the West, winter precipitation in the mountains occurs as snowfall, where it accumulates in seasonal snowpack and is released during the spring and summer-melt seasons to sustain streamflow during late spring and summer months (Brooks et al., 2012). The flowing portions of river networks tend to have their maximum extent during seasons with the highest



C. Crystal River, CO [2009 annual runoff = 679 mm]

A. Rapidan River, VA [2005 annual runoff = 450 mm]

D. San Pedro River, AZ [2005 annual runoff = 9 mm]

B. Noyo River, CA [2006 annual runoff = 1338 runoff]

E. Metolius River, OR [2008 annual runoff = 1744 mm]

Figure 3-15. Map of annual runoff in contiguous United States showing locations of five example streams that illustrate daily runoff patterns and total annual runoff depths. (A) Rapidan River, VA; (B) Noyo River, CA; (C) Crystal River, CO; (D) San Pedro River, AZ; and (E) Metolius River, OR. All data from http://waterdata.usgs.gov/usa/nwis/sw (downloaded June 27, 2011). Runoff can be conceived as the difference between precipitation and evapotranspiration at the watershed scale. Varied runoff patterns in the five rivers result from divergent climate, geology, and topography.

water surplus (see Section 3.2.3; Figure 3-10), when conditions for flooding are most likely to exist. Typically, the occurrence of ephemeral and intermittent streams is greatest in watersheds with low annual runoff and high water surplus seasonality but is also influenced by watershed geologic and edaphic features (Gleeson et al., 2011).

Rainfall intensity can affect hydrologic connectivity in localities where watershed surfaces have low infiltration capacities relative to rainfall intensities. Overland flow occurs when rainfall intensities exceed watershed surface infiltration, and it can be an important mechanism providing water to wetlands and river networks (Levick et al., 2008). Overland flow is common at low elevations in the Southwest, due to the presence of desert soils with low infiltration capacities combined with relatively high rainfall intensities (see Section 4.8). The Pacific Northwest has low rainfall intensities, whereas many locations in the Mid-Atlantic, Southeast, and Great Plains have higher rainfall intensities. The prevalence of impermeable surfaces in urban areas can generate overland flow in virtually any setting (Booth et al., 2002).

River system topography and landscape form can have a profound impact on river network drainage patterns, distribution of wetlands, and groundwater and surface water flowpaths. Winter (2001) described six generalized hydrologic landscape forms (see Figure 3-16) common throughout the United States. Mountain Valleys (see Figure 3-16A) and Plateaus and High Plains (see Figure 3-16C) have constrained valleys through which streams and rivers flow. The Mountain Valleys form has proportionately long steep sides with narrow to nonexistent floodplains resulting in the rapid movement of water downslope. In contrast, Riverine Valleys (see Figure 3-16D) have extensive floodplains that promote strong surface water, hyporheic water, and alluvial groundwater connections between wetlands and rivers. Small changes in water table elevations can influence the water levels and hydrologic connectivity of wetlands over extensive areas in this landscape form (see Figure 3-16D). Local groundwater flowpaths are especially important in Hummocky Terrain (see Figure 3-16F). Constrained valleys, such as the Mountain Valley landform (see Figure 3-16A), have limited opportunities for the development of floodplains and alluvial aquifers, whereas unconstrained valleys, such as the Riverine Valley landform (see Figure 3-16D), provide opportunities for the establishment of floodplains. River basins can be contained within a single hydrologic landscape form, but larger river basins commonly comprise hydrologic landscape form complexes. For example, the James River in Virginia, which flows from mountains through the Piedmont to the Coastal Plain, is an example of a Mountain Valley, High Plateaus and Plains, Coastal Terrain, and Riverine Valley complex.

Floodplain hydrologic connectivity to rivers and streams occurs primarily through overbank flooding, shallow groundwater flow, and hyporheic flow (see Section 3.2). Water-table depth can influence connectivity across a range of hydrologic landscape forms, but

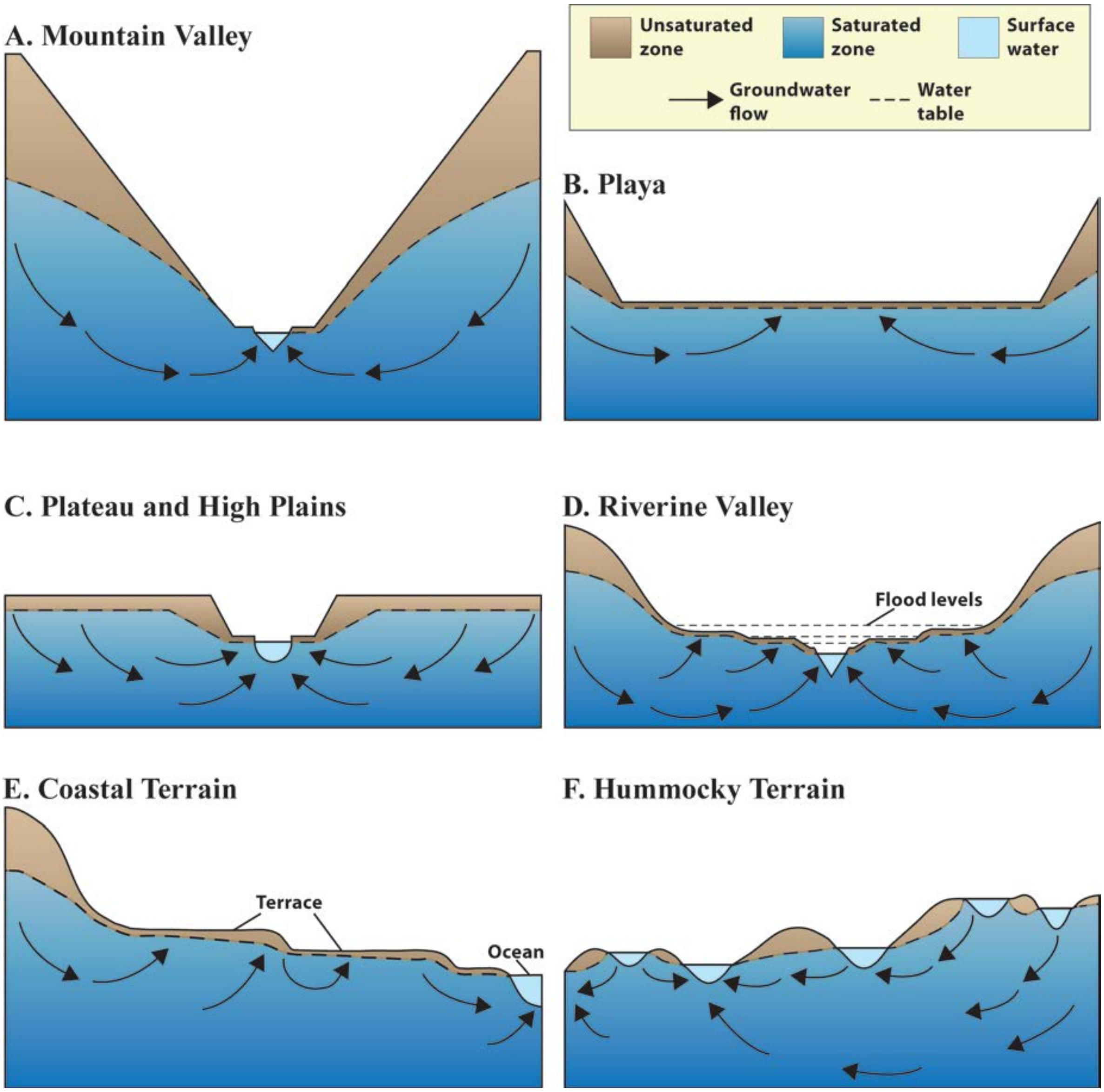


Figure 3-16. Generalized hydrologic landscape forms. (A) Mountain Valley: narrow uplands and lowlands separated by a large steep valley side; (B) Playa: large broad lowland separated from narrow uplands by steeper valleys sides (playas and basins of interior drainage); (C) Plateau and High Plains: small narrow lowlands separated from broad uplands by steeper valley sides; (D) Riverine Valley: small fundamental landscape units nested inside broader fundamental landscape unit; (E) Coastal Terrain: small fundamental landscape units nested inside broader fundamental landscape unit (coastal plain with terraces and scarps); and (F) Hummocky Terrain: small fundamental landscape units superimposed randomly on larger fundamental landscape unit. A fundamental hydrologic landscape unit is defined by land-surface form, geology, and climate.

Modified from Winter (2001).

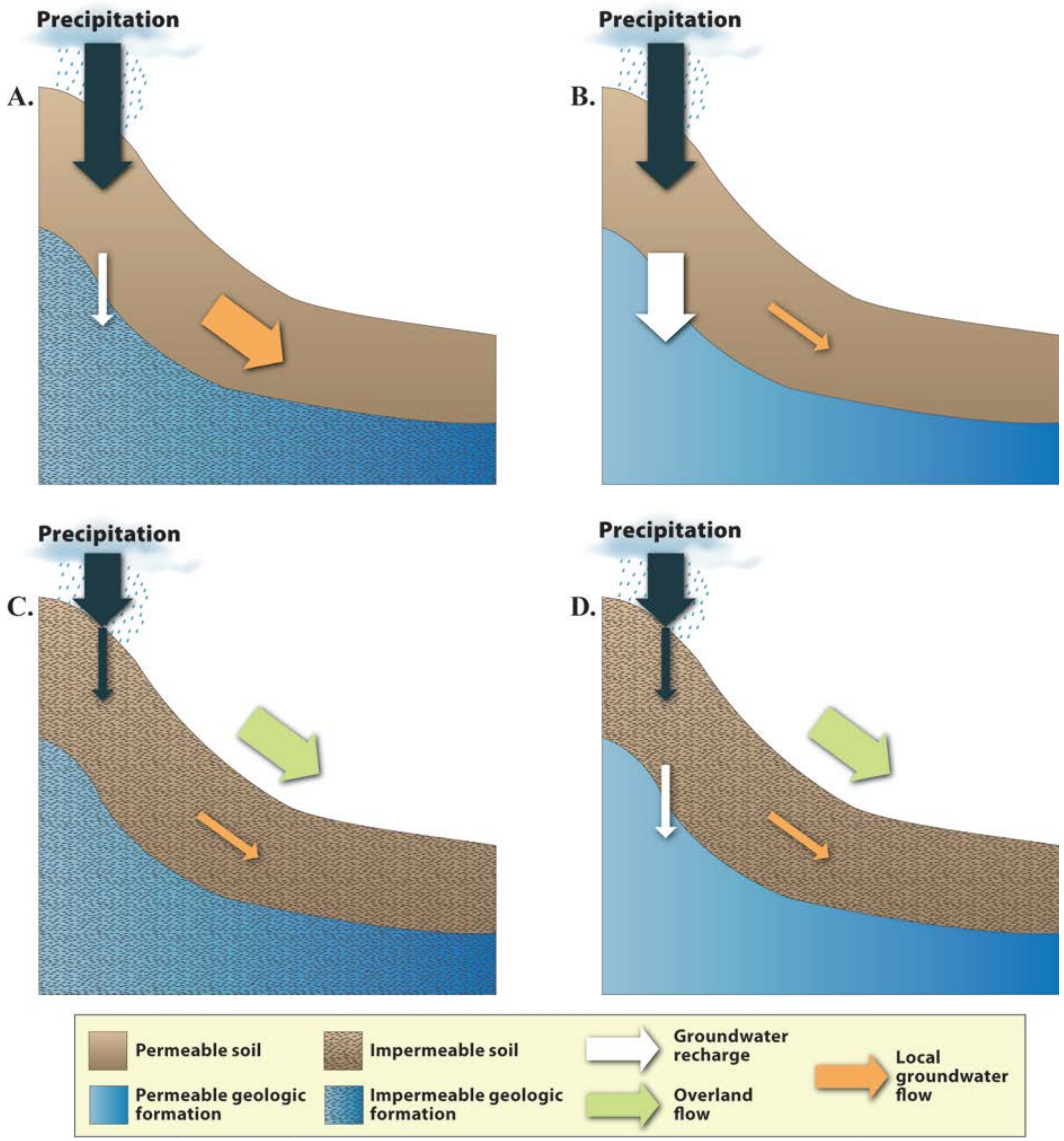


Figure 3-17. Major hydrologic flowpaths for hillslopes with combinations of permeable and impermeable soils and geologic formations. (A) Permeable soil and impermeable underlying geologic formation; (B) permeable soil and permeable underlying geologic formation; (C) impermeable soil and impermeable underlying geologic formation; and (D) impermeable soil and permeable underlying geologic formation. Width of arrow indicates relative magnitude of flow. Note that pavement can be another source of impermeable surfaces and subsequent overland flow in anthropogenically influenced settings.

especially in floodplains. Rivers and wetlands can shift from losing reaches (or recharge wetlands) during dry conditions to gaining reaches (or discharge wetlands) during wet conditions. Wet, high water-table conditions influence both groundwater and surface water connectivity. When water tables are near the watershed surface, they create conditions in which swales and small stream channels fill with water and flow to nearby water bodies (Wigington et al., 2003; Wigington et al., 2005). Nanson and Croke (1992) noted that floodplains are formed by a complex interaction of fluvial processes, but their character and evolution are essentially a product of stream power (the rate of energy dissipation against the bed and banks of a river or stream) and sediment characteristics. They proposed three floodplain classes based on the stream power-sediment characteristic paradigm: (1) high-energy noncohesive, (2) medium-energy noncohesive, and (3) low-energy cohesive. The energy term describes stream power during floodplain formation, and the cohesiveness term depicts the nature of material deposited in the floodplain. The cohesiveness term is also related to the hydraulic properties of alluvial aquifers. Alluvium for Class 1 and 2 floodplains will tend to have higher hydraulic conductivity, or a higher rate at which water moves through a saturated, permeable soil or rock layer, than Class 3 floodplains. The higher the hydraulic conductivity of an alluvial aquifer, the greater the exchange rate between the alluvial aquifer and river waters (Whiting and Pomeranets, 1997). In addition, hyporheic and alluvial aquifer exchanges are more responsive to seasonal discharge changes in floodplains with complex topography (Poole et al., 2006).

Within hydrologic landscape forms, soil and geologic formation permeabilities are also important determinants of hydrologic flowpaths (see Figure 3-17). Permeable soils promote infiltration that results in groundwater hydrologic flowpaths (see Figures 3-17A and B), whereas the presence of impermeable soils with low infiltration capacities is conducive to overland flow (see Figures 3-17C and D). In situations in which groundwater outflows from watersheds or landscapes dominate, the fate of water depends in part on the permeability of deeper geologic strata. The presence of an aquiclude near the watershed surface leads to shallow subsurface flows through soil or geologic materials (see Figure 3-17A). These local groundwater flowpaths connect portions of watersheds to nearby wetlands or streams (see Figure 3-3). Alternatively, if a deep permeable geologic material (an aquifer) is present, water is likely to move further downward within watersheds and recharge deeper aquifer (see Figure 3-17B). The permeability of soils and geologic formations can both influence the range of hydrologic connectivity between unidirectional wetlands and river networks. For example, a wetland that is the origin of a stream can have a permanent or temporary surface water connection with downstream waters through a channelized outlet (see Figure 3-18A); a wetland can be connected to downstream waters by transient surface water flows through swales (see Figure 3-18B) or by shallow groundwater flows (see Figure 3-18C); or a wetland can be hydrologically isolated from downstream waters

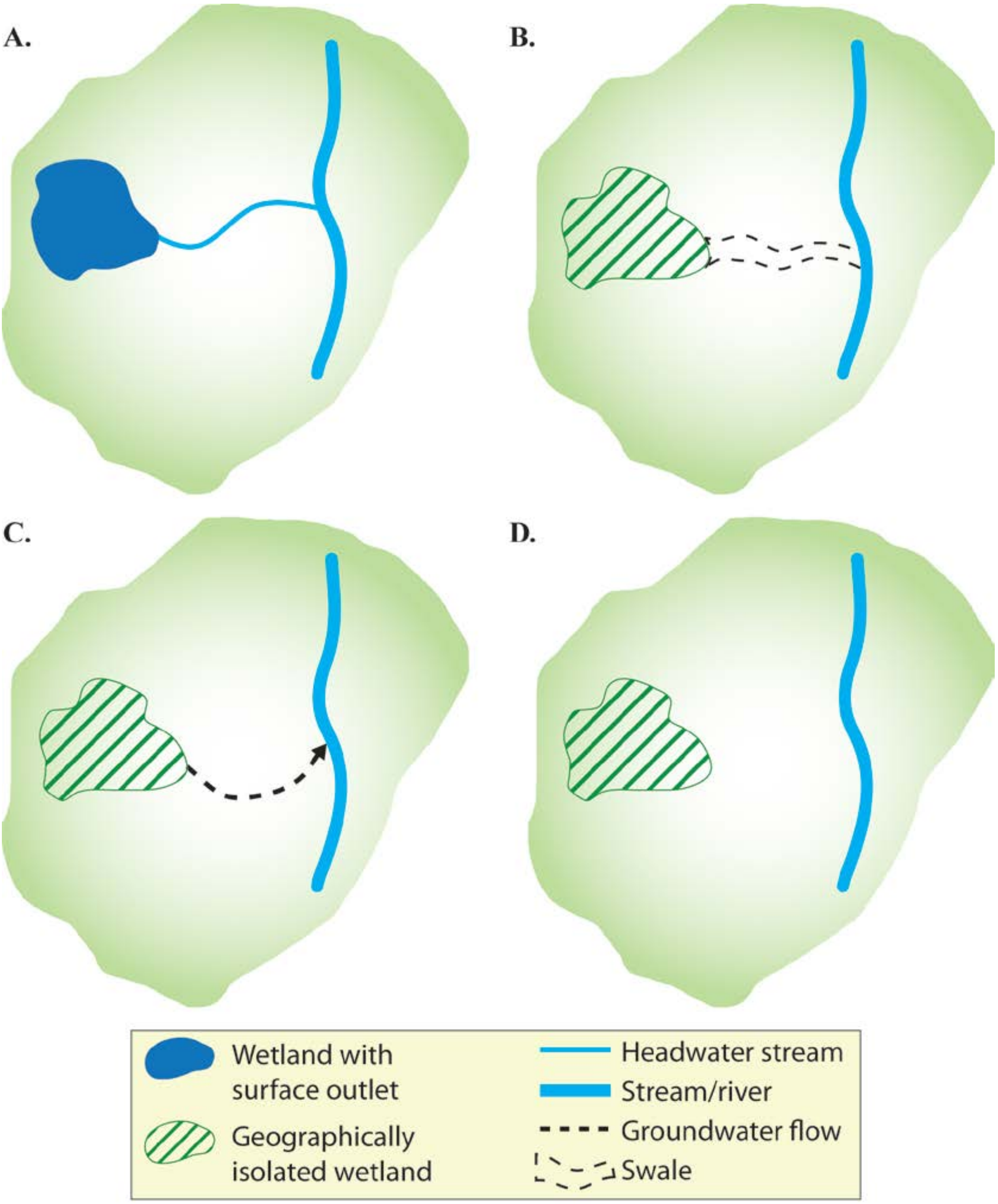


Figure 3-18. Types of hydrologic connections between unidirectional wetlands and streams or rivers. (A) Wetland connected to a river by surface flow through a headwater stream channel. (B) A wetland connected to a river by surface flow through a nonchannelized swale. Such a wetland would be considered geographically isolated if the swale did not meet the Cowardin et al. (1979) three-attribute wetland criteria. (C) A geographically isolated wetland connected to a river by groundwater flow (flowpath may be local, intermediate, or regional). (D) A geographically isolated wetland that is hydrologically isolated from a river.

Note that in A–C, flows connecting the wetland and river may be perennial, intermittent, or ephemeral.

(see Figure 3-18D) because it recharges a deep groundwater aquifer that does not feed surface waters, or it is located in a basin where evapotranspiration is the dominant form of water loss.

The importance of climate-watershed interactions in determining the amount and seasonality of water surpluses, the timing and duration of streamflow, and thus the timing and extent of hydrologic connectivity, is illustrated by annual hydrographs for five rivers in different regions of the United States (see Figure 3-15). The hydrograph for the Rapidan River in Virginia (see Figure 3-15A) illustrates the uniform annual precipitation pattern of the East (with small variations due to increased evapotranspiration in the summer months) interacting with a steep Blue Ridge Mountain watershed that is comprised of metamorphic bedrock with alluvial and colluvial fill in the lower riparian areas (Castro and Hornberger, 1991). Hydrologic events driven by rainfall can occur anytime during the year, but are especially common in winter and spring months; these events result in expansion of the river network as ephemeral streams flow. Baseflow sustains perennial flow over a large part of the network.

Located in a region of steep slopes and impermeable bedrock (Mayer and Naman, 2011), the Noyo River drainage basin in California (see Figure 3-15B) has highly seasonal water surplus because rainfall occurs primarily from November through May and the impermeable bedrock prevents precipitation water from moving to deep groundwater. Consequently, runoff timing is similar to precipitation temporal patterns. Total runoff for the basin is high, and baseflow levels are high during the winter and low during the dry summer season. These low baseflow periods create conditions favorable for intermittent flows in streams with significant channel alluvium (Wigington et al., 2006).

The Crystal River of Colorado (see Figure 3-15C) drains a glaciated landscape in the upper portion of the Gunnison River in the Colorado Rocky Mountains. It has protracted high flow during the spring that is controlled by the accumulation and melt of snow in the basin's higher elevations during the winter and subsequent melt during spring and summer. This streamflow pattern also promotes the occurrence of intermittently flowing streams due to large water surplus differences between the high-flow and low-flow periods.

Total runoff in the San Pedro River, Arizona (see Figure 3-15D) is low and hydrologic events are commonly driven by short, intense rainstorms during the summer monsoons (Levick et al., 2008). Because a major proportion of water reaching the San Pedro River originates as overland flow to ephemeral streams that ultimately flow to the mainstem river, baseflow is limited. In other San Pedro River mainstem reaches, baseflow is supported by groundwater flow from regional and alluvial aquifers (Dickinson et al., 2010).

Like the Crystal River, the Metolius River in Oregon (see Figure 3-15E) also has snowpack in its higher elevations, but geologic conditions in the watershed alter the climate signal. Meltwaters in the Metolius River flow through long flowpaths in porous bedrock to springs in or adjacent to the river (James et al., 2000; Gannett et al., 2001). Although intermittent and ephemeral streams occur in the Metolius basin, most streams are spring-fed and are perennial.

3.4.2. Spatial Distribution Patterns

Climate and watershed characteristics have a direct effect on spatial and temporal patterns of connectivity between streams and wetlands and rivers via their effects on the timing and extent of river network expansion and contraction. They also have an indirect effect by influencing the spatial distribution of water bodies within a watershed (e.g., Tihansky, 1999), and in particular, the spatial relationship between those water bodies and the river.

Hydrologic connectivity between streams and rivers can be a function of the distance between the two water bodies (Bracken and Croke, 2007; Peterson et al., 2007). If channels functioned as pipes, this would not be the case, and any water and its constituent materials exported from a stream would eventually arrive in the river. Because streams and rivers are not pipes (Bencala, 1993; see Section 3.2.3), water can be lost from the channel through evapotranspiration and bank storage and diluted through downstream inputs. Thus, material from a headwater stream that flowed directly into the river would be subject to less transformation or dilution. On the other hand, the greater the distance a material travels between a particular stream reach and the river, the greater the opportunity for that material to be altered (e.g., taken up, transformed, or assimilated) in intervening stream reaches; this alteration could reduce the material’s direct effect on the river, but it could also allow for beneficial transformations. For example, organic matter exported from a headwater stream located high in a drainage network might never reach the river in its original form, instead becoming reworked and incorporated into the food chain (see Figure 3-14). Similarly, higher order streams are generally located closer to rivers and, therefore, can have higher connectivity than upstream reaches of lower order. Note that although an individual low-order stream can have less connectivity than a high-order stream, a river network has many more low-order streams, which can represent a large portion of the watershed (see Section 4.2); thus, the magnitude of the cumulative effect of these low-order streams can be significant.

The relationship between streams and the river network is a function of basin shape and network configuration. Elongated basins tend to have trellis networks where relatively small streams join a larger mainstem (see Figure 3-19A); compact basins tend to have dendritic networks with tree-like branching, where streams gradually increase in size before joining the mainstem (see Figure 3-19B). This network configuration describes the incremental accumulation of drainage area along rivers, and therefore informs questions about the relative contributions of streams to downstream waters. Streams in a trellis network are more likely to connect directly to a mainstem, compared with a dendritic network. The relationship between basin shape, network configuration, and connectivity, however, is complex. A mainstem in a trellis network is also more likely to have a lower stream order than one in a dendritic network. For example, the lower-most reach in the trellis network in Figure 3-19A is a third-order stream, while that of the dendritic network (see Figure 3-19B) is a fourth-order stream.

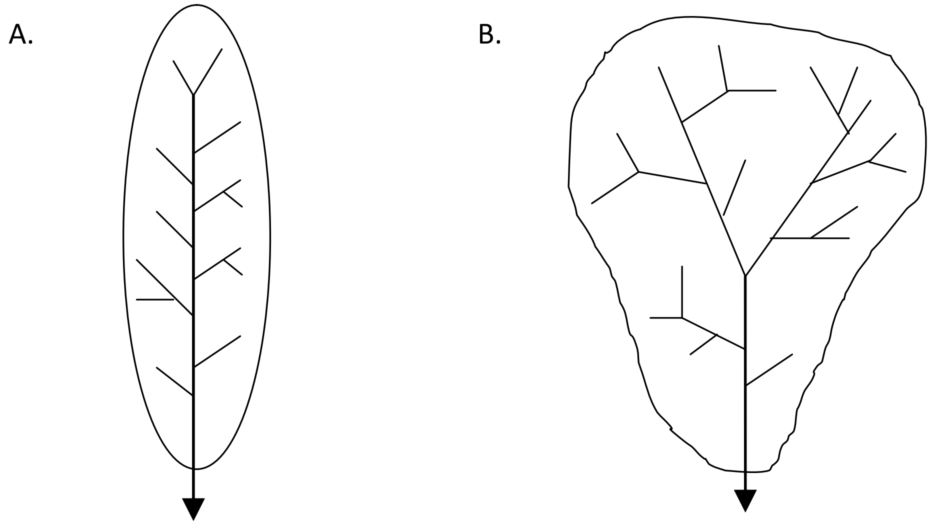


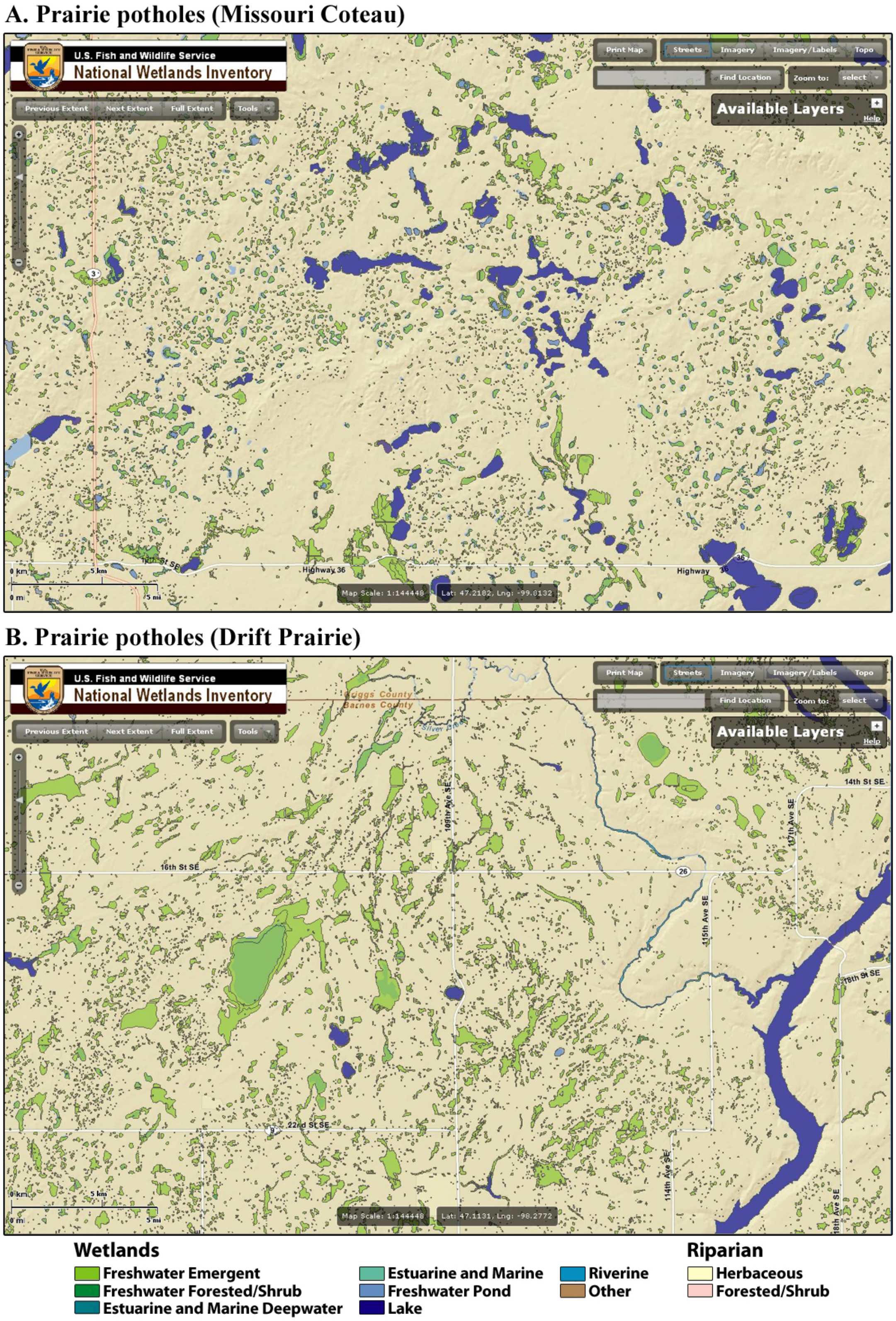
Figure 3-19. Major types of basin shapes and network configurations. (A) A rectangular basin with trellis network, and (B) a compact basin with dendritic network.

Distance also affects connectivity between unidirectional and riparian/floodplain wetlands and downstream waters. Riverine wetlands that serve as origins for lateral source streams that connect directly to a mainstem river have a more direct connection to that river than wetlands that serve as origins for terminal source streams high in a drainage network. This also applies to riparian/floodplain wetlands that have direct surface water connections to streams or rivers. If geographically isolated unidirectional wetlands have surface water outputs (e.g., depressions that experience surface water spillage or groundwater seeps; see Figure 3-18B), the probability that surface water will infiltrate or be lost through evapotranspiration increases with distance. For unidirectional wetlands connected through groundwater flows, less distant areas are generally connected through shallower flowpaths (see Figure 3-5), assuming similar soil and geologic properties. These shallower groundwater flows have the greatest interchange with surface waters (see Section 3.2.2) and travel between points in the shortest amount of time. While elevation is the primary factor determining areas that are inundated through overbank flooding, connectivity with the river will generally be higher for riparian/floodplain wetlands located near the river’s edge compared with riparian/floodplain wetlands occurring near the floodplain edge.

Biological connectivity among streams and wetlands is also influenced by distance from the river network. For example, mortality of a given organism due to predators and natural hazards generally increases with the distance it has to travel. The likelihood that organisms or propagules traveling randomly or by diffusive mechanisms such as wind will arrive at the river network decreases as distance increases.

The distribution of distances between wetlands and river networks depends on both the drainage density of the river network (the total length of stream channels per unit area) and the density of wetlands. Climate and watershed characteristics influence these spatial patterns, which can vary widely. For example, a subset of fens in New York State was located closer to each other, on average, than a subset of Carolina bays at the Savannah River Site: the proportion of wetlands located at distances of 0−100, 100−500, and >500 m was 27, 39, and 35%, respectively, for the fens and 12, 44, and 44% for the Carolina bays, respectively (Bedford and Godwin, 2003; Sharitz, 2003). When interpreting such distributions, however, other factors that affect connectivity (e.g., differences in soils or slope) should be considered.

Figure 3-20 compares the spatial distribution of wetlands and streams to the river network in six different landscape settings. A comparison of these figures shows landscape settings ranging from no nearby streams and dense small wetlands (see Figure 3-20A), to a few nearby streams with high wetland density (see Figures 3-20B and 3-20C), to less spatially uniform wetlands (see Figure 3-20D), to areas with higher drainage densities and riparian (see Figure 3-20E) or larger, more extensive (see Figure 3-20F) wetlands. The maps on Figure 3-20 represent single examples of these different settings, and so might not be representative. They are useful, however, for illustrating the degree to which landscape setting can affect the interspersion—and thus average distance—between wetlands and the river network, and the large variability that can result. In settings with many wetlands and relatively low drainage density (see Figures 3-20B, C, and D), there can be a large range in the distances between individual wetlands and the stream. In contrast, areas with a higher drainage density (see Figure 3-20E and F) can have a narrower range of shorter distances. All things being equal, wetlands with shorter distances to the stream network will have higher hydrologic and biological connectivity than wetlands located farther from the same network.

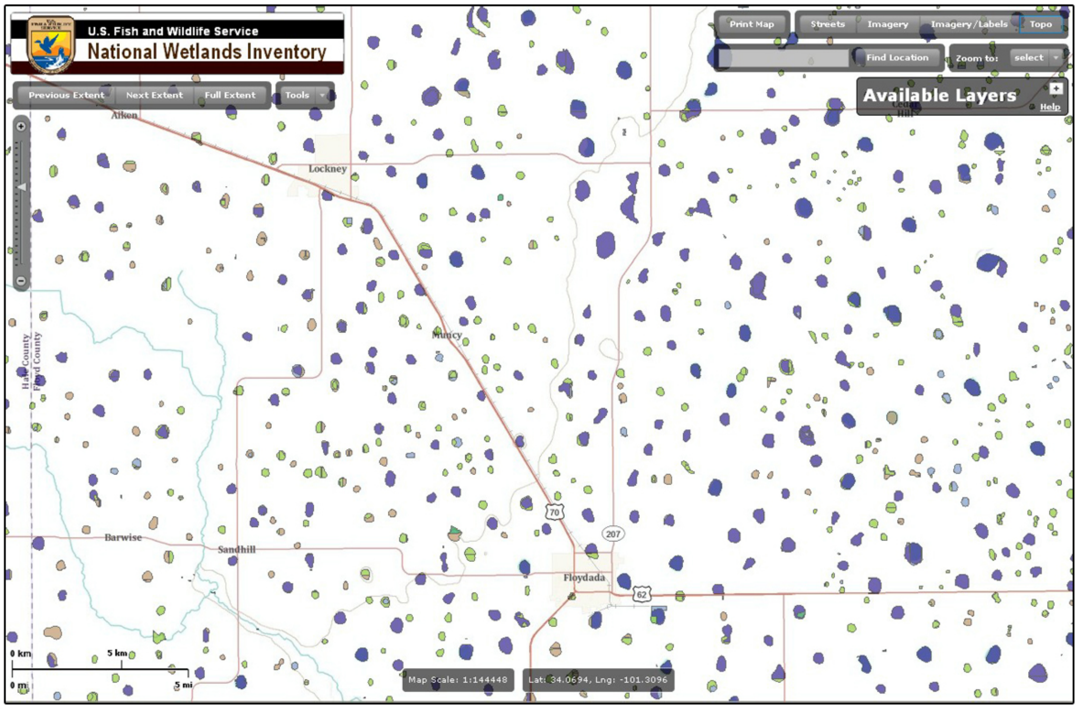


A. Prairie potholes (Missouri Coteau)

B. Prairie potholes (Drift Prairie)

Figure 3-20. Examples of different landscapes showing interspersion of wetlands and streams or rivers.

C. Playa



D. Vernal pools

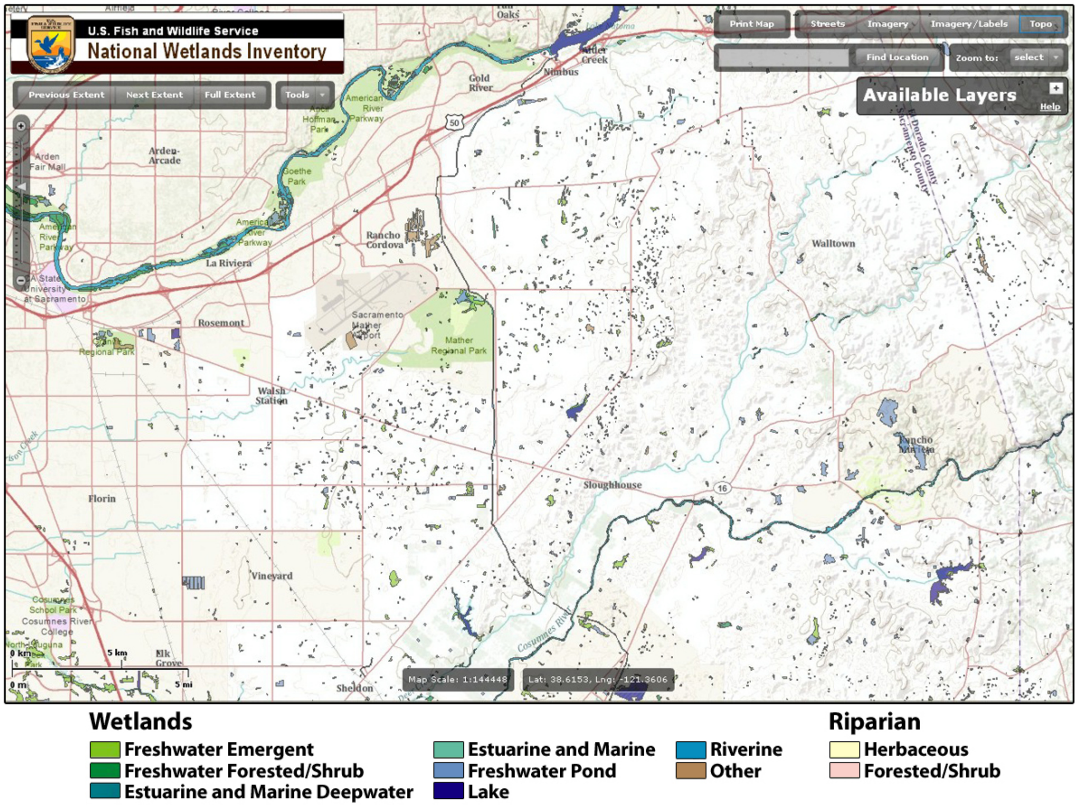
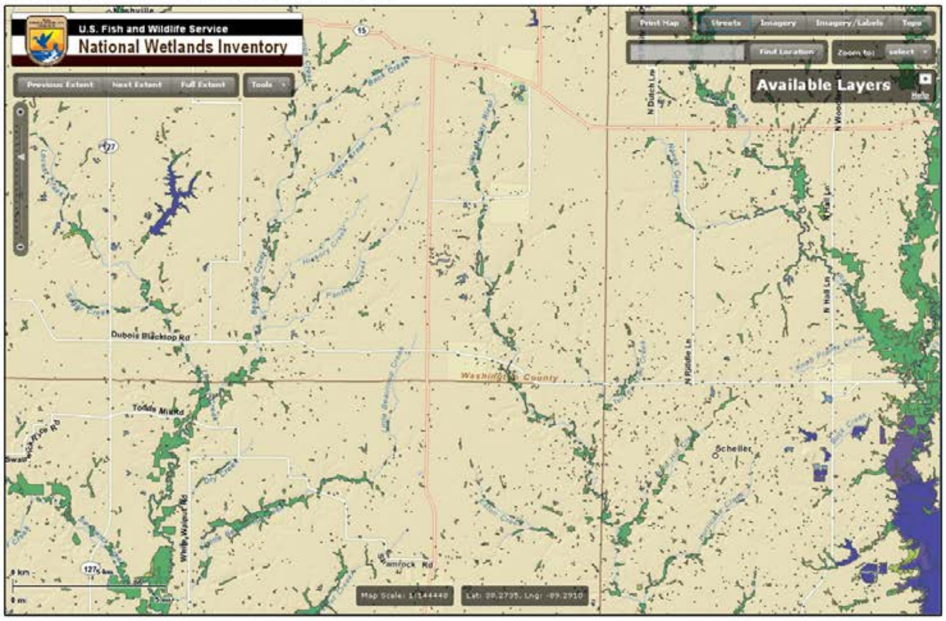


Figure 3‒20. Examples of different landscapes showing interspersion of wetlands and streams or rivers (continued).

E. Bottomland hardwood wetlands



F. Carolina bays

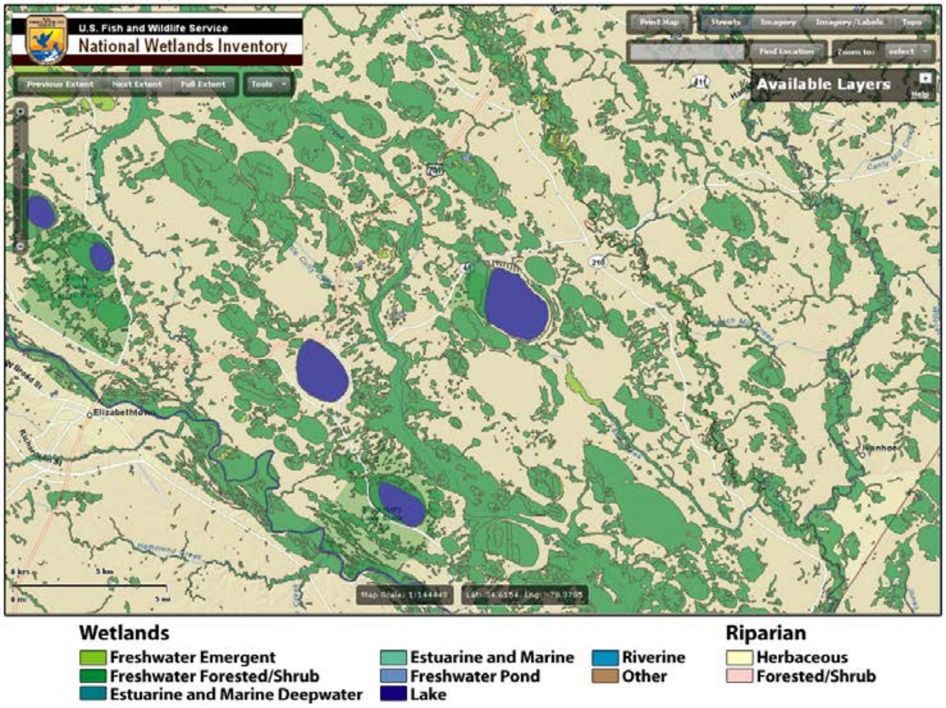


Figure 3−20. Examples of different landscapes showing interspersion of wetlands and streams or rivers (continued). (A) Prairie potholes within the Missouri Coteau in North Dakota; (B) prairie potholes within the Drift Prairie in North Dakota; (C) playas in Texas; (D) vernal pools in California; (E) bottomland hardwood wetlands in Illinois; and (F) Carolina bays in North Carolina. Note all maps are at the same scale. Wetlands smaller than the minimum mapping unit (currently 0.4 ha) may not appear on maps.

Source: National Wetlands Inventory Wetlands Mapper (http://www.fws.gov/wetlands/Data/Mapper.html).

3.4.3. Biota

Biological connectivity results from the interaction of physical characteristics of the environment—especially those promoting or restricting dispersal—and species' traits or behaviors, such as life-cycle requirements, dispersal ability, or responses to environmental cues. Thus, the biota within a river system are integral in determining its connectivity, and species traits that necessitate or facilitate movement of organisms or their reproductive elements tend to increase biological connectivity among water bodies.

Diadromous fauna (e.g., Pacific and Atlantic salmon, certain freshwater shrimps and snails, American eels), which require both freshwater and marine habitats over their life cycles and therefore migrate along river networks, provide one of the clearest illustrations of biological connectivity. Many of these taxa are either obligate or facultative users of headwater streams (Erman and Hawthorne, 1976; Wigington et al., 2006), meaning that they either require (obligate) or can take advantage of (facultative) these habitats; these taxa thereby create a biological connection along the entire length of the river network. For example, many Pacific salmon species spawn in headwater streams, where their young grow for a year or more before migrating downstream, living their adult life stages in the ocean, and then migrating back upstream to spawn. Many taxa can also exploit temporary hydrologic connections between rivers and floodplain wetland habitats, moving into these wetlands to feed, reproduce, or avoid harsh environmental conditions and then returning to the river network (Copp, 1989; Junk et al., 1989; Smock, 1994; Richardson et al., 2005).

Biological connectivity does not solely depend on diadromy, however, as many nondiadromous organisms are capable of significant movement within river networks. For example, organisms such as pelagic-spawning fish and mussels release eggs or larvae that disperse downstream with water flow (e.g., Platania and Altenbach, 1998; Schwalb et al., 2010); many fish swim significant distances both upstream and downstream (e.g., Gorman, 1986; Hitt and Angermeier, 2008); and many aquatic macroinvertebrates actively or passively drift downstream (e.g., Elliott, 1971; Müller, 1982; Brittain and Eikeland, 1988; Elliott, 2003). Taxa capable of movement over land, via either passive transport (e.g., wind dispersal or attachment to animals capable of terrestrial dispersal) or active movement (e.g., terrestrial dispersal or aerial dispersal of winged adult stages), can establish biotic linkages between river networks and wetlands, as well as linkages across neighboring river systems (Hughes et al., 2009).

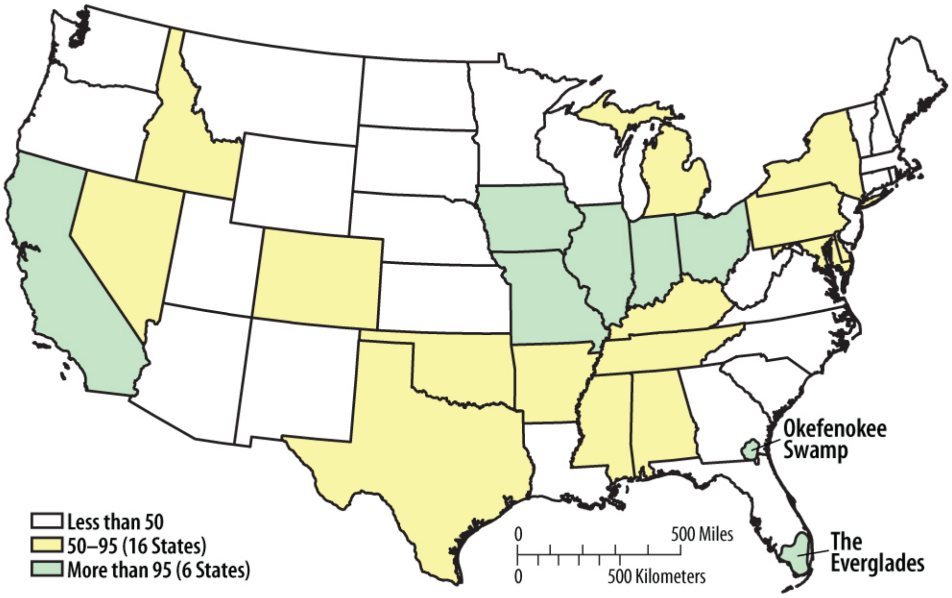
3.4.4. Human Activities and Alterations

Human activities frequently alter connectivity between headwater streams, riparian/floodplain wetlands, unidirectional wetlands, and downgradient river networks, thereby altering the transfer and movement of materials and energy between river system components. In fact, the individual or cumulative effects of headwater streams and wetlands on river networks often only become discernible following human-mediated changes in degree of connectivity. These human-mediated changes can result in increased or decreased hydrologic and biological connectivity (or, alternatively, decreased or increased hydrologic and biological isolation). For example, activities and alterations such as dams, levees, water abstraction, and piping, channelization, and burial can reduce hydrologic connectivity between streams and wetlands and rivers, whereas activities and alterations such as wetland drainage, irrigation, impervious surfaces, interbasin transfers, and channelization can enhance hydrological connections. Biological connectivity can be affected similarly: for example, dams and impoundments might impede biotic movement, whereas nonnative species introductions artificially increase biotic movement. Further complicating the issue is that a given activity or alteration might simultaneously increase and decrease connectivity, depending on which part of the river network is considered. For example, channelization and levee construction reduce lateral expansion of the river network (thereby reducing hydrologic connections with floodplains), but might increase this connectivity downstream due to increased magnitude and frequency of high flows.

To illustrate, we describe two notable alterations that affect river system connectivity: dams (and their associated impoundments) and wetland drainage. The United States has more than 80,000 dams, over 6,000 of which exceed 15 m in height (USACE, 2009). Numerous studies have shown that dams impede biotic movements, reduce biological connectivity between upstream and downstream locations (e.g., Greathouse et al., 2006; Hall et al., 2011), and form a discontinuity in the normal stream-order related progression in stream ecosystem structure and function (Stanford and Ward, 1982). Upstream of large dams, riparian areas are permanently inundated, increasing lateral hydrologic connectivity. Downstream, dams decrease peak stream volumes during the normal high runoff seasons, while increasing minimum flows during normal low-flow seasons—an overall dampening of stream-flow variability (Poff et al., 2007). Because many riverine organisms are adapted (life history, behavioral, and morphological) to the seasonality of natural flow regimes, dampening flow variability can have deleterious effects on species persistence where dams have been built (Lytle and Poff., 2004). This reduction in high flows also decreases the connectivity of riparian wetlands with the stream by reducing the potential for overbank lateral flow. This can affect downstream water quality, because overbank flow deposits sediment and nutrients that would otherwise remain entrained in the river (Hupp et al., 2009).

The greatest human impact on riparian/floodplain wetlands and unidirectional wetlands has been through wetland drainage (see Figure 3-21), primarily for agricultural purposes. Estimates show that the conterminous United States have lost more than 50% of their original

A. Percent of Wetlands Lost, 1780s–1980s



B. Artificially Drained Agricultural Land, 1985 (1 dot = 8100 ha)

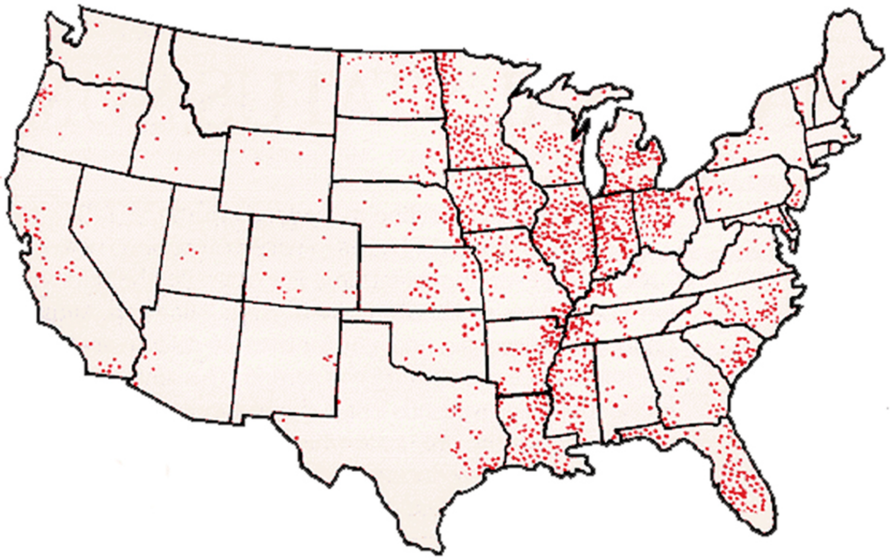


Figure 3-21. Comparison of percent wetland loss between (A) the 1780s and mid-1980s with (B) the distribution of artificially drained agricultural land in 1985. One dot equals 8100 ha.

From Blann et al. (2009), as modified from Dahl (1990).

wetlands, with some states losing more than 90%; wetland surface areas also have declined significantly (Dahl, 1990).

Drainage causes a direct loss of function and connectivity in cases where wetland characteristics are completely lost. Wetland drainage, however, also increases hydrologic connectivity between the landscape—including drained areas that retain wetland characteristics—and downstream waters. Effects of this enhanced hydrologic connectivity include (1) reduced water storage and more rapid conveyance of water to the network, with subsequent increases in total runoff, baseflows, stormflows, and flooding risk (Wiskow and van der Ploeg, 2003; Blann et al., 2009); (2) increased delivery of sediment and pollutants to downstream waters; and (3) increased transport of water-dispersing organisms (Babbitt and Tanner, 2000; Baber et al., 2002; Mulhouse and Galatowitsch, 2003). Biological connectivity, however, also can decrease with drainage and ditching, as average distances between wetlands increase and limit the ability of organisms to disperse between systems aerially or terrestrially (Leibowitz, 2003). Groundwater withdrawal also can affect wetland connectivity by reducing the number of wetlands. Of particular concern in the arid Southwest is that groundwater withdrawal can decrease regional and local water tables, reducing or altogether eliminating groundwater-dependent wetlands (Patten et al., 2008). However, groundwater withdrawal also can increase connectivity in areas where that groundwater is applied or consumed.

Particularly noteworthy is that restoration of hydrologic connectivity, particularly in systems with widespread human alterations, also might adversely affect downstream waters (Jackson and Pringle, 2010). For example, dam removal can result in the downstream transport of previously sequestered pollutants (Jackson and Pringle, 2010); dam releases to restore flows, without simultaneous restoration of sediment supplies, can result in downstream channel degradation (Germanoski and Ritter, 1988; Schmidt and Wilcock, 2008). Hammersmark et al. (2008) used a modeling study to show how the restoration of incised stream channels can improve connectivity between streams and floodplains and thus restore predisturbance hydrology (i.e., increased floodplain water storage, reduced peak stormflow, and reduced baseflow).

3.4.5. Interactions Among Factors

Interactions among the factors discussed above can be complex. Here we provide an example of temporary surface water connections between wetlands in the prairie pothole region (PPR) to illustrate these complex interactions (Leibowitz and Vining, 2003). Further details on wetlands in the PPR are provided in Section 5.8.

During high water conditions in 1995, a temporary surface water connection was observed between two geographically isolated prairie potholes in the region's Drift Prairie. Based on a spatial analysis during similarly wet conditions in 1996, 28% of the wetlands in a 40 km2 area containing the sites had a temporary surface water connection to at least one other wetland. This included a complex (defined in the study as a group of wetlands interconnected through temporary surface water connections) of 14 wetlands.

In considering these findings, Leibowitz and Vining (2003) suggested that precipitation and local relief are the primary factors controlling the spatial distribution of these temporary surface connections. Precipitation is the ultimate source of water that fills these wetlands, whereas relief controls how much the water level in a wetland must rise before spillage occurs (water level is also influenced by evapotranspiration and groundwater, but groundwater dynamics are difficult to predict for individual wetlands). Relief also controls mixing—which could occur in flatter areas when the boundaries of expanding wetlands overlap—by determining the change in surface area per change in water level. Thus, for a given level of precipitation, the number of surface connections occurring between wetlands should be inversely proportional to local relief. Within the PPR, precipitation generally decreases from east to west, while relief generally increases. The easternmost physiographic region in the PPR is the Red River Valley, a relatively flat ancient lakebed (Lake Agassiz) having deep deposits of silt and clay. Water can pond easily on these deposits, producing shallow wetlands and integrated drainage (i.e., the presence of stream networks). The Missouri Coteau, which forms the western boundary of the PPR, consists of dead-ice glacial moraine. This area has hummocky terrain, and local relief can be as great as 15−45 m in steeper areas (Winter et al., 1998). As a result, the Coteau has deeper wetlands and little to no integrated drainage. The Drift Prairie, located between the Red River Valley and the Missouri Coteau, is an undulating plain formed on ground moraine. Relief, wetland depth, and the level of integrated drainage in the Drift Prairie are intermediate in comparison with the other two regions.

Leibowitz and Vining (2003) hypothesized that the combined effect of these patterns in precipitation and relief should produce a strong east-west gradient across the PPR in the occurrence of intermittent surface-water connections. Both the absolute number of connections and complex size (the number of wetlands contained in a complex) should be highest in the Red River Valley. Given the relative flatness of this area, mixing should be the more common mechanism for temporary connections. The number of temporary connections and complex size should be lower in the Drift Prairie, and spillage might dominate in this hillier terrain. In the Missouri Coteau, where relief is greatest, the occurrence of these temporary connections should be rare and limited to small complex sizes. Human impacts, however, could affect these trends (see Section 3.4.4).

Beyond these regional trends in relief and precipitation, local variation in the occurrence of intermittent surface-water connections should be influenced strongly by groundwater dynamics. The groundwater hydrology of prairie potholes has been well investigated at several sites (e.g., Winter et al., 1998; Winter and Rosenberry, 1998). However, the specific groundwater interactions—and hence the effects of groundwater movement on spillage or mixing—are unknown for most prairie potholes. It would generally be expected that, all else being equal, groundwater discharge wetlands should receive more water, and so have a higher probability of spillage, than groundwater recharge wetlands, since recharge should reduce the amount of water available for spillage.

A major factor influencing the temporal distribution of intermittent connections within the PPR is wet-dry cycles. These cycles are driven by climatic changes that have occurred throughout the Holocene. For example, there is evidence of 20-, 22-, 50-, 100-, and 200-year climatic cycles (Ashworth, 1999). Wetland hydrology responds dramatically to these wet-dry cycles as groundwater levels and precipitation patterns fluctuate. In 1996, the average monthly Palmer Hydrological Drought Index for central North Dakota was 4.02 (88th percentile), compared with a median of 1.00 for annually calculated monthly averages between 1895 and 2001. Moisture levels of this magnitude—and consequently the degree of connectivity observed (Leibowitz and Vining, 2003)—would be expected to occur during wetter portions of wet-dry cycles.

4. STREAMS: PHYSICAL, CHEMICAL, AND BIOLOGICAL CONNECTIONS TO RIVERS

4.1. ABSTRACT

The physical structure of a river network inherently demonstrates connectivity between all streams and their downstream rivers. Substantial evidence supports physical, chemical, and biological connections from headwater streams—including those with ephemeral, intermittent, and perennial flows—to waters immediately downstream through transport of water and associated materials, as well as movement of organisms and reproductive propagules, and bidirectional geomorphic adjustments. Among the most compelling evidence for the effects of headwater streams on rivers is as sources of water, nitrogen, organic carbon, and contaminated sediment; as sinks of nitrogen, carbon, and contaminants; and as providers of essential habitat for migratory animals such as anadromous salmon. Small streams as a class provide substantial quantities of water to larger water bodies. For example, first-order streams contribute approximately 60% of the total mean annual flow to all northeastern U.S. streams and rivers. Infrequent, high-magnitude events are especially important for transmitting materials from headwater streams in most river networks. The strongest lines of evidence supporting the effects of headwater streams are from basins where headwater streams drain a unique (in terms of hydrology, geology, human alteration) portion of the basin. Our examination of the literature makes clear that investigation of connections among river network components continues to be an active area of scientific research. Additional empirical data and further breakthroughs in our ability to quantify linkages across large spatio-temporal scales will continue to enhance our understanding of the complexity of river networks.

4.2. INTRODUCTION

The purpose of this chapter is to describe the state of knowledge of stream connectivity and its effects on the physical, chemical, and biological condition of downstream waters. Although we recognize that streams also are important sources of water and other materials to nearby terrestrial and groundwater systems (e.g., Gray, 1993; Shentsis and Rosenthal, 2003; Walters et al., 2008), we focus here on surface water connections between streams and rivers, as well as subsurface water interactions integral to surface water connections and downstream water condition. The evidence primarily focuses on the downstream connections of small (headwater) streams to downstream waters, but some evidence is drawn from connections of larger streams to rivers, reservoirs, lakes, and coastal waters. We consider the peer-reviewed evidence for connectivity and its effects on downstream rivers in terms of physical (see Section 4.3), chemical (see Section 4.4), and biological (see Section 4.5) connections between upstream and downstream habitats. While recognizing that many linkages between streams and downstream waters cross physical, chemical, and biological boundaries, we have chosen this format for ease of presentation. We close this general section on stream-river connections with a synthesis of the evidence in terms of the conceptual framework (see Section 4.6), and then consider in greater detail the evidence for connectivity in two specific stream types: prairie streams (see Section 4.7) and arid streams of the Southwest (see Section 4.8). Prairie streams and arid streams of the Southwest were selected for case studies in part because a high proportion of these river networks are composed of intermittent and ephemeral streams.

Streams range greatly in size in terms of both drainage area and discharge, and generally, their abundance is inversely related to their size. First-order streams typically are most abundant, although individually they have the smallest drainage areas and shortest average stream lengths (Horton, 1945; Schumm, 1956; Ijjasz-Vasquez et al., 1993). When drainage area and stream length of headwater streams are combined, however, they can represent most of the river catchment and network.

The contribution of headwater streams to river networks in terms of stream number, length, or drainage area over large geographic regions has been difficult to determine, even with advances in remote sensing and geographic information systems (GIS). The small size of headwater streams makes distinguishing them from surrounding areas and overlying tree canopies in most regions difficult (Gilvear and Bryant, 2003). Numerous studies have shown that existing U.S. hydrographic databases and topographic maps underestimate the extent of headwater streams (Morisawa, 1957; Gregory, 1976; Hansen, 2001; Heine et al., 2004; Stoddard et al., 2005; Colson et al., 2008; Roy et al., 2009). Therefore, most first-order streams portrayed on databases and maps are second- or third-order streams when ground truthed. For example, over 80% of mapped (1:25,000 scale topographic maps) stream terminuses in a Massachusetts watershed that were surveyed underestimated the upstream extent of the channels (Brooks and Colburn, 2011). On average these unmapped upstream segments were nearly 0.5 km in length and 40% had one or more upstream tributaries (Brooks and Colburn, 2011). Despite the widely known underestimation by databases and maps, first-order streams recognized by the U.S. Geological Survey (USGS) medium-resolution (1:100,000-scale) National Hydrographic Database (NHD) represented 53% (2,900,000 km) of total stream length (Nadeau and Rains, 2007b). Moreover, approximately 50% of these first-order streams were classified as not having year-round flow (i.e., nonperennial; Nadeau and Rains, 2007b; see Section 3.2.2). Because most databases and maps do not portray the true extent of headwater and nonperennial streams, these resources do not accurately reflect the true geomorphic definition of stream order and should not be used to define the upper extent of what is and is not a stream within a watershed. Nevertheless, given what we do know from hydrographic databases and about the distribution of streams by size, it is clear that headwater and nonperennial streams represent a large fraction of river networks in the United States.

In the following sections, we consider connectivity between streams and downstream rivers in terms of the physical, chemical, and biological connections between them. These types of connections are not independent, however. For example, the physical connection of water flow through the river network largely forms the foundation for chemical and biological connections. The scientific community is increasingly aware that integration across multiple disciplines is fundamental to obtaining deeper understanding, and riverine science is no exception (Paola et al., 2006; Wood et al., 2007; Thorp et al., 2008).

4.3. PHYSICAL CONNECTIONS

Physical connections result from the transport of nonliving materials that do not chemically change (or change slowly) from streams to downstream rivers. In this section we discuss factors controlling water, temperature (or heat energy), sediment, and wood in streams; how these materials are transported downstream; and evidence that these connections affect the condition of downstream rivers.

4.3.1. Water

The recurrent, concentrated surface flow of water from surface runoff and groundwater develops and maintains river networks, and water is the primary medium carrying other materials from streams to rivers (see Section 3.3). Most (although not all) rivers receive most of their water from tributaries rather than through direct precipitation on or groundwater input to river segments (Winter, 2007; Bukaveckas, 2009). Alexander et al. (2007) modeled flow through stream networks in the northeastern United States and estimated that first-order streams (designated on the 1:100,000-scale NHD river network) provide approximately 70% of the mean annual water volume in second-order streams and about 55% and 40% of the mean water volume in fourth- and higher order rivers, respectively. Overall, first-order streams contribute about 60% of the total volume of mean annual flow to all northeastern streams (Alexander et al., 2007). Contributions of headwaters to downstream baseflow vary among river networks, depending on large-scale factors (see Section 3.4). For example, headwater streams which have stronger connections to groundwater or which consistently receive more precipitation, relative to downstream reaches, will have a larger effect on river baseflows. Hydrologic data from 11 nested gages distributed throughout a 176 km^2-basin in the Catskill Mountains, NY were used to assess the extent of spatial correlation in baseflow discharge (Shaman et al., 2004). Baseflow discharge in smaller streams (i.e., with watersheds <8 km^2) was more weakly correlated with mainstem discharge than discharge in larger streams; the authors concluded that this pattern reflected greater contributions by deep groundwater as drainage area increased (Shaman et al., 2004). Using geochemical tracers and hydrologic data from 32 nested stations in a 1,849 km^2-basin of the River Dee in Scotland, Tetzlaff and Soulsby (2008) determined that streams draining the upper 54% of the catchment contributed 71% of baseflow. This finding is particularly significant because the upper catchment received only 58% of the total annual precipitation, indicating that groundwater storage in the headwater catchments was important in maintaining downstream baseflows (Tetzlaff and Soulsby, 2008). In contrast, headwater streams (0.11−3.5 km^2) making up 33% of the total area in a northern Sweden basin (78 km^2) contributed only 18% of the summer baseflow at the basin outlet (Temnerud et al., 2007). The specific discharge contribution ($L\ s^{-1}\ km^2$) for headwater streams, however, varied by an order of magnitude (~0.5−8.0) reflecting the heterogeneity (i.e., mires, lakes, forest) of the study catchment (Temnerud et al., 2007).

The role of headwater streams also can be inferred from variation in river hydrologic response over space. Discharge increases with drainage area, and the general assumption is that they have a positive relationship such that drainage area is a common proxy for discharge. The relationship can be written as $Q = kA^c$, where Q is discharge ($m^3\ s^{-1}$), k is a constant representing hydrologic factors such as antecedent moisture and precipitation, A is drainage area (km^2), and c is the scaling power constant. This scaling power reflects how the rate of discharge increases with drainage area and can be useful for qualitatively assessing the contributions of headwaters to downstream discharge. Where $c \approx 1$, discharge is generated proportionally with increasing drainage area; where $c < 1$, upstream portions of the catchment (where small streams tend to be most abundant) generate more discharge per unit area than downstream portions; where $c > 1$, downstream portions generate more discharge per area than upstream reaches. Data from multiple USGS gages along large, unregulated rivers showed that mean and peak annual discharge does not always increase proportionally with drainage area (Galster, 2007, 2009). Of the 40 rivers examined, only 16 had linear peak annual discharge-area relationships ($c \approx 1$) throughout their period of record (Galster, 2009). Eleven rivers had relationships where $c < 1$, three rivers had relationships where $c > 1$, and ten showed changes in the relationship over their period of record. Rivers having $c < 1$ suggests that these rivers derive a higher proportion of their flow from headwater streams. Rivers having $c > 1$ suggests that the upstream portions might store more water per unit area than downstream areas. In some cases, however, urbanization in the lower portions of the catchment can cause greater flow generation per unit area, leading to a similar relationship (Galster et al., 2006).

Despite the variability in area-discharge relationships, most watersheds have a value of c between 0.8 and 1 (Galster, 2007), suggesting that to a first approximation, drainage area can be used to estimate the proportion of flow that arises from headwater streams. For example, Alexander et al. (2007) found that the catchments of first-order streams accounted for 57% of the total drainage area, and 55% of the total annual river flow of the New England states. Caruso and Haynes (2011) reported that first-order catchments made up 61% of the total drainage area of the Upper Colorado River basin. In this case, however, the first-order streams produced a lower proportion (41%) of the total annual river flow than suggested by their total drainage area, explained in part by the fact that 84% of the streams were intermittent. Both studies used the 1:100,000-scale NHD, in which first-order catchments generally correspond to second-order catchments at the 1:24,000 scale (Alexander et al., 2007). These results, representing two very different parts of the United States, strongly suggest that headwater streams, even where seasonally dry, generate a large fraction of the nation's stream and river flows.

The propagation of stormflow through river networks provides clear evidence supporting the existence of hydrologic connectivity between headwater streams and rivers, particularly when an intense storm occurs over only the headwater portions of a river network. In these cases, the hydrograph peaks sharply in the headwater streams, indicating a quick response to precipitation (see Figures 3-8 and 3-11). Timing of the storm and onset of the peak will be increasingly delayed with increasing distance down the network (see Figure 3-11 and further discussion on hydrologic dispersion below). Typically, discharge magnitude increases as stormflow accumulates incrementally over the stream network (Allan, 1995). The contribution of tributaries to rivers during widespread floods manifests as stepped increases in discharge immediately below confluences, as water flows through a river network (see Figure 4-1).

Such propagation was recorded following a monsoonal storm event through an arid network of ephemeral channels in the Río Grande, NM (see Figure 4-2). The high intensity storm dropped approximately 18−25% of the annual rainfall over a 2-day period on the stream's approximately 16,000-km^2 drainage area. Discharge recorded at two gages on the stream and three gages on the Rio Grande downstream of the confluence illustrated lag time and peak hydrograph broadening at least 127 km downstream (Vivoni et al., 2006). The contributions of the stormflow from the ephemeral stream accounted for 76% of the flow at the Rio Grande, despite being considered to have a flood return interval only ranging from 1.11 to 1.84 years across the USGS gages in the network (Vivoni et al., 2006).

Here we describe how water flowing through the streams in river networks shapes the hydrologic response (time to peak flow, peak flow magnitude, and recession of peak flow) in downstream rivers (see also Section 3.2). A key effect streams have in a network structure on the hydrologic response is dispersion, or the spreading of water output from a drainage basin over time. Hydrologic dispersion is the combined effect of several mechanisms across spatial

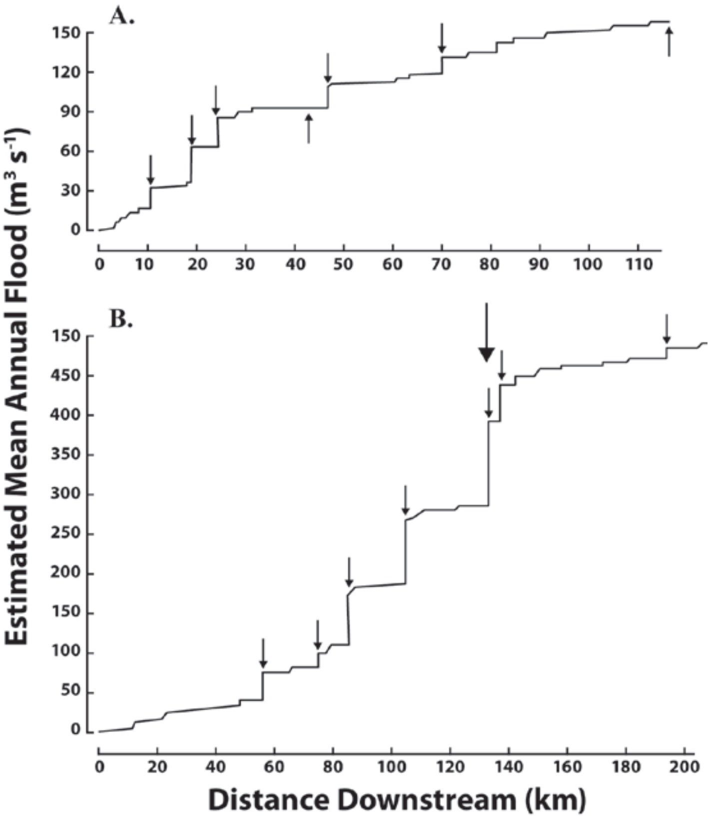


Figure 4-1. Longitudinal pattern of flow along (A) River Derwent and (B) River Trent, illustrating stepped increases in flow associated with contributions from tributaries. Small arrows indicate location of tributary confluences along the mainstem; bold arrow in (B) indicates the confluence of the two rivers.

Modified from Knighton (1998).

scales that influence the travel time and volume of water reaching a river network outlet (Saco and Kumar, 2002).

The components of hydrologic dispersion most relevant to river networks include **hydrodynamic dispersion**, **geomorphologic dispersion**, and **kinematic dispersion**. At the scale of individual channels within the network, hydrodynamic dispersion represents storage, turbulence, and shear stress processes that make portions of a channel's volume move downstream faster than others, rather than as a discrete pulse. Hydrodynamic dispersion, which can be visualized by placing a volume of dye tracer in an upstream location and watching how the dye disperses longitudinally as it moves downstream, takes into account the water flowing into and out of the streambed and adjacent bank sediments (hyporheic flow, see Section 3.2).

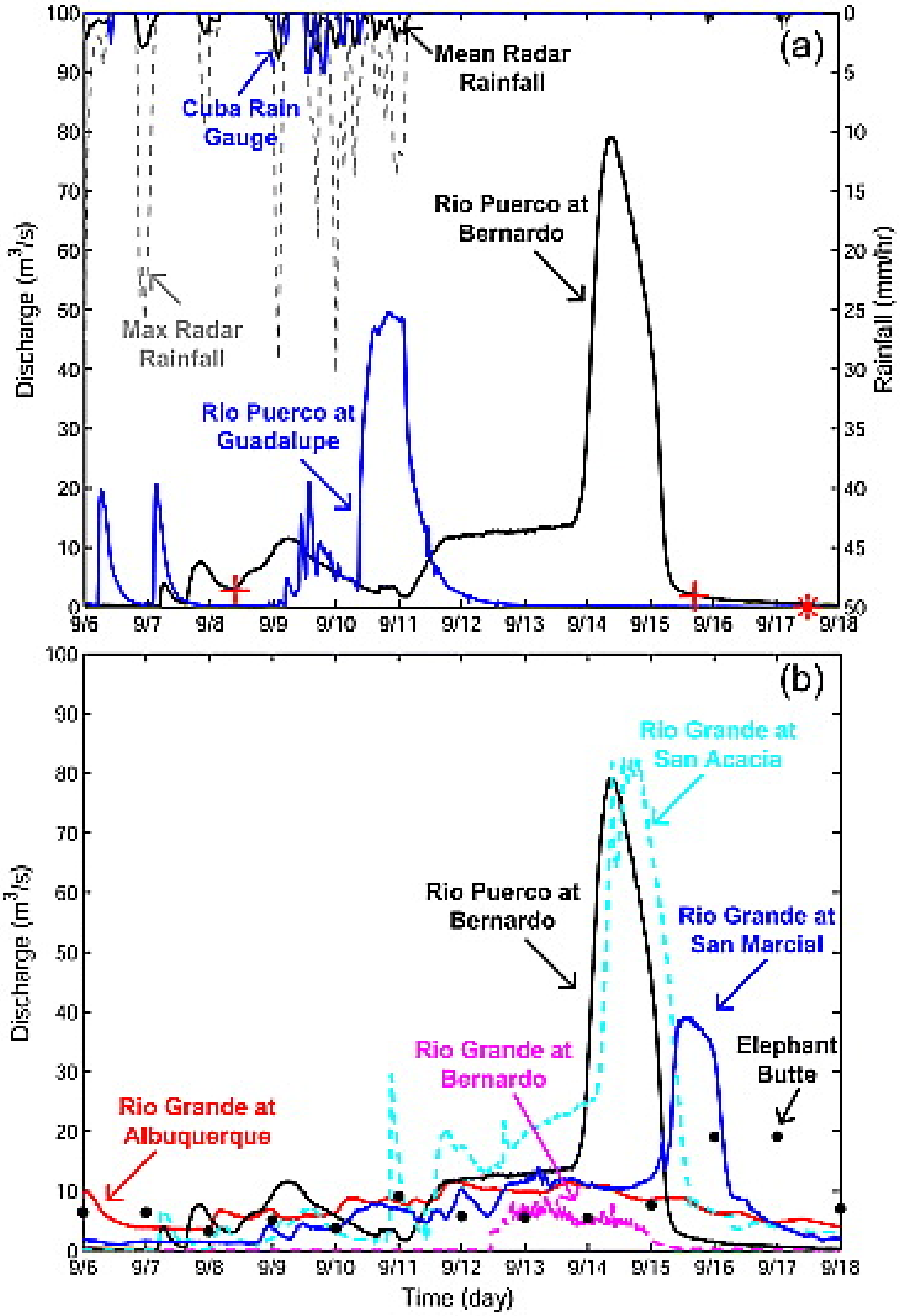


Figure 4-2. Time series of rainfall and streamflow observations in the Rio Puerco and Rio Grande, 6−18 September 2003.

Reprinted with permission from Vivoni et al. (2006).

Geomorphologic dispersion is the effect of different travel distances over the larger spatial scale of entire river networks (Rodríguez-Iturbe and Valdes, 1979; Gupta et al., 1980;

Rinaldo et al., 1991; Snell and Sivapalan, 1994). Not all points along the river network (or even headwater streams) are the same distance from the network outlet, so water entering the network simultaneously will not arrive at the outlet simultaneously.

Considering only geomorphologic dispersion assumes water flowing through the distribution routes moves at a constant velocity. Water velocity (and related hydrodynamics), however, changes over space and time within river networks; for example, channel slope or channel dimensions are not uniform across all pathways through the river network (Saco and Kumar, 2002; Paik and Kumar, 2004). Kinematic dispersion is the effect of spatially variable velocity of water as it moves through river networks (Saco and Kumar, 2002). The physical configuration and the variable channel form of streams within a river network (which influence components of hydrologic dispersion at varying scales) are the primary controls mediating the arrival time of pulses in rivers following rain storms, dispersing the flow from streams to rivers over time (Saco and Kumar, 2008).

Another factor that influences hydrologic response is transmission, or the loss of surface flow volume due to infiltration into unconsolidated alluvium (see Section 3.2). Transmission is another process in which streams, particularly in arid and semiarid regions, can slow or divert water from downstream rivers and minimize downstream flooding. Over relatively short time frames, transmission losses usually are dominated by infiltration or seepage through channel bed and banks, but evapotranspiration losses can be significant in stream reaches with prolonged surface flows (Hamilton et al., 2005; Costelloe et al., 2007). Because streams collect and concentrate surface water, they tend to have more water available for infiltration, be more permeable (have coarser sediment) than upland soils, have higher antecedent moisture, and be closer to shallow groundwater, being the topographic low in catchments. Infiltration is especially significant in arid, semiarid, and karst river networks, where water in intermittent and ephemeral streams recharge groundwater aquifers (Brahana and Hollyday, 1988; Hughes and Sami, 1992; Sharma and Murthy, 1995; Constantz et al., 2002). These aquifers supply water to rivers and other water bodies downgradient.

Channel bed and bank permeability also governs the degree to which infiltration is an important pathway between streams and groundwater aquifers. Fine bed and bank sediments slow infiltration; in many semiarid and arid streams, bed sediments become finer in the downstream direction because flow competence declines (Dunkerley, 1992). Because fine sediments can become concentrated in channels following moderate flows, higher flows that scour out fine sediments or submerge more permeable floodplains have higher infiltration rates (Lange, 2005). In Walnut Gulch, Arizona, transmission losses over 54 km of channel resulted in a 57% decrease in flow volume associated with a storm (Renard and Keppel, 1966). Tang et al. (2001) used chemical and isotopic tracers to confirm that ephemeral streams are important areas for floodwaters to recharge groundwater aquifers in desert regions, and infiltration losses accounted for up to half of the flow volume along three ephemeral channels in the southwestern United States (Constantz et al., 2002). Although transmission losses represent disruptions of surface connectivity between streams and downstream waters, such losses are hydrologic pathways that reduce downstream flooding and recharge groundwater aquifers that eventually support springs and flow in downgradient streams and rivers (Izbicki, 2007).

4.3.2. Sediment

Sediment carried with water flow from streams to downstream waters is critical for maintaining the river network. Fluvial sediments scour channels, deposit to form channel features, and influence channel hydrodynamics (Church, 2006). Although essential to river systems, excess sediment also can impair ecological integrity by filling interstitial spaces, reducing channel capacity, blocking sunlight transmission through the water column, and increasing contaminant and nutrient concentrations (Wood and Armitage, 1997).

Sediment in headwater streams originates from adjacent hillslopes and enters these streams via overland flow, bank erosion (Grimshaw and Lewin, 1980), and infrequent disturbances such as landslides and debris flows (e.g., Benda and Dunne, 1987; Swanson et al., 1998; Eaton et al., 2003). Sediment transported within river networks can be divided into two major categories: suspended and bed load. Suspended sediment is fine sediment (clay, silt, and fine sand) that requires slow velocities and little turbulence to remain entrained in the water column; bedload sediment is coarser particles that slide, roll, and bounce along the streambed during faster, more turbulent flows (Church, 2006; Wilcock et al., 2009).

The dynamic balance between sediment supply and transport capacity (Lane, 1955; Bull, 1991; Trimble, 2010)—with variables of sediment flux and sediment grain size on one side, and discharge and channel slope on the other side—is a principal paradigm of fluvial geomorphology. If one of these variables changes, a compensatory change occurs in at least one of the other variables. For example, if discharge increases, a lower channel slope is needed to transport the same amount of sediment of that grain size; alternatively, to move a load of fine sediment, less discharge or lower channel slope is needed relative to the same load of coarse sediment. Associated with this balance is the relationship between channel geometry (width and depth) and discharge (Leopold and Maddock, 1953), and adjustments to maintain a dynamic balance also can include channel dimensions. This balance is particularly relevant to geomorphologic connectivity in river networks because these variables commonly differ between streams and rivers (Ferguson et al., 2006; Ferguson and Hoey, 2008), with slope and grain size decreasing and discharge and channel size increasing downstream (Church, 2002). Thus, streams affect rivers through changing sediment supply or transport capacity at confluences.

Relatively small contributions in sediment and discharge from a stream might elicit no detectable change or only a short-lived spike in downstream sediment characteristics, discharge, or channel geometry. In contrast, streams making large relative contributions at mainstem confluences elicit strong stepped changes in mainstem characteristics. Because small streams can make large contributions (e.g., floods, debris flows) during infrequent disturbances, even small streams have long-lasting effects on rivers.

Streams transport and store sediment. Small streams tend to have low competence to transport sediment during baseflow (Gooderham et al., 2007), but they have structures (boulders, woody debris) that entrain and store colluvial sediments between infrequent disturbances (i.e., stormflows) that are the dominant means for downstream transport (e.g., Gomi and Sidle, 2003).

Ephemeral desert streams can exhibit high sediment export efficiency. The amount of bed load per unit stream power from an ephemeral Negev Desert stream was estimated to be substantially higher than from a forested perennial stream (Laronne and Reid, 1993). Despite infrequent flows with short durations, flood waves (bores) in ephemeral desert streams carry substantial amounts of sediment downstream (Hassan, 1990). The transport distance associated with these floods, however, often is insufficient to link them to perennial rivers. For example, a reach-scale study in Walnut Gulch, Arizona estimated sand transport distances of only 401 and 734 m in two consecutive years marked by nine floods (Powell et al., 2007). Streams also can store substantial amounts of sediment that are only released during rare export events. A series of experimental sediment introductions (to mimic road surface sediment) into steep, ephemeral second-order streams in southwestern Washington revealed that between 30 and 45% of the sediment (ranging from clay to coarse sand) was exported to the mainstem, 95−125 m downstream, during stormflows representing 66−69% of bank full discharge (Duncan et al., 1987). Virtually all of the fine clay particles introduced were exported from the ephemeral streams to the mainstem, presumably because this fraction remained suspended at even moderate flows (Duncan et al., 1987). Streams in the Coastal Range of Oregon stored 23% of the sediment within a 2.5-km^2 basin compared with only 9% within the mainstem channel (May and Gresswell, 2003). A long-term sediment budget for the Coon Creek watershed (360 km^2), a stream to the Mississippi River in Wisconsin, was constructed over periods coinciding with major land use changes (Trimble, 1999). Over a period when agricultural practices caused major soil erosion (1853−1938), streams acted as net sources of sediment (42×10^3 Mg y^{-1}); after erosion control, streambank stabilization, and revegetation (1975−1993) , streams changed to net sinks of sediment (9×10^3 Mg y^{-1}; Trimble, 1999).

Several studies identify abrupt changes in sediment size and channel morphology coinciding with stream confluences with sufficiently high symmetry ratios (Knighton, 1980; Rhoads, 1987; Rice and Church, 1998; Rice et al., 2001). In his review of available data, Rhoads

(1987) determined that for a stream to create a discernible sediment or channel morphology discontinuity along a mainstem river, the symmetry ratio needed to be at least 0.7. A similar review of 168 confluences across the western United States and Canada found that a symmetry ratio needs to be greater than 0.2 to affect a downstream river's sediment supply or transport capacity (Benda, 2008). Suspended particulate matter (inorganic + organic) and bed particle size were measured above and below eight confluences on the Acheron River in Australia to determine stream contributions (Wallis et al., 2008; Wallis et al., 2009). Suspended particulate matter downstream of confluences approximated the sum of mainstem and stream exports during high flow, but stream contributions were negligible during low flows (Wallis et al., 2009). Four of the eight confluences showed expected changes in bed particle size below confluences with streams, and the bed particle sizes were similar in the mainstem and stream for the remaining confluences so particle size change associated with streams was not discernible (Wallis et al., 2008).

Streams, through their connections to rivers at confluences, can disrupt longitudinal trends in discharge of water and sediment in rivers (Best, 1988; Benda et al., 2004; Ribeiro et al., 2012). For example, dams often remove much of the sediment from transport, whereas most streams are sediment sources. The objective of a study on the Agigawa River in Japan was to examine contrasting disruptions associated with a dam (sediment removal) and a stream confluence (sediment discharge) located downstream from the dam (Katano et al., 2009). The stream contributions to the river reversed many of the dam-related changes to the river, including restoring the turbidity level and the proportion of sand and gravel substrate in the river bed (Katano et al., 2009).

4.3.3. Wood

Large woody debris (typically considered >10 cm diameter and >1 m long) has a strong influence on hydrodynamics, sediment transport and storage, and channel morphology (e.g., Harmon et al., 1986; Nakamura and Swanson, 1993; Abbe and Montgomery, 1996; Naiman and Decamps, 1997; Montgomery et al., 2003). More specifically, woody debris dissipates energy, traps moving material, and forms habitat for aquatic plants and animals (Anderson and Sedell, 1979; Harmon et al., 1986; Abbe and Montgomery, 1996; Naiman and Decamps, 1997; Gurnell et al., 2002). The debris can redirect water movements, create pools, and slow water movement through a channel (Nakamura and Swanson, 1993; Abbe and Montgomery, 1996; Naiman and Decamps, 1997). Wood recruitment to forested streams occurs as a result of chronic tree mortality; episodic disturbances such as fire, debris flows, landslides, and windthrow; and bank erosion. The steeper topography associated with hillslopes along many headwater streams increases the likelihood that trees will fall toward the channel (Sobota et al., 2006), relative to streams in flatter terrain.

Wood tends to accumulate in, rather than be exported from, most forested headwater streams, due to their low discharge and relatively small channel widths (Keller and Swanson, 1979; Bilby and Ward, 1989; Gurnell, 2003). For example, wood in a headwater stream in North Carolina was determined to have entered the channel more than 60 years earlier (Wallace et al., 2001) and more than a century earlier in some Pacific Northwest streams (Swanson et al., 1976; Keller et al., 1981). Because of the large occurrence of wood and small size of streams, wood has a stronger influence on hydrologic and geomorphic processes in headwater streams than in most larger rivers (Bilby and Bisson, 1998). Large, infrequent disturbance events are the primary drivers for wood movement in headwater streams (Benda and Cundy, 1990; Benda et al., 2005; Bigelow et al., 2007). Reeves et al. (2003) determined that 65% of the wood pieces and 46% of the wood volume in a fourth-order stream in the Coastal Range in Oregon were delivered downstream by debris flows from headwater streams rather than the riparian zone adjacent to the fourth-order channel. Using data from 131 reservoirs in Japan, investigators identified a curvilinear relationship between watershed area and large woody debris export (Seo et al., 2008), meaning that wood export per unit area increased from small streams (6−20 km^2), peaked at intermediate-sized streams (20−100 km^2), and decreased from large streams (100−2,370 km^2). The amount of wood in low-gradient streams in the Midwest was determined to be supply-limited mainly because human alteration depletes large wood sources and altered hydrology and channel structure enhances transport of small wood downstream (Johnson et al., 2006). Topography and topology also govern wood delivery from headwaters. Downstream segments draining steep, finely dendritic networks will receive a greater proportion of wood from headwater streams than networks that are low gradient and weakly dissected (Benda and Cundy, 1990; Reeves et al., 2003).

Several studies have assessed the distribution of wood associated with confluences. Wood volumes were measured upstream and downstream of 13 confluences (symmetry ratios ranged from 0.05 to 0.49) in the Cascade Range of western Washington (Kiffney et al., 2006). Wood volumes tended to peak at or immediately downstream from stream confluences (Kiffney et al., 2006), suggesting that streams are either important sources of wood to mainstems or alter channel form to enhance wood storage at confluences. Elevated wood density, however, was not associated with confluences of eight streams to the Acheron River in Australia (Wallis et al., 2009). The authors concluded that the study streams did not have sufficient capacity for transporting wood to the mainstem, because streams had similar slope to the mainstem but lower discharges (Wallis et al., 2009).

Large wood can shorten sediment transport and debris flow runout by entrainment (Lancaster et al., 2003). Woody debris in 13 Coastal Range streams in Oregon had accumulation rates ranging from 0.003 to 0.03 $m^3\ m^{-1}\ yr^{-1}$, which were subsequently driven by time since the last debris flow (May and Gresswell, 2003). The volume of instream wood was strongly related to the volume of sediment stored. On average, 73% of stream sediment, prone to debris flow transport, was stored behind instream wood (May and Gresswell, 2003). Wood (and associated sediment) movement from headwater streams to downstream segments occurs through infrequent, high-magnitude events (e.g., debris flows, fire). Once in larger streams, wood and sediment can be stored in alluvial fans and floodplains between stormflows that trigger further downstream movement through the network (Benda et al., 2005). Because of the long distances and infrequent triggers associated with wood transport from most headwater streams to rivers, the relevant periods for governing transport are decades to centuries (Benda et al., 1998). Wood entering headwater streams can affect the downstream transport of water and materials in headwater streams, but also can be transported downstream from headwater streams where it is important habitat for aquatic life, a source of dissolved and particulate organic matter (POM), and influential in controlling hydrodynamics and channel morphology of rivers.

4.3.4. Temperature (Heat Energy)

Connections between streams and downstream rivers can affect water temperature in river networks (Knispel and Castella, 2003; Rice et al., 2008). Water temperature is an important physical factor governing the distribution and growth of aquatic life, both directly (through its effects on organisms) and indirectly (through its effects on other physicochemical properties, such as dissolved oxygen and suspended sediments; Allan, 1995). The primary factors governing water temperature in streams and rivers are climate (e.g., solar radiation, air temperature), water source (e.g., groundwater, runoff, meltwater), channel characteristics (e.g., width, bed topography, hydraulic exchange), topography (e.g., aspect, upland shading, canopy cover), and discharge (e.g., volume of water, turbulence; Poole and Berman, 2001; Caissie, 2006).

Perennial and intermittent streams that derive much of their flow from intermediate or regional groundwater have water temperatures similar to groundwater. Groundwater temperature is largely buffered from seasonal and short-term changes that affect air temperature, so that in temperate climates, groundwater tends to be cooler than air temperature in summer but warmer in winter. Streams deriving water from other sources (e.g., local groundwater, runoff, or snowmelt) have water temperatures and associated fluctuations reflecting these sources. Typically a nonlinear increase in mean daily water temperature occurs from headwaters to large rivers, and a unimodal trend is observed in daily variation (i.e., daily maximum-minimum) of water temperature (Caissie, 2006). Stable groundwater temperatures (in headwater streams) and greater depth and volume of water (in large rivers) buffer water temperatures from the daily changes typical in intermediate-sized streams. The steep increase in water temperature immediately downstream of headwaters is associated with more rapid flux of heat into small streams, as shallow water contacts the surrounding air and receives direct radiation (Caissie, 2006). This longitudinal pattern, however, does not hold for all river networks, because some river networks receive substantial deep groundwater contributions at lower reaches. As water moves from streams through stream networks, water temperature is influenced by heat exchange associated with solar radiation and hyporheic exchange (mixing with groundwater). These factors vary with geographic location. For instance, water in headwater streams draining steep, forested regions will be buffered from solar radiation and move downstream rapidly, compared to a headwater stream draining a low-gradient, prairie catchment where shading by riparian trees is minimal (see Section 4.7.2).

The empirical evidence supporting thermal connections between small streams and rivers includes studies that have gauged the spatial relationship of water temperature over stream networks and studies that have detected discontinuities in river temperature associated with stream confluences. Geospatial analyses are used to assess the degree of spatial dependence of a variable across a river network, and are particularly well suited for studying connectivity within these systems. Water temperature data collected at 72 locations throughout a Catskill Mountain, NY drainage basin were used to spatially predict daily mean summer water temperatures throughout approximately 160 km of channel (Gardner and Sullivan, 2004). Results showed that water temperatures at points along the river network separated by up to nearly 20 km were related. Johnson et al. (2010) similarly used geostatistical analyses to determine the influence of headwater streams on downstream physicochemistry, including water temperature. Water temperature within the eastern Kentucky catchment was correlated across the river network over an average distance of approximately 5 km (Johnson et al., 2010). Ebersole et al. (2003) identified and characterized cold patches along a river network in northeastern Oregon that largely had summer water temperatures exceeding the tolerance of native salmonids. Floodplain springbrook streams were among the cold patches identified and were determined to contribute the coldest water to the river network (Ebersole et al., 2003).

Thermal infrared sensors are a recent remote sensing tool that can provide snapshots of thermal heterogeneity along river corridors (Torgersen et al., 2001; Torgersen et al., 2008; Cristea and Burges, 2009). Thermal maps and plots of longitudinal profiles overlaid by the locations of streams show that confluences coincide with distinct peaks and troughs in river temperature (see Figure 4-3). The effect of streams was discernible when temperature differences of streams and the mainstem exceeded 1°C and streams had large symmetry ratios (Cristea and Burges, 2009).

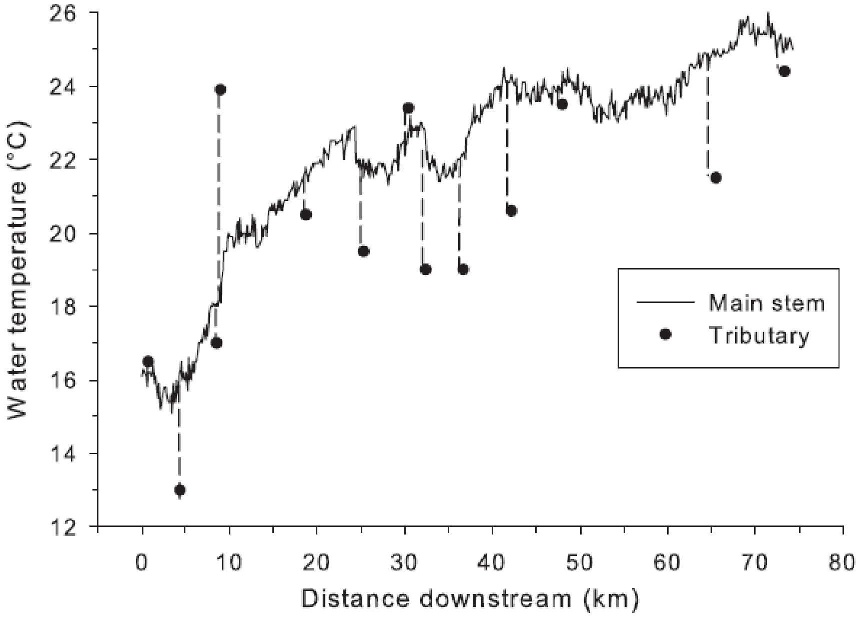


Figure 4-3. Airborne thermal infrared remotely sensed water temperature in the mainstem and at tributary confluences of the North Fork John Day River, OR, on 4 August 1998. Line indicates main stem, black dots indicate tributary confluences, and dashed vertical lines indicate location of tributary confluences along the mainstem.

Reprinted with permission from Torgersen et al. (2008).

In most cases, the effect of the stream on river water temperature was minor in relation to longitudinal changes over the course of the river (Torgersen et al., 2001; Cristea and Burges, 2009). Despite having a relatively minor effect on temperature over the length of entire rivers, however, streams provide constant cold-water habitats that are important for aquatic life (see Section 4.5.2).

4.4. CHEMICAL CONNECTIONS

Chemical connections are linkages between headwater and other tributary streams to their downstream waters based on the transport of chemical elements and compounds, such as nutrients, dissolved and particulate organic matter, ions, and contaminants. Chemical connectivity between streams and rivers involves the transformation, removal, and transport of these substances; in turn, these processes influence water quality, sediment deposition, nutrient availability, and biotic functions in rivers.

Because water flow is the primary mechanism by which chemical substances are transported downstream, chemical connectivity is closely related to hydrologic connectivity (see Sections 3.2 and 4.3.1). The movement of water across and through landscapes and into stream networks integrates potential sources and sinks of solutes throughout the watershed, making solute concentrations an integration of upstream mixing processes and transport processes in the stream channel. A simplified characterization has streams operating in two modes: a high-discharge throughput mode in which solutes and particles entering the stream channel are quickly transported downstream, and a low-discharge processing mode whereby solutes and particles are processed or stored in proximity to where they entered the stream network (Meyer and Likens, 1979).

Factors that affect hydrologic connectivity (including precipitation patterns and human alterations) modify these upstream-downstream chemical linkages. For example, the spatial and temporal variability of rainfall affects chemical connectivity between tributaries and rivers. Many small tributaries receive pulse inputs of water, sediment, organic matter, and other materials during rain events. Periodic flows in ephemeral or intermittent tributaries can have a strong influence on biogeochemistry by connecting the channel and other landscape elements (Valett et al., 2005); this episodic connection can be very important for transmitting a substantial amount of material into downstream rivers (Nadeau and Rains, 2007b). Alteration of channel characteristics (e.g., channel shape and depth) and organic matter input also will affect the ability of streams to cycle materials.

4.4.1. Nutrients

Alexander et al. (2007) investigated how nitrogen transport in a northeastern U.S. stream network was affected by stream size, which ranged from headwater streams to large rivers. First-order headwater streams contributed approximately 65% of the nitrogen mass in second-order streams, and approximately 40% of that mass in fourth-order and higher order streams (Alexander et al., 2007). Alexander et al. (2000) conducted a study of major regional watersheds of the Mississippi River basin. Instream nitrogen loss was inversely related to mean stream depth, most likely because denitrification and settling of particulate nitrogen occur less in deeper channels, due to reduced contact and exchange between streamwater and benthic sediments (Alexander et al., 2000). Both studies highlight how chemical connections are affected by stream size, with small streams within the network affecting downstream water quality.

Research in the Mississippi River basin on the hydrologic control and seasonality of nutrient export from streams provides evidence of downstream connectivity from two studies (see also Section 4.7.3). In the first, the export of dissolved reactive phosphorus from second- and fourth-order streams in agricultural watersheds occurred mainly during conditions of high discharge, with 90th percentile and greater discharges exporting 84% of the dissolved reactive phosphorus primarily during January and June (Royer et al., 2006). Similar patterns have been documented in total phosphorus concentrations of first- through fourth-order streams from another Mississippi River basin watershed (Bayless et al., 2003). In the second study, researchers focused on the January-to-June period to model riverine dissolved reactive phosphorus yield of 73 watersheds as a function of nutrient sources and precipitation in the Mississippi River basin. Jacobson et al. (2011) showed that riverine dissolved reactive phosphorus yield was positively related to fertilizer phosphorus inputs, human sources of phosphorus (e.g., sewage effluent), and precipitation. The surface runoff from precipitation moves the phosphorus from fertilizer in fields into streams and rivers which transport them downstream (Jacobson et al., 2011). These studies demonstrate the connections and processes by which nutrients exported from streams in the Mississippi River basin contribute to anoxia in the Gulf of Mexico (Rabalais et al., 2002).

The underlying geology of the Mokelumne River in the central Sierra Nevada of California affected the spatial and temporal variability in chemical connections. Holloway et al. (1998) examined water quality in that watershed to identify primary sources of nitrate entering downstream reservoirs. They conducted a paired watershed comparison with two ephemeral streams in adjacent catchments, which were underlain with different rock types (diorite vs. biotite schist) but had similar land use, vegetation, topography, and catchment area. Many samples from the diorite watershed had nitrate concentrations below detection limits (<4 μM), with a median concentration of 3.3 μM; concentrations were not strongly associated with the start or end of the high precipitation period. In the biotite schist watershed, maximum stream concentrations of nitrate (>300 μM) occurred at the start of the high precipitation period, and concentrations decreased over time. An adjacent perennial stream, also in a biotite schist watershed, displayed this same temporal trend, with highest nitrate concentrations at the beginning of the rainy season and decreasing concentrations during the spring. By monitoring the stream network in this watershed, Holloway et al. (1998) concluded that biotite schist streams in watersheds having this geological source of nitrogen, contributed a disproportionately large amount of total nitrate to downstream reservoirs despite draining only a small area of the entire watershed.

Chemical connectivity throughout a river network also is dynamic due to environmental and biological processes. Nitrate concentrations were measured at 50 sites across the West Fork watershed of the Gallatin River in the northern Rocky Mountains of southwestern Montana under different hydrologic conditions and across two seasons, growing or dormant (Gardner and McGlynn, 2009). Streams ranged from first-order mountain streams to fourth-order streams near the West Fork-Gallatin River confluence. In the dormant season, the distance over which nitrate concentrations were spatially correlated ranged from 3.2 to 5.5 km. In the growing season, this range decreased to 1.9−2.7 km. This seasonal difference could have resulted from greater biological uptake and use of nitrate during the growing season, limiting its transport by streamflow; when these processes were reduced during the dormant season, greater spatial dependence in nitrate concentrations was detected among sites.

Another example of seasonal variability in chemical connectivity was observed in the San Pedro River in Arizona where differences in dissolved organic nitrogen concentration were detected among three segments of the river during the dry season (Brooks and Lemon, 2007). In the wet season, however, streamwater was well-mixed, the system was hydrologically connected, and no differences in dissolved organic nitrogen concentration were detected (Brooks and Lemon, 2007). The seasonal differences in the longitudinal pattern of nitrogen occurs because nitrogen accumulates locally at varying levels during drier periods but is mixed and transported downstream during large infrequent storm events, making nitrogen levels more longitudinally uniform (Fisher et al., 2001).

Peterson et al. (2001) examined chemical connectivity by studying similar network components across different types of stream networks. After measuring nitrogen export from 12 headwater tributaries distributed throughout the contiguous United States, Alaska, and Puerto Rico, they found that uptake and transformation of inorganic nitrogen were most rapid in the smallest streams (Peterson et al., 2001). Given the prevalence of headwater streams on the landscape (see Section 4.2) and their hydrologic connectivity to other network components (see Sections 3.2 and 4.3.1), this level of nitrogen processing could improve the water quality in the downstream receiving waters. Other studies also highlight the processing of nitrogen in headwater streams (e.g., Hill et al., 1998; Hill and Lymburner, 1998; Triska et al., 2007). Mulholland et al. (2008) measured in situ rates of nitrate removal by denitrification and used those rates to model how small and large tributaries in a network respond to simulated increases in nitrate loading. At low loading rates, the biotic removal of dissolved nitrogen from water is high and occurs primarily in small tributaries, reducing the loading to larger tributaries and rivers downstream. At moderate loading rates, the ability of small tributaries to remove nitrogen is reduced, but downstream the larger tributaries can remove the excess nitrogen. At high loading rates, removal by small and large tributaries in the network is ineffective, resulting in high nitrogen export to rivers (Mulholland et al., 2008). Similar results were obtained by Wollheim et al. (2008) in the Ipswich River, MA.

In the Ispwich River (MA) and Flat Creek (WY) networks, the effect of connectivity was illustrated through simulation experiments by Helton et al. (2011) of a river-network model of nitrate dynamics. The nitrate models under-predicted nitrogen removal in many reaches. That under-prediction was attributed to connections between the river channels and adjacent wetlands, which were thought to function as nitrogen sinks. The wetland functionality and connectivity were not characterized by the model, resulting in the under-predictions (see Section 5.3.2.2).

The influences of headwater and other tributary streams on nutrient concentrations in larger downstream waters, such as detailed in the examples given above, reflect the combined processes of nutrient cycling and downstream transport that occur throughout the river network, but most intensively in small tributaries. The concept of nutrient spiraling provides an approach to quantifying these processes as well as a relatively simple framework for understanding their implications. As nutrients cycle through various forms or ecosystem compartments, being consumed and regenerated for reuse, they complete a "cycle" only after having been displaced some distance downstream, thus in concept, stretching the cycle into a helix or "spiral" (Webster and Patten, 1979). The stretching, or openness between loops, of the spiral is primarily determined by flow, and the diameter of the loops is mainly determined by biotic activity (Cummins et al., 2006). Nutrients such as dissolved phosphorus and nitrogen, which enter the stream via groundwater or overland flow, are removed from the water column by streambed algal and microbial populations. From there, the nutrients can be consumed by higher trophic levels, detach and travel farther downstream as suspended particles, or return to the dissolved pool through cell death and lysis. Nutrients flowing through the food web also are eventually regenerated to the dissolved pool via excretion and microbial decomposition. In each phase of the cycling process, the nutrient is subject to downstream transport, whether in dissolved, particulate, or living tissue form, so that with each transition from one form to another it moves some distance downstream. The average downstream distance associated with one complete cycle—from a dissolved inorganic form in the water column, through microbial uptake, subsequent transformations through the food web, and back to a dissolved available form—is termed the "spiraling length."

Measurement of total spiraling length requires detailed study of tracer dynamics through multiple compartments of the stream ecosystem, but Newbold et al. (1981; 1983a) have shown that it can be approximated by the "uptake length" or distance traveled in the water column before microbial and algal assimilation occurs. Uptake lengths for phosphorus and nitrogen can be estimated precisely only from tracer additions of radioactive or stable isotopes, but they can be roughly estimated from experimental additions that briefly raise the concentration of the natural form of the nutrient. Ensign and Doyle (2006) compiled results of 404 measurements of uptake length of phosphate, ammonium, and nitrate in streams and rivers ranging from first to fifth order. For a given stream order, they estimated the number of cycles that each nutrient had undergone as the ratio of median uptake length to the average length of stream for that stream order (from Leopold et al., 1964). They found roughly that the three nutrient forms cycle between 8 (nitrate) and 40 (ammonium) times within the length of a first-order stream, and between 8 and 90 times within the respective lengths of first- to fourth-order streams.

Downstream ecosystems depend on ecosystem processes that occur in headwater streams. Given that roughly half the water reaching larger tributaries and rivers originates from headwater (first- and second-order) streams (see Section 4.3.1), the results of Ensign and Doyle (2006) make clear that phosphorus and nitrogen arrive at downstream waters having already been cycled many times in headwater and smaller tributaries. The cycling is, fundamentally, a complex of ecosystem processes that intensively use nutrients and yet regenerate them to be delivered to downstream waters much in their original form. Because nutrients undergo transformations across various forms (e.g., dissolved, particulate, inorganic, living) while being transported downstream (i.e., spiraling), explicitly identifying their exact origin to the network can be difficult. If this cycling had been seriously impaired so that nutrient regeneration is inhibited, for example, or nutrients in biologically unavailable or toxic forms are generated, then the downstream effects could be large.

Although headwater nutrient cycling, or spiraling, functions largely to deliver regenerated nutrients downstream, headwater processes measurably alter the delivery of nutrients to downstream waters in many ways. Some of the nutrients taken up as readily available inorganic forms are released back to the water as organic forms (Mulholland et al., 1988) that are less available for biotic uptake (Seitzinger et al., 2002). Similarly, nutrients incorporated into particulates are not entirely regenerated (Merriam et al., 2002; Hall et al., 2009), but accumulate in longitudinally increasing particulate loads (Whiles and Dodds, 2002). The concentrations of phosphorus and nitrogen that are delivered downstream by headwater streams have seasonal cycles due to the accumulation of nutrients in temporarily growing streambed biomass (Mulholland and Hill, 1997; Mulholland, 2004). Such variations have been demonstrated to affect downstream productivity (Mulholland et al., 1995) and explain seasonality in spatial correlations of nutrient concentration as described above. Nitrification, or the microbial transformation of ammonium to nitrate, affects the form of downstream nutrient delivery. Nitrification occurs naturally in undisturbed headwater streams (e.g., Bernhardt et al., 2002), but increases sharply in response to ammonium inputs (e.g., Newbold et al., 1983b), thereby reducing potential ammonium toxicity from pollutant inputs (Chapra, 1996). Denitrification, which removes nitrate from streamwater through transformation to atmospheric nitrogen, is widespread among headwater streams, as demonstrated by stable isotope tracer additions to 72 streams in the conterminous United States and Puerto Rico (Mulholland et al., 2008).

Mulholland et al. (2008) estimated that small streams (<100 L s^{-1}, about third order or less), free from agricultural or urban impacts, reduce downstream delivery of nitrogen by 20−40%. Alexander et al. (2007) and Wollheim et al. (2008), using earlier and less extensive measurements of denitrification rates, estimated nitrogen removal of 8 and 16% by headwater networks of orders 1−3 and order 1−5, respectively. In headwater agricultural streams, denitrification in stream sediments might not be effective at removing nitrate from streamwater because of altered hydrology. In these watersheds with tile drains and channelized headwaters, stream nitrate concentration is positively correlated with stream discharge, so these streams could be in a through-put mode whereby nitrate inputs to streams are rapidly transported downstream with little retention or processing (Royer et al., 2004).

Small tributaries also affect the downstream delivery of nutrients through abiotic processes. Meyer (1979) showed that phosphorus concentrations in a forested first-order New Hampshire stream were reduced by sorption to stream sediments. A much stronger sorption of phosphorus by stream sediments was observed by Simmons (2010) in first- to third-order West Virginia streams impacted by acid mine drainage. In the latter case, phosphorus sorbed to metal hydroxide precipitates introduced by mine drainage, illustrating the potential for headwater streams to absorb impacts while transforming them to downstream benefit.

4.4.2. Dissolved and Particulate Organic Matter

Headwater streams supply downstream ecosystems with organic carbon in both dissolved and particulate forms, which supports biological activity throughout the river network. Organic carbon enters headwater streams from the surrounding landscape, including wetlands (see Sections 5.3.2.4 and 5.4.3.1), in the form of terrestrial leaf litter and other seasonal inputs (e.g., catkins), dissolved organic carbon (DOC) in subsurface and surface runoff, and fine particulate organic matter in surface runoff including eroded soil. Ågren et al. (2007) determined that small headwaters exported the largest amount of terrestrial dissolved organic carbon on a per unit basis in the Krycklan watershed in Sweden. Organic carbon is also produced within the stream by photosynthesis. These inputs were first documented and quantified by Fisher and Likens (1973) for a forested headwater stream in New Hampshire. Fisher and Likens (1973) followed the fate of these inputs, concluding that 34% of the inputs were mineralized through respiration by consumers and microbes within the reach; this was the "ecosystem efficiency" of the reach. The remaining 66% was exported downstream constituting, as Fisher and Likens observed, "… inputs to the next stream section where they are assimilated, or passed on (throughput) or both." Vannote et al. (1980) recognized that the exported carbon was not simply the unutilized fraction but was also greatly modified in character. They proposed, as one of the basic tenets of their River Continuum Concept, that longitudinal variations in the structure of stream ecosystems reflect, in part, the cumulative effects of upstream organic matter processing. Here we focus on a subset of the large body of literature on organic matter dynamics in streams and rivers, citing basic evidence that headwaters modify and export organic carbon that significantly affects downstream ecosystem processes throughout the river network.

Most organic matter inputs (66%) to a headwater stream in New Hampshire were exported (Fisher and Likens, 1973), which is comparable to results from other studies. Webster and Meyer (1997) compiled organic matter budgets from 13 North American first- and second-order streams. The median ecosystem efficiency was 31%, implying a median export of 69% of inputs. Much or most of the organic carbon exported from headwater streams has been altered either physically or chemically by ecosystem processes within the headwater reaches. Leaf litter contributes an average of 50% of the organic matter inputs to forested headwater streams (Benfield, 1997), but leaves and leaf fragments (>1 mm) only account for 2% or less of organic matter exports (Naiman and Sedell, 1979; Wallace et al., 1982; Minshall et al., 1983). The conversion of whole leaves to fine particles (<1 mm) involves physical abrasion, microbial decomposition, and invertebrate feeding and egestion (Kaushik and Hynes, 1971; Cummins et al., 1973; Petersen and Cummins, 1974). The rate of that conversion is affected by whether the leaves are in an aerobic environment, such as riffles, or an anaerobic environment, such as depositional pools (Cummins et al., 1980). Aquatic invertebrates that feed on leaves that have entered streams are called shredders (Cummins and Klug, 1979; Cummins et al., 1989). Invertebrate activity is particularly important, as demonstrated by large reductions of fine particle export that followed experimental removal of invertebrates from a headwater stream (Cuffney et al., 1990; Wallace et al., 1991). Strong invertebrate influence on fine particle export also has been inferred from analysis of seasonal (Webster, 1983) and daily (Richardson et al., 2009) variations. Headwater reaches also export organic carbon produced within the stream by photosynthesis, both as dissolved organic carbon (Kaplan and Bott, 1982) and suspended particles (Marker and Gunn, 1977; Lamberti and Resh, 1987).

Organic carbon exported from headwater streams is consumed by downstream organisms, supporting metabolism throughout the river network. In part this results from direct feeding by consumers on detrital organic matter (Wallace et al., 1997; Hall et al., 2000), but much of the metabolic consumption of organic matter in streams occurs via microbial decomposition (Fisher and Likens, 1973). The microbes themselves are then fed upon by consumers (Hall and Meyer, 1998; Augspurger et al., 2008), whose energy in turn supports the food web through what is known as the “microbial loop” (Meyer, 1994).

The organic carbon turnover length, derived from the spiraling concept (Newbold et al., 1982a; see Section 4.4.1), is a measure of the downstream fate of exported carbon. Carbon turnover length is computed as the ratio of the downstream flux of organic carbon to ecosystem respiration per length of stream. It approximates the average distance that organic carbon is expected to travel before being consumed and mineralized by aquatic biota. Carbon turnover length for first-order streams is on the order of 1−10 km (Newbold et al., 1982a; Minshall et al., 1983), suggesting that organic carbon exported from small streams is likely to be used primarily in the somewhat larger streams of which they are direct tributaries (i.e., second- or third-order streams). The carbon turnover length, however, actually represents a weighted average of widely varying turnover lengths associated with the diverse array of particulate and dissolved forms of organic carbon in stream and river ecosystems (Newbold, 1992). Turnover lengths of specific forms can be estimated if their rates of downstream transport and mineralization (or assimilation) are known. For example, Webster et al. (1999) estimated a turnover length of 108 m for whole leaves in a North Carolina second-order stream whereas the estimate for fine (<1 mm) organic particles was far longer at 40 km. Newbold et al. (2005) obtained similar estimates of 38 and 59 km for the turnover lengths of two different size fractions of fine organic particles in a second-order Idaho stream. Similarly, Kaplan et al. (2008) concluded that dissolved organic carbon in a third-order stream in southeastern Pennsylvania consisted of a rapidly assimilated “labile” fraction with a turnover length of 240 m, a more slowly assimilated “semilabile” fraction with a turnover length of 4,500 m, and a “refractory” fraction with immeasurably slow assimilation, implying an indefinitely long turnover length sufficient, at least, to carry the carbon to coastal waters.

Organic carbon that travels to a larger-order stream is likely to travel farther than its original turnover length predicts, because turnover length increases with stream size (Minshall et al., 1983; Webster and Meyer, 1997). For example, the organic turnover length of the Salmon River, ID increased from 3.7 km in a second-order headwater to 1,200 km in the eighth-order reach, about 600 km downstream from the headwaters (Minshall et al., 1992). In a modeling study, Webster (2007) estimated that turnover length increased from several hundred meters in the headwaters to greater than 100 km in a large downstream river. This progression of increasing turnover length through the river continuum implies that organic carbon exported from headwaters supports metabolism throughout the river network.

Although turnover length reflects the spatial scale over which upstream exports of organic carbon are likely to support downstream metabolism, it does not provide direct evidence for or quantify the actual use of organic carbon in the downstream reaches. Such evidence, however, is provided by studies of transport and mass balance throughout the river network. Shih et al. (2010) applied the SPARROW model to organic carbon (C) data from 1,125 monitoring sites throughout the conterminous United States. They estimated that all river reaches (large and small) delivered an annual average of 72 kg C ha^{-1} of incremental drainage area, whereas the river systems as a whole exported 30 kg C ha^{-1}. Thus, 58% of the carbon

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inputs were respired within the river networks, while the rest (42%) were transported downstream. Shih et al. (2010) did not specify the proportion of inputs originating from headwater streams but using their results with some assumptions, we can get a rough estimate that river networks receive approximately a third of their organic carbon from headwater streams. We begin with the proportion of carbon originating from allochthonous sources being 0.78 (Shih et al., 2010). If we assume that the proportion of headwater streams in a drainage area is 0.50 (see Section 4.2; Alexander et al., 2007; Caruso and Haynes, 2011). Headwater streams then provide 0.39 (= 0.78 × 0.50) of the total organic carbon supply, with the input from the larger downstream network being 0.61 (i.e., 61%) of the carbon supply. Using the ecosystem efficiency for headwater streams of 31% (Webster and Meyer, 1997), we calculate that the proportion of carbon originating in headwater stream that is delivered downstream is $0.39 \times (1 - 0.31) = 0.27$. The proportion of carbon exported from headwater streams (0.27), plus the proportion of carbon input directly to the downstream network (0.61), equals the carbon input to the downstream network of 0.88. Thus, 0.31 (= 0.27/0.88 = 31%) of the total carbon supplied to downstream reaches originates from headwater streams.

Most terrestrial organic matter that enters headwater tributaries is transported downstream (Gomi et al., 2002; MacDonald and Coe, 2007), typically as fine particulate or dissolved organic matter (Bilby and Likens, 1980; Naiman, 1982; Wallace et al., 1995; Kiffney et al., 2000). These small streams also can export significant amounts of autochthonous organic matter via the downstream transport of benthic algae (Swanson and Bachmann, 1976). Both allochthonous and autochthonous organic matter can be transported significant distances downstream (Webster et al., 1999), especially during high flows (Bormann and Likens, 1979; Naiman, 1982; Wallace et al., 1995). For example, Wallace et al. (1995) examined coarse particulate organic matter export in three headwater streams in North Carolina and found that 63−77% of export over a 9-year period occurred during the 20 largest floods. This finding suggests that headwater tributaries (including ephemeral and intermittent streams) can provide temporary storage for organic matter (Gomi et al., 2002), which is then transported downstream during storms or snowmelt. Exports also can vary seasonally, increasing in autumn and winter when deciduous trees drop their leaves (Wipfli et al., 2007) and in the spring when flowers and catkins are shed.

The amount of organic matter exported from headwater tributaries can be large, and often depends on factors such as abiotic retention mechanisms within the channel (Bilby and Likens, 1980), biotic communities (Cuffney et al., 1990), and the quality and quantity of riparian vegetation in headwater catchments (Wipfli and Musslewhite, 2004). For example, Wipfli and Gregovich (2002) found that organic matter export ranged from <1 to 286 g of detritus (dead organic matter) per stream per day in 52 small coastal streams in Alaska. When debris dams were removed from a small stream in New Hampshire, export of fine particulate organic carbon increased by 632% (Bilby and Likens, 1980); this finding illustrates the interdependence of physical and biological connections within the river network.

Although organic matter clearly is exported from headwater tributaries, effects on downstream biota, and how far these effects propagate down the river network, are difficult to quantify (Wipfli et al., 2007). Many downstream biota rely on organic matter and its associated microbes for food, but demonstrating where in the river network such material originates presents a challenge. Similarly, the conversion of organic matter to other forms (e.g., invertebrate or fish biomass via consumption), having their own transport dynamics, makes tracking sources of downstream contributions difficult. Given the prevalence of headwater tributaries in both the landscape and the river network (Leopold et al., 1964), and their primacy in organic matter collection and processing, concluding that they exert a strong influence on downstream organic matter dynamics is logical. In addition, headwater tributaries also serve as a source of colonists for downstream habitats. For example, headwater springs might provide algae a winter refuge from freezing, then provide propagules that can recolonize downstream reaches upon spring thaws (Huryn et al., 2005).

4.4.3. Ions

Measurements of ions and conductivity from nested study designs provide evidence for connectivity by various transport mechanisms. Rose (2007) collected data at 52 sampling stations in the Chattahoochee River basin, north-central Georgia, over a 2-year period. The basin included the heavily urbanized Atlanta Metropolitan Region. The study sought to characterize baseflow hydrochemistry across a rural-to-urban land use gradient. A plot of the major ion concentrations (sodium, bicarbonate alkalinity, chloride, and sulfate) versus downstream river distance showed distinct peaks relative to baseflow measurements in the Atlanta Metropolitan Region, with elevated concentrations persisting downstream.

In a study of mined and unmined streams in the Buckhorn Creek basin in Kentucky, water measurements taken at several locations within the same tributary had similar conductivity values (Johnson et al., 2010). As expected, confluences disrupted this spatial similarity along the river network. Conductivity values along the mainstem decreased at confluences with unmined streams and increased at confluences with mined streams, demonstrating that streams were transporting ions downstream and affecting downstream conductivity. This spatial pattern in conductivity was consistent between spring and summer surveys of the stream network.

In a study in Sweden, measurements of pH from the outlets of seven catchments were related to their headwater pH measurements in those catchments (Temnerud et al., 2010). Under low-flow conditions, as pH at outlets increased, so did median pH of the headwater streams.

This study illustrates the connectivity between the headwater components of the stream network and the outlets of the catchments.

4.4.4. Contaminants

The movement of contaminants, or substances that adversely affect organisms when present at sufficient concentrations, provides another line of evidence for chemical connectivity between tributaries and the river network. Existing information typically has been derived from empirical experiments using tracer substances released into streams to monitor movement along a longitudinal gradient. In the case of trace metals, studies also have examined data collected at multiple sites throughout a specific watershed, relative to a point source or a complex mixture of point-source inflows (e.g., active mining areas or wastewater treatment plant discharges). The studies using metals as tracers provide a way to understand sediment transport in streams and rivers and to determine how metals are dispersed spatially and temporally in the watershed (Rowan et al., 1995).

Another example of chemical connections along the river network is how inputs of water associated with natural gas (coalbed methane) extraction and hardrock mining can influence trace element and dissolved solute concentrations in perennial rivers. Patz et al. (2006) examined trace elements and other water quality parameters in ephemeral tributaries resulting from coalbed methane extraction activities connected to the perennial Powder River, WY. Iron, manganese, arsenic, and fluoride and dissolved oxygen, pH, and turbidity differed across sample locations, demonstrating connectivity between wellhead discharge and ephemeral channels. The contribution of ephemeral channels was detected in the Powder River, where pH was consistently elevated downstream of the confluence with a high-pH tributary (Patz et al., 2006).

In a broader study, Wang et al. (2007) investigated spatial patterns in major cation and anion concentrations related to coalbed methane development in the Powder River basin (33,785 km^2) in Wyoming and Montana, using retrospective USGS data (1946−2002). The study indicated that coalbed methane development could have detrimental effects on the Powder River, especially concerning sodium adsorption ratio (sodicity). Although the authors indicated connectivity and adverse affects in stream quality with increased sodium and stream sodicity, data also revealed inconsistent patterns associated with complex spatial variability within the basin (due to the geographic distribution of the coalbed methane wells). In addition, the use of annual medians rather than monthly medians from the entire data set likely smoothed seasonal variation inherent in the data.

The spatial extent of metal transport was shown in a study of the upper Arkansas River in Colorado, where the headwaters have been affected by past mining activities (Kimball et al., 1995). Bed sediments sampled from the headwaters to approximately 250 km downstream showed an inverse relationship between sediment concentrations of cadmium, lead, and zinc and downstream distance. That same spatial distribution pattern in metals in bed sediments from headwaters to downstream was observed for the Clark Fork River in Montana, which has been impacted by mining and smelting activities in its headwaters (Axtmann and Luoma, 1991). Based on regression models, metal concentrations in bed sediments from river sites were inversely related to distance downstream, and predictions from those models indicated that sediments with metals originating from the mining and smelting areas in the headwaters were reaching Lake Pend Oreille, more than 550 km downstream. Hornberger et al. (2009) used a 19–year data set on sediments from the Clark Fork River with sites spanning from the headwaters to 190 km downstream and found that copper concentrations in bed sediments at downstream sites were positively correlated with concentrations at upstream sites.

In two studies examining the downstream transport of heavy metals to perennial systems via ephemeral and intermittent channels, both Lewis and Burraychak (1979) and Lampkin and Sommerfeld (1986) explored the impacts of active and abandoned copper mines in Arizona. In the first study, water chemistry in Pinto Creek was monitored biweekly for 2 years at four stations, one above and three below a point discharge associated with the Pinto Valley Mine in east-central Arizona (Lewis and Burraychak, 1979). Surveys of fish, aquatic macroinvertebrates, and vegetation were conducted during the same period at 13 sampling stations along the total stream length. Contaminants from the Pinto Valley Mine entered Pinto Creek via accidental discharge of tailings pond wastes (Lewis, 1977). Monitoring revealed that mine wastes comprised up to 90% of total flow in Pinto Creek, and that most chemical parameters increased in concentration below the discharge point, then decreased progressively downstream. Increases in sulfate, conductivity, and total hardness between above-mine and below-mine locations were most apparent, although increases in heavy metals and suspended solids were considered most detrimental to biota. Suspended solids settled in and buried intermittent channels, which contained up to 50 cm of mine waste sediment; these sediments were present all the way to the stream terminus. Increased heavy metal concentrations in the food chain and sediments also were detected below the discharge point.

An additional example of intermittent streams contributing highly mineralized, acidic waters to a perennial tributary occurs in a study that characterized acid mine drainage impacts on water and sediment chemistry (particularly major cations, silica, sulfate, selected heavy metals, and acidity) in Lynx Creek, a small intermittent stream in east-central Arizona (Lampkin and Sommerfeld, 1986). Six stations, two above and four below an abandoned copper mine, were monitored (water and sediment samples) monthly for 1 year. Specific conductance, pH, and dissolved ion concentrations varied with proximity to the mining complex. Concentrations of most constituents were higher near the mine and progressively decreased downstream toward the terminus of Lynx Creek due to precipitation and dilution by tributary streams. All heavy metals and sulfate had significantly higher levels at the immediate discharge location versus the above-mine stations; sulfate concentrations downstream of mine-drainage inputs also significantly differed from the rest of the creek. Sediments throughout the creek were high in metals, suggesting downstream transport of contaminated sediments. Acid-mine drainage from the mine had a major but mostly localized impact on Lynx Creek. Evidence of connectivity was apparent, with noticeable increases in dissolved metals, major cations, and sulfate and a three-unit depression in pH.

Studies of the distribution, transport, and storage of radionuclides (e.g., plutonium, thorium, uranium) have provided convincing evidence for distant chemical connectivity in river networks because the natural occurrence of radionuclides is extremely rare. The production, use, and release of radionuclides, however, have been monitored for military and energy production for more than 50 years. Like metals, radionuclides adsorb readily to fine sediment; therefore, the fate and transport of radionuclides in sediment generally mirrors that of fine sediment. From 1942 to 1952, prior to the full understanding of the risks of radionuclides to human health and the environment, plutonium dissolved in acid was discharged untreated into several intermittent headwater streams that flow into the Rio Grande at the Los Alamos National Laboratory, NM (Graf, 1994; Reneau et al., 2004). These intermittent headwaters drain into Los Alamos Canyon, which has a 152 km^2 drainage area and joins the Rio Grande approximately 160 km upriver from Albuquerque. Also during this time, nuclear weapons testing occurred west of the upper Rio Grande near Socorro, NM (Trinity blast site) and in Nevada. The San Juan Mountains in the northwestern portion of the upper Rio Grande basin (farther upstream from the site where Los Alamos Canyon enters the Rio Grande) are the first mountain range greater than 300 m in elevation east of these test locations. The mountains therefore have higher plutonium concentrations than the latitudinal and global averages because of their geographic proximity to the test sites. The mountain areas are steep with thin soils, so erosion and subsequent overland movement of plutonium from the testing fallout readily transported it to headwater streams in the upper Rio Grande basin. The distribution of plutonium within the Rio Grande illustrates how headwater streams transport and store contaminated sediment that has entered the basin through fallout and from direct discharge. Los Alamos Canyon, while only representing 0.4% of the drainage area at its confluence with the Rio Grande, had a mean annual bedload contribution of plutonium almost seven times that of the mainstem (Graf, 1994). Much of the bedload contribution occurred sporadically during intense storms that were out of phase with flooding on the upper Rio Grande. Total estimated contributions of plutonium between the two sources to the Rio Grande are approximately 90% from fallout to the landscape and 10% from direct effluent at Los Alamos National Laboratory (Graf, 1994). Based on plutonium budget calculations, only about 10% of the plutonium directly discharged into Los Alamos Canyon and less than 2% of the fallout over the upper Rio Grande basin have been exported to the Rio Grande. Much of the plutonium is adsorbed to sediment and soil that has either not yet been transported to the river network or is stored on floodplains or in tributary channels (Graf, 1994). Approximately 50% of the plutonium that entered the Rio Grande from 1948−1985 is stored in the river and its floodplain; the remaining amount is stored in a downriver reservoir.

4.5. BIOLOGICAL CONNECTIONS

Biological connections are linkages between headwater streams, including those with intermittent and ephemeral flow, and their downstream waters that are mediated by living organisms or organism parts. In this section, we examine biological connections in terms of the materials (invertebrates, fishes, and genes) that move along river networks, and their effects on downstream waters (for discussion of particulate organic matter dynamics, see Section 4.4.2).

Because biological connectivity often results from passive transport of organisms or organism parts with water flow, these connections often depend on hydrologic connectivity (see Section 4.3.1). Many living organisms, however, can also actively move with or against water flow; others disperse actively or passively over land by walking, flying, drifting, or "hitchhiking." All of these organism-mediated connections form the basis of biological connectivity between headwater tributaries and downstream waters.

Biological connectivity between upstream and downstream reaches can affect downstream waters via multiple pathways or functions. For example, headwater tributaries provide food resources to downstream waters. As Progar and Moldenke (2002) state, "…headwater streams are the vertex for a network of trophic arteries flowing from the forest upland to the ocean." For downstream organisms capable of significant upstream movement, headwater tributaries can increase both the amount and quality of habitat available to those organisms. Under adverse conditions, small streams provide refuge habitat, allowing organisms to persist and recolonize downstream areas once adverse conditions have abated (Meyer and Wallace, 2001; Meyer et al., 2004; Huryn et al., 2005).

4.5.1. Invertebrates

Headwater streams provide habitat for diverse and abundant stream invertebrates (Meyer et al., 2007) and serve as collection areas for terrestrial and riparian invertebrates that fall into them (Edwards and Huryn, 1995; Kawaguchi and Nakano, 2001). These aquatic and terrestrial invertebrates can be transported downstream with water flow and ultimately serve as food resources for downstream biota. Many fish feed on drifting insects (Nakano and Murakami, 2001; Wipfli and Gregovich, 2002), and these organisms can also settle out of the water column and become part of the local invertebrate assemblage in downstream waters. However, drift has been shown to significantly increase invertebrate mortality (Wilzbach and Cummins, 1989), suggesting that most drifting organisms are exported downstream in the suspended detrital load (see Section 4.3.2).

The downstream drift of stream invertebrates (Müller, 1982; Brittain and Eikeland, 1988) and the contribution of terrestrial and riparian invertebrates to overall drift (Edwards and Huryn, 1995; Kawaguchi and Nakano, 2001; Eberle and Stanford, 2010) have been well documented. For example, drift estimates in 52 small coastal streams in Alaska ranged from 5 to 6,000 individuals per stream per day (Wipfli and Gregovich, 2002). The amount of invertebrate drift often is closely related to stream discharge (e.g., Harvey et al., 2006) and diel invertebrate behavioral patterns that are independent of flow (Rader, 1997). To compensate for loss of individuals to downstream drift, invertebrate populations in headwater streams are maintained and replenished by a combination of high productivity and upstream dispersal (Hershey et al., 1993; Humphries and Ruxton, 2002).

As with organic matter, assessing the effect of headwater invertebrate production and export on downstream waters is difficult. Wipfli and Gregovich (2002) estimated that drifting insects and detritus (i.e., particulate organic matter; see Section 4.4.2) from fishless headwater tributaries in Alaska supported between 100 and 2,000 young-of-year salmonids per km in a large, salmon-bearing stream. This estimate of headwater importance in systems where juvenile salmonids move into headwater tributaries to feed and grow is likely conservative (see Section 4.5.2). Other studies have shown increased fish growth with increased invertebrate drift (Wilzbach et al., 1986; Nielsen, 1992; Rosenfeld and Raeburn, 2009), indicating that drift does provide a valuable food resource, especially when food is limiting (Boss and Richardson, 2002).

Small streams also serve as habitat for invertebrates. Many invertebrate species are well adapted to seasonal or episodic periods of drying (Feminella, 1996; Williams, 1996; Bogan and Lytle, 2007) or freezing temperatures (Danks, 2007) and can be found throughout a range of stream sizes (e.g., Hall et al., 2001b) and flow regimes (intermittent and perennial, e.g., Feminella, 1996). After disturbance, these habitats can provide colonists to downstream reaches; this phenomenon can be especially important in intermittent streams, where permanent upstream pools can serve as refuges during drying. For example, Fritz and Dodds (2002, 2004) examined invertebrate assemblages before and after drying in intermittent prairie streams and found that initial recovery of invertebrate richness, richness of invertebrate drift, and richness of aerially colonizing insects were negatively related to distance from upstream perennial water. Intermittent streams can also provide refuge from adverse biotic conditions. For example, Meyer et al. (2004) found that native amphipods can persist in intermittent reaches but are replaced by nonnative amphipods in perennial reaches.

4.5.2. Fishes

Although some fish species maintain resident headwater populations, many species move into and out of headwater streams at some point in their life cycles (Ebersole et al., 2006; Meyer et al., 2007). Some fish species occur only in small streams, which contribute to regional aquatic biodiversity (e.g., Paller, 1994). However, as with invertebrates, certain fish species can be found throughout a range of stream sizes (Freeman et al., 2007) and flow durations (Schlosser, 1987; Labbe and Fausch, 2000), and the fish species found in headwater streams often are a subset of species found in downstream habitats (Horwitz, 1978). Use of headwater streams as habitat is especially obvious for the many diadromous species that migrate between small streams and marine environments during their life cycles (e.g., Pacific and Atlantic salmon, American eels, certain lamprey species), and the presence of these species within river networks provides robust evidence of biological connections between headwaters and larger rivers. Return migration of diadromous fishes provides a feedback loop in which marine-derived nutrients are transported upstream to headwaters, for subsequent processing and export (see Section 4.4.1). Even nonmigratory taxa, however, can travel substantial distances within the river networks (Gorman, 1986; Sheldon, 1988; Hitt and Angermeier, 2008).

Hydrologic connectivity must exist for the exchange of fish between upstream and downstream reaches. Fish assemblages tend to be more similar among connected streams, in that assemblages in reaches located more closely together tend to have more species in common than in distantly separated reaches (Matthews and Robinson, 1998; Hitt et al., 2003; Grenouillet et al., 2004). Measures of river network structure also can explain fish assemblage structure, with studies showing that metrics such as link magnitude (the sum of all first-order streams draining into a given stream segment) and confluence link (the number of confluences downstream of a given stream segment) are significant predictors (e.g., Osborne and Wiley, 1992; Smith and Kraft, 2005).

For certain taxa, headwater tributaries provide habitat for a specific part of their life cycle. Many salmonids spawn in small streams, including those with intermittent flow (Erman and Hawthorne, 1976; Schrank and Rahel, 2004; Ebersole et al., 2006; Wigington et al., 2006; Colvin et al., 2009); many nonsalmonids also move into these habitats to spawn (Meyer et al., 2007). After spawning, these fish sometimes return downstream for feeding and overwintering. For example, Bonneville cutthroat trout moved from less than 1 km to more than 80 km downstream postspawning, typically within 30 days (Schrank and Rahel, 2004).

Many salmonids also grow in headwater streams (Brown and Hartman, 1988; Curry et al., 1997; Bramblett et al., 2002). In some cases, these headwaters (including intermittent streams) can provide higher quality habitat for juvenile fish, as evidenced by increased growth, size, and overwinter survival in these habitats (Ebersole et al., 2006; Wigington et al., 2006; Ebersole et al., 2009), perhaps due to warmer temperatures and higher prey and lower predator densities (Limm and Marchetti, 2009).

In prairie streams (see Section 4.7), the importance of hydrologic connectivity is especially evident, as many fishes broadcast spawn, or release eggs into the water column, which then develop as they are transported downstream (Cross and Moss, 1987; Fausch and Bestgen, 1997); adult fish then migrate upstream prior to egg release (Fausch and Bestgen, 1997). Thus, these fishes require hydrologic connectivity for egg development and upstream migration of adult fish, to maintain populations (Fausch and Bestgen, 1997).

When abiotic or biotic conditions farther downstream in the river network are adverse, upstream reaches can provide refuge habitat for downstream fishes. Examples of adverse abiotic conditions include temperature (Curry et al., 1997; Cairns et al., 2005) or flow (Pires et al., 1999; Wigington et al., 2006) extremes, low dissolved oxygen concentrations (Bradford et al., 2001), and high sediment levels (Scrivener et al., 1994). Examples of adverse biotic conditions include the presence of predators, parasites, and competitors (Fraser et al., 1995; Cairns et al., 2005; Woodford and McIntosh, 2010).

Because headwater tributaries often depend on groundwater inputs, temperatures in these systems tend to be warmer in winter (when groundwater is warmer than ambient temperatures) and colder in summer (when groundwater is colder than ambient temperatures), relative to reaches farther downstream (see Section 4.3.4; Power et al., 1999). Thus, these headwaters can provide organisms with both warmwater and coldwater refuges at different times of the year (Curry et al., 1997; Baxter and Hauer, 2000; Labbe and Fausch, 2000; Bradford et al., 2001). In some cases, loss of coolwater refuges can facilitate invasion by species more tolerant of warmwater conditions (Karr et al., 1985).

Headwater tributaries also can provide refuge from flow extremes. Fish can move into headwaters (including intermittent streams) to avoid high flows downstream (Wigington et al., 2006); fish also can move downstream during peak flows (Sedell et al., 1990), demonstrating the bidirectionality of biological connections within these systems. Low flows can cause adverse conditions for biota, as well, and residual pools, often fed by hyporheic flow, can enable organisms to survive dry periods within intermittent streams (Pires et al., 1999; May and Lee, 2004; Wigington et al., 2006).

Biotic conditions within the river network—the taxa found in the system—also can create an adverse environment, as the presence of invasive species or other predators and competitors can negatively affect native taxa. In some cases, headwater tributaries can provide these taxa refuge from other species and allow populations to persist. For example, Fraser et al. (1995) found that prey fish moved downstream when piscivores (fish-eating fish) were excluded, but moved upstream into headwaters when they were present. The role of headwaters as refuges from adverse biotic conditions can be closely related to where along the connectivity-isolation continuum these habitats fall, with isolation allowing for persistence of native populations (Letcher et al., 2007). Physical barriers (which reduce connectivity and increase isolation) have been used to protect headwater systems from invasion (Middleton and Liittschwager, 1994; Freeman et al., 2007); similarly, most genetically pure cutthroat trout populations are confined to small, high-elevation streams that are naturally or anthropogenically isolated (Cook et al., 2010).

When adverse conditions have abated and these organisms move back down the river network, they can serve as colonists of downstream reaches (Meyer and Wallace, 2001). Hanfling and Weetman (2006) examined the genetic structure of river sculpin and found that upstream populations were emigration biased (i.e., predominant movements were out of these reaches), whereas downstream populations were immigration biased (i.e., predominant movements were into these reaches).

4.5.3. Genes

Genetic connectivity results from biotic dispersal and subsequent reproduction and gene flow, or the transfer of genetic material within and among spatially subdivided populations. Populations connected by gene flow have a larger breeding population size, making them less prone to inbreeding and more likely to retain genetic diversity or variation—a basic requirement for adaptation to environmental change (Lande and Shannon, 1996). Genetic connectivity exists at multiple spatial and temporal scales. It can extend beyond a single river catchment (Hughes et al., 2009; Anderson et al., 2010), and in diapausing organisms, can be a direct link between distant generations (dispersal through time; Bohonak and Jenkins, 2003).

Although physical barriers can protect headwater habitats and populations by isolating them from colonization and hybridization with invasive species (see Section 4.5.2), isolation also can have serious adverse effects on native species via reductions in genetic connectivity. For example, Hanfling and Weetman (2006) found that man-made weirs intensified natural patterns of limited headwater immigration, such that headwater (above-barrier) sculpin populations diverged genetically from downstream (below-barrier) populations and lost significant amounts of genetic diversity. This pattern of strong genetic divergence accompanied by loss of headwater genetic diversity above natural and man-made barriers has been documented in multiple fish species and regions (Yamamoto et al., 2004; Wofford et al., 2005; Deiner et al., 2007; Guy et al., 2008; Gomez-Uchida et al., 2009; Whiteley et al., 2010). Loss of headwater-river genetic connectivity might be exerting selection pressure against migrant forms in fish with life cycles requiring movement along the entire river corridor (Morita and Yamamoto, 2002). Ultimately, tradeoffs exist between the risks associated with headwater-river genetic connectivity (e.g., hybridization with nonnative species and hatchery fish) and those associated with genetic isolation (e.g., reduced reproductive fitness, increased risk of local extinction, deterioration of overall genetic variation, and selection against migratory traits; Fausch et al., 2009).

In general, genetic connectivity decreases with increasing spatial distance (Wright, 1943). Genetic connectivity in river networks is also strongly influenced by the hierarchical structure of a river network (see Section 3.4.2), the direction of dispersal (upstream, downstream, or both), dispersal modes and pathways used (e.g., swimming, flying), and species life history (Hudy et al., 2010).

Computer simulation approaches examine the spatial and temporal processes of genetic connectivity for realistic behaviors and life histories of species inhabiting complex, dynamic landscapes and riverscapes (Epperson et al., 2010). For example, Morrissey and de Kerckhove (2009) demonstrated that downstream-biased dispersal in dendritic river networks (which by definition have more tributaries than mainstems) can promote higher levels of genetic diversity than other geographical habitat structures. Under these conditions, low-dispersing headwater stream populations can act as reservoirs of unique genetic alleles (units of genetic variation) that occasionally flow into and mix with highly dispersing downstream populations. Although the number of headwater streams (i.e., potentially unique genetic reservoirs) is important in maintaining genetic diversity, networks with more complex hierarchical structures (see Figure 4-4) are more efficient at maintaining genetic diversity than networks in which all tributaries flow directly into the mainstem (Morrissey and de Kerckhove, 2009). In another simulation, Chaput-Bardy et al. (2009) demonstrated that out-of-network gene flow (e.g., terrestrial dispersal by insects or amphibians) or very high levels of within-network gene flow (e.g., fish that move and reproduce throughout the network) can counteract the effects of network structure; thus, individual species behavior can profoundly affect observed genetic patterns.

Most empirical evidence for the role of headwaters in maintaining genetic connectivity and diversity comes from studies of economically important fish species, but correlations of river network structure or landscape alteration with genetic patterns have been reported for other species. Consistent with the model of Morrissey and de Kerckhove (2009), Fer and Hroudova (2008) found higher genetic diversity in downstream populations of yellow pond-lily (*Nuphar lutea*), which disperses over long distances via water-mediated dispersal of detached rhizomes. Frequent dispersal and high gene flow among headwater and downstream populations of the giant Idaho salamander (*Dicamptodon aterrimus*; Mullen et al., 2010) are expected to contribute to genetic diversity of upstream and downstream populations.

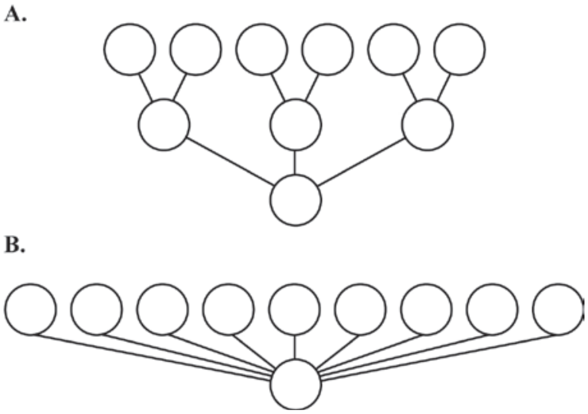

Figure 4-4. (A) A dendritic network with multilevel hierarchical structure, and (B) a uninodal network with all headwater streams feeding directly into a river mainstem.

Modified from Morrissey and de Kerckhove (2009).

Headwater populations contribute to the maintenance of genetic diversity even in animals capable of overland dispersal. In a field study of the common stream mayfly *Ephemerella invaria*, which emerges into streamside forests to mate and disperse, Alexander et al. (2011) found that regional genetic diversity is strongly correlated with tree cover in first-order (headwater) stream catchments. Observed loss of genetic diversity in this species could be related to degradation of stream habitats, degradation of out-of-network dispersal pathways, or both (Chaput-Bardy et al., 2009; Grant et al., 2010; Alexander et al., 2011).

In summary, genetic connectivity in river systems reflects the breeding potential of a metapopulation. The maintenance of genetic diversity is directly related to genetic connectivity, and thus is critical to a species' regional persistence. Genetic connectivity is influenced by the landscape, riverscape, and biology of the organisms involved; spatially subdivided stream and river populations can maintain genetic diversity, provided they remain connected by at least low levels of gene flow (Waples, 2010).

4.6. STREAMS: SYNTHESIS AND IMPLICATIONS

A substantial body of evidence unequivocally demonstrates connectivity between streams and downstream rivers via both structural and functional connectivity (as defined in Wainwright et al., 2011). Streams are structurally connected to rivers through the network of continuous channels (beds and banks) that make these systems physically contiguous, and the very existence of a continuous bed and bank structure provides strong geomorphologic evidence for connectivity (see Section 3.2.1). A stream must be linked to a larger, downstream water body by a channel in order for the two to have surface water (hydrological) connection. While there are streams that lack a channel connection to larger water bodies (i.e., small endorheic basins), these are the exception. Streams that link larger water bodies through networks of continuous bed and bank are the rule. Streams are functionally connected to rivers by the movement of water and other materials through this network of channels. Even losing-stream reaches that at times lack sufficient flow for hydrological connection can still influence downstream waters by functioning as sinks for water and materials carried by water. The river network and its flow of materials represent the integration of its streams' cumulative contributions to downstream waters.

Existing evidence indicates that headwater streams (including intermittent and ephemeral streams) transform, store, and export significant amounts of material (water, organic matter, organisms, etc.) to downstream waters. The most compelling evidence linking headwater streams to downstream habitats supports source, sink (or lag), and transformation functions (see Section 3.3.1, Table 3-1). For example, studies that involved sampling throughout river networks have documented headwater streams as sources of water (via floods and baseflow) to rivers (see Section 4.3.1). Nitrogen and carbon transported from headwaters contribute substantially to nitrogen and carbon levels in downstream rivers, and headwater streams can function as nitrogen and carbon sinks for river networks (see Sections 4.4.1 and 4.4.2). Studies documenting the fate and transport of contaminants through headwater streams to downstream waters also represent clear lines of evidence for headwater streams as sources and sinks (see Section 4.4.4). Many organisms, such as anadromous salmon, have complex life cycles that involve migration through the river network, from headwaters to downstream rivers and oceans, over the course of their lives (see Section 4.5). In fact, the importance of headwater streams (including intermittent and ephemeral streams) in the life cycles of many organisms capable of moving throughout river networks provides strong evidence for connectivity among these systems.

Most of the evidence relevant to issues of connectivity between headwater streams and large rivers is based on data collected either in the upper (i.e., from headwater streams to intermediate tributaries) or lower (i.e., from large tributaries to mainstem rivers) portions of the river network. Although few studies have explicitly examined the movement of materials along entire river networks, the exchange of materials among adjacent stream reaches—which numerous studies have documented, for a variety of materials—can be extended over large spatial scales.

Table 4-1. Examples of functions by which streams influence downstream waters. See relevant section numbers in parentheses for greater detail. Note that there is not always a clear distinction between types of functions. For example, denitrification could be considered a sink or transformation function

Source Function
• Streams supply water downstream through baseflow and floods that influence discharge and habitat (4.3.1, 4.7.2.5, 4.7.3.1.1, 4.8.4.2, 4.8.5.1).
• Streams supply downstream waters with sediment (4.3.2, 4.4.4, 4.7.3.1.3, 4.8.4.2).
• Streams supply downstream waters with nutrients and other ions (4.4.1, 4.4.3, 4.7.4.2.1, 4.8.4.2).
• Streams can transport to downstream waters contaminants that adversely affect organisms (4.4.4, 4.7.3.1.3).
• Streams supply dissolved and particulate organic matter that can fuel heterotrophy in downstream waters and influence physicochemical conditions (4.3.3, 4.4.2, 4.7.3.2.2, 4.8.4.2).
• Organisms actively and passively move from streams to downstream waters (4.5, 4.7.2.4, 4.7.3.3).
Sink Function
• Streams can divert surface flow from downstream waters via infiltration into underlying alluvium and evapotranspiration to the atmosphere (4.3.1, 4.8.3, 4.8.4.2, 4.8.5.1).
• Streams can divert nitrate from downstream waters via denitrification (4.4.1, 4.7.3.2.1)
• Streams can divert sediment and associated contaminants from being transported to downstream waters through deposition on floodplains (4.3.2, 4.4.4).
Refuge Function
• Streams can offer protection from temperature extremes, drying, predators, and competition with nonnative species for organisms that inhabit downstream waters (4.5, 4.7.3.3).
Transformation Function
• Streams mediate the form of nutrients before entering downstream waters via nutrient spiraling (4.4.1, 4.7.3.2.1)
• Streams mediate the form of organic matter before entering downstream waters via carbon spiraling (4.4.2, 4.7.3.2.2)

Table 4-1. Examples of functions by which streams influence downstream waters. See relevant section numbers in parentheses for greater detail. Note that there is not always a clear distinction between types of functions. For example, denitrification could be considered a sink or transformation function (continued)

Lag Function
• Streams can delay water from arriving at downstream waters through local and network structures, thus reducing flood magnitudes, but increasing baseflows in downstream waters (4.3.1, 4.3.3, 4.7.3.1.1, 4.8.3, 4.8.4.2).
• Streams can delay sediment from arriving at downstream waters through local and network structures (4.3.3, 4.3.2, 4.4.4).
• Streams can delay nutrients from arriving at downstream waters through local and network structures and biological uptake (4.4.1, 4.7.2.4, 4.7.3.2.1).
• Streams can delay organic matter from arriving at downstream waters through local and network structures and biological uptake (4.3.3, 4.4.2, 4.7.3.2.2).

4.7. CASE STUDY: PRAIRIE STREAMS

4.7.1. Abstract

Prairie streams drain temperate grasslands in the central United States. Their hydrology is characterized by periods of flooding and drying, with spring-fed, perennial pools and reaches embedded within more intermittently flowing reaches; thus, water flow along prairie stream networks exhibits high temporal and spatial variability. Existing evidence indicates that small prairie streams are connected to downstream reaches, most notably via flood propagation and the extensive transport and movement of fish species throughout these networks. Nutrient retention in small prairie streams also significantly influences nutrient loading in downstream rivers.

4.7.2. Introduction

4.7.2.1. *Geography and Climate*

Prairies are temperate grasslands located in the Great Plains physiographic region of the central United States and Canada (see Figure 4-5). Grasses and forbs (broad-leaf plants other than grasses) dominate the region, particularly in upland areas. Shrubs and trees can be found in lowlands, and are commonly called gallery forests. Native prairie ecosystems once covered approximately 1.62 million km^2 in North America but have been almost completely lost since European settlement, mainly replaced by row-crop agriculture (Samson and Knopf, 1994). Because of drastic alterations to much of the historical eastern plains (Iowa, Illinois, Missouri, Indiana, and Minnesota), our discussion centers principally on river networks in the high plains subregion of the Great Plains (see Subregion 2 in Figure 4-5), where drier climate and thin, rocky soil have limited row-crop agriculture.

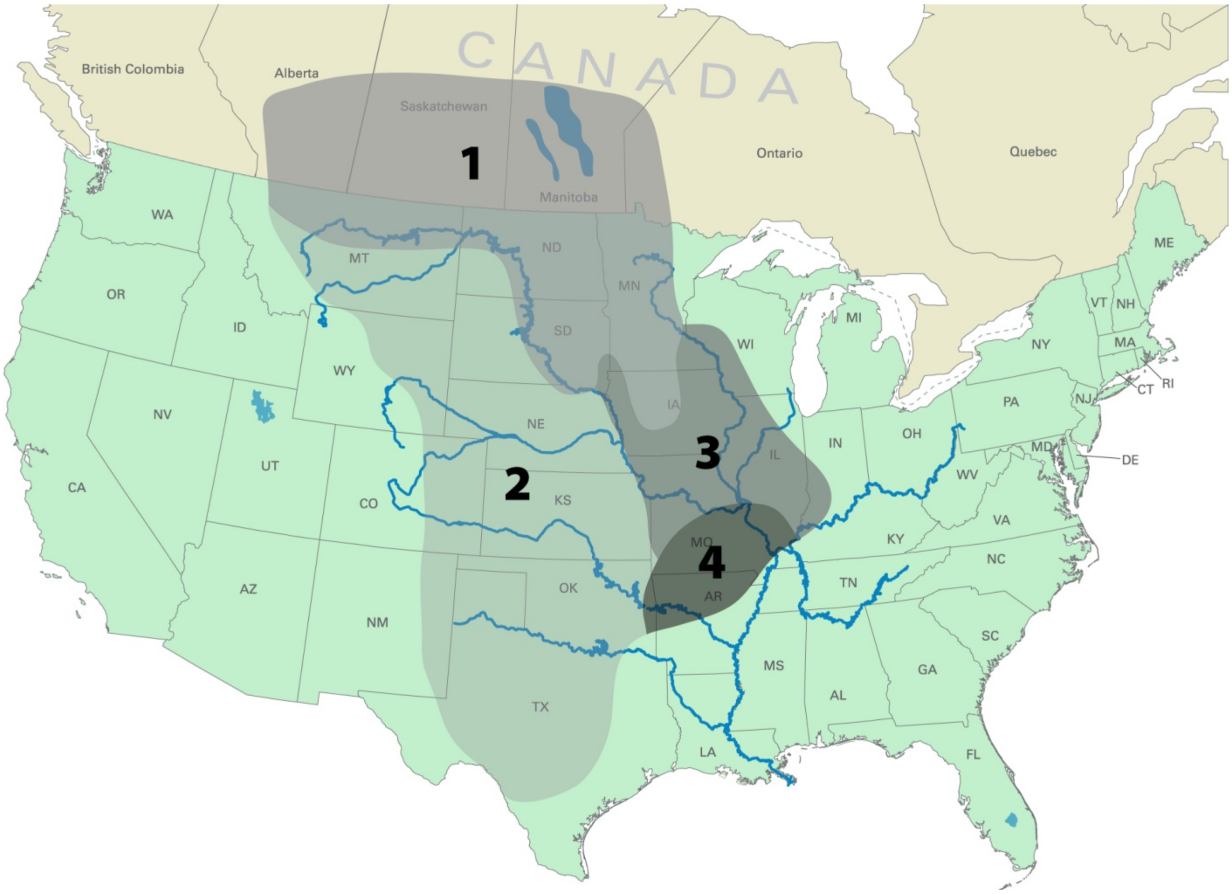

Figure 4-5. Map of the United States showing physiographic subregions and major rivers of the Great Plains. (1) Glaciated prairie; (2) high plains; (3) eastern plains; and (4) Ozark Plateau.

Modified from Covich et al. (1997).

Prairies generally can be characterized by their relatively low topographic relief, although areas such as the Flint Hills in eastern Kansas, the Arikaree Breaks in northwestern Kansas, and the Arbuckle Mountains in south-central Oklahoma have relatively steep terrain compared to that of western Kansas or the Oklahoma panhandle (Osterkamp and Costa, 1987; Matthews, 1988). The underlying geology consists of extensive limestone deposits, but other areas are characterized by sandstone and shale deposits or unconsolidated sands, silts, and clays (Brown and Matthews, 1995). Soils in the Great Plains are predominately loess, but some areas such as

Nebraska's Sand Hills have high percentages of sand (Wolock et al., 2004). Although prairie soils tend to be less permeable than more humic forest soils, fractures and macropores of the limestone geology in some prairie areas, such as the Flint Hills, allow for relatively rapid percolation and recharge of local groundwater (Macpherson and Sophocleous, 2004).

Most of the large rivers draining the high plains subregion (e.g., the Missouri, Yellowstone, Milk, Cheyenne, White, Niobrara, Platte, Kansas-Republican, Arkansas, Cimarron, Canadian, Red, and Washita Rivers) are major tributaries to the Mississippi River. The southern portions of the subregion contain the headwaters of the Rio Grande River (Pecos River) or rivers that flow directly into the Gulf of Mexico (the Guadalupe, San Antonio, Colorado of Texas, Brazos, and Nueces Rivers). Some rivers in the northern portions of the glaciated prairie flow north, eventually into the Hudson Bay (notably the Red River of the North).

The climate in this region ranges from semiarid in the western portions to moist subhumid in the eastern portions. Mean annual precipitation ranges from 200 to 1,000 mm y^{-1} from west to east across the Great Plains (Lauenroth et al., 1999). Potential evaporation typically exceeds precipitation (Transeau, 1905, 1935). Mean annual temperatures increase from north (4−8°C) to south (16–20°C; Lauenroth et al., 1999). Winters tend to be dry, with less than 20% of the annual precipitation (Borchert, 1950; Lauenroth et al., 1999; Boughton et al., 2010). Most precipitation falls in late spring and early summer (Borchert, 1950; Lauenroth et al., 1999), and much of the summer precipitation results from localized convective thunderstorms. Because of the region's geographic location relative to the Gulf of Mexico and the Rocky Mountains, however, substantial interannual variation exists, particularly in terms of summer rainfall deficit (Borchert, 1950).

4.7.2.2. *Hydrology and Geomorphology*

The hydrology of most prairie river networks is highly variable (Matthews, 1988; Brown and Matthews, 1995; Dodds et al., 2004). These systems are frequently subjected to the extremes of drying and flooding, and intermittent or flashy hydrology is prevalent in river networks throughout most of the Great Plains (Matthews, 1988; Zale et al., 1989; Poff, 1996; Dodds et al., 2004). The topology of most prairie river networks is dendritic due to the relatively flat landscape and uniform geology (Brown and Matthews, 1995). Prairie river networks tend to have high drainage density (see Section 3.4.2), and are therefore efficient at transferring rainfall from uplands to downstream reaches (Gregory, 1976; Osterkamp and Friedman, 2000). Flood magnitudes tend to be higher in the semiarid Great Plains than in other regions, despite comparable rainfall intensities, due to low infiltration and vegetation interception (Osterkamp and Friedman, 2000). Although floods tend to occur in late fall through late spring, they can occur any time during the year (Brown and Matthews, 1995; Poff, 1996). Like most river networks, those draining prairie landscapes often contain ephemeral, intermittent, and perennial streams. Although many headwater prairie streams are ephemeral or intermittent (Matthews, 1988; Brown and Matthews, 1995; Dodds et al., 2004), some have perennial spring-fed reaches located at the network origins or distributed between intermittent reaches along headwater streams (Matthews et al., 1985; Sawin et al., 1999; Dodds et al., 2004; Bergey et al., 2008).

The flow regimes of streams draining the Rocky Mountains, Black Hills, and northern prairies are largely tied to snowmelt. Most systems originating in the mountains quickly transition in flow and morphology as they cross the Great Plains, becoming intermittent and then slowly gaining flow from large streams before joining the Mississippi River (Brown and Matthews, 1995). Some areas, however, have stable streamflow with few intermittent streams because flow is derived from large, permeable groundwater sources (e.g., Sand Hills in Nebraska; Winter, 2007).

The High Plains (Ogallala) aquifer system and other aquifers (e.g., Edwards-Trinity) are important hydrologic features interconnected with Great Plains river networks. The High Plains aquifer system is the largest (450,658 km^2) and most intensively pumped U.S. aquifer, underlying much of the Great Plains from southern South Dakota and southeastern Wyoming to central Texas (Sophocleous, 2005; Ashworth, 2006; Sophocleous, 2010). The High Plains aquifer is composed of blanket sand and gravel derived mainly from alluvial deposits and ancient marine sands. It is unconfined regionally, but locally can be confined where beds of silt, clay, or marl are present. Regional movement of water through the aquifer is from west to east, but locally the water moves toward major tributaries. Northern areas of the Great Plain are underlain by glacial deposit aquifers that can be a mixture of till (unsorted material ranging from clay to boulders) and outwash (stratified sand and gravel) that was deposited by glacial meltwater.

Most headwater streams originating in the prairie have riffle-pool morphology with alluvial gravel; only headwater streams originating in the western mountains have high gradient, cobble-boulder channels (Brown and Matthews, 1995). Southern prairie headwater streams tend to have finer substrate than those in the northern and central Great Plains (Brown and Matthews, 1995). Larger streams tend to have broad sand beds that are frequently braided (but see Section 4.7.2.5). In contrast to headwater streams in forested regions, the riparian areas of prairie headwater streams typically lack overhanging trees. Grasses and shrubs are the dominant riparian vegetation, so channels lack woody debris and are generally well lit. Because of intense flooding, prairie streams tend to form wide, deep channels relative to their drainage areas, regardless of flow permanence (Hedman and Osterkamp, 1982; Brown and Matthews, 1995). Because of similarity in topography, climate, geology, and soils, stream geomorphology across the Great Plains is largely comparable (Miller and Onesti, 1988). High plains channels, however, tend to be slightly steeper in gradient and more sinuous than wider and deeper channels of the eastern plains (Miller and Onesti, 1988). During floods, the relatively incised channels and lack of woody debris in prairie headwater streams make them less retentive of organic matter and other materials than those of high-gradient forested channels; their pool-riffle morphology, high sinuosity, and seasonal drying, however, can enhance retention (Brown and Matthews, 1995).

4.7.2.3. *Physicochemistry*

The factors discussed above are strong drivers of prairie stream physicochemistry (Matthews, 1988; Brown and Matthews, 1995). Hot summers and cold winters in this region cause substantial direct and indirect changes in water temperature, dissolved oxygen, and nutrient concentrations. Isolation of surface water into pools during summer drying exacerbates these changes (Zale et al., 1989; Ostrand and Marks, 2000; Ostrand and Wilde, 2004). For example, water surfaces can be covered with ice in winter, whereas summer water temperatures can reach 35−40°C with 9−10°C diel (i.e., daily) fluctuations (Matthews, 1988; Matthews and Zimmerman, 1990). Concomitant fluctuations in dissolved oxygen occur, which when combined with stream respiration, contribute to dissolved oxygen values approaching anoxic conditions.

Prairie rivers and streams naturally have higher concentrations of dissolved solids (e.g., calcium (Ca), carbonate, bicarbonate, sodium (Na), chloride, magnesium, sulfate) due to dissolution of the underlying geologic layers (Huntzinger, 1995). Associated with these high levels of dissolved ions are elevated alkalinity and pH. Mean total dissolved solids concentrations for many Great Plains rivers are among the highest in the United States, exceeding 500 mg L^{-1}; many Great Plains rivers, however, also receive anthropogenic total dissolved solid inputs from wastewater treatment effluents, agricultural runoff, irrigation contributions to baseflow, and disposal of produced water associated with fossil fuel production (Mathis and Dorris, 1968; Huntzinger, 1995; Farag et al., 2010). Some river networks, such as the headwaters of the Red River in Texas and Oklahoma, are saline because they derive from brine springs (Taylor et al., 1993).

Streams and rivers of the central United States are often cited as having elevated nutrient (i.e., nitrogen and phosphorus) loads. These loads are primarily attributable to nonpoint source runoff from fertilizer application and livestock waste, especially during higher flows in winter and spring (e.g., Huntzinger, 1995; Royer et al., 2006; Alexander et al., 2008). Data from streams draining native prairie indicate that nitrogen and phosphorus concentrations and fluxes are lower or comparable to other intact ecosystems (McArthur et al., 1985a; Dodds et al., 1996a; Kemp and Dodds, 2001).

4.7.2.4. *Ecology*

The low diversity of aquatic flora and fauna of prairie river networks, especially compared to assemblages in the eastern and southeastern United States (Jewell, 1927; Fausch and Bestgen, 1997), is likely due to the environmental instability of these river networks, their evolutionary history, and the magnitude and extent of human alterations. Most organisms have adapted to erratic hydrologic regimes and harsh physiochemical conditions in prairie streams by having rapid growth, high dispersal ability, resistant life stages, fractional or extended reproduction (i.e., spawn multiple times during a reproductive season), broad physiological tolerances, and life cycles timed to avoid predictably harsh periods (Matthews, 1988; Dodds et al., 1996b; Fausch and Bestgen, 1997).

Algae are foundational components of prairie streams, acting to retain nutrients and provide an important energy source to consumers (Gelwick and Matthews, 1997; Dodds et al., 2000; Evans-White et al., 2001; Evans-White et al., 2003). Flooding and drying in prairie streams reset algal assemblages, spur successional sequences, and maintain high levels of primary production (Power and Stewart, 1987; Dodds et al., 1996b; Murdock et al., 2010). Algal assemblages are composed primarily of diatoms (e.g., *Cymbella*, *Cocconeis*, *Pinnularia*, *Achnanthes*, *Navicula*, and *Gomphonema*), filamentous green algae (e.g., *Cladophora*, *Spirogyra*, *Rhizoclonium*, *Stigeoclonium*, *Zygnema*, and *Oedogonium*), and cyanobacteria (e.g., *Oscillatoria*, *Nostoc*).

Because of high light availability, algal primary production in prairie streams can at times be substantially higher than in forested headwaters (Hill and Gardner, 1987a; Dodds et al., 1996b; Mulholland et al., 2001; Bernot et al., 2010). Gallery forests farther downstream provide shade and contribute organic matter. Shade from the gallery forests lowers light transmission to algae, resulting in lower algal primary production in these reaches than in unshaded prairie headwater reaches. Thus, in contrast to conventional longitudinal paradigms like the River Continuum Concept, the organic matter driving prairie headwater streams is derived mainly from within the channel (autochthonous production), whereas leaf litter and other detritus from adjacent gallery forests (allochthonous production) dominate in intermediate-sized streams (Gurtz et al., 1982; Gurtz et al., 1988; Wiley et al., 1990). Despite having greater primary production than forested headwaters, prairie streams, like forested ones, tend to also be net heterotrophic systems (Mulholland et al., 2001), but those influenced by agricultural activities (e.g., elevated nutrients, channelization) may at times be net autotrophic (Prophet and Ransom, 1974; Gelroth and Marzolf, 1978; Wiley et al., 1990).

Invertebrates in prairie streams are represented by various aquatic insect groups (e.g., Diptera, Coleoptera, Plecoptera, Ephemeroptera, Trichoptera), crustaceans (crayfish, isopods, amphipods), mollusks, and oligochaetes. Consumers of fine benthic organic matter, epilithic algae, and other invertebrates tend to dominate invertebrate communities (Gray and Johnson, 1988; Harris et al., 1999; Stagliano and Whiles, 2002). Diversity and abundance of invertebrates tend to increase with flow permanence, but there is generally high overlap in species composition, with intermittent stream assemblages representing a nested subset of those from perennial streams (McCoy and Hales, 1974; Miller and Golladay, 1996; Fritz and Dodds, 2002).

As with algae, flooding and drying are important drivers of invertebrate assemblages in prairie streams. Distinct successional transitions are apparent following these disturbances (Chou et al., 1999; Fritz and Dodds, 2002), and recovery to predisturbance levels can be rapid (Miller and Golladay, 1996; Miller and Nudds, 1996; Fritz and Dodds, 2004). Woody debris is often rare in prairie streams, but where it is present, invertebrates tend to be more abundant and more resistant to flooding, relative to those associated with less stable sand and gravel substrates (Golladay and Hax, 1995; Hax and Golladay, 1998; Johnson and Kennedy, 2003).

Fish are a well-studied component of river networks in the Great Plains, and are among the most threatened (Rabeni, 1996; Fausch and Bestgen, 1997; Hubert and Gordon, 2007; Hoagstrom et al., 2010). Approximately 200 fish species are found across prairie river networks, about 50 of which are endemic to these streams. The most common taxa are minnows (Cyprinidae), suckers (Catastomidae), darters (Percidae), sunfishes (Centrarchidae), and catfishes (Ictaluridae).

Longitudinal organization of fish assemblages has been widely recognized in Great Plains river networks (e.g., Harrell et al., 1967; Smith and Powell, 1971; Schlosser, 1987), and like macroinvertebrates these assemblages often are nested such that intermittent headwater communities are subsets of those in downstream perennial segments. Unlike algae and macroinvertebrates, fish inhabiting intermittent headwater streams do not have terrestrial or drying-resistant life stages. Fish, however, are highly mobile and avoid desiccation by moving into downstream perennial reaches or perennial spring-fed pools in upstream segments (Deacon, 1961; Fausch and Bramblett, 1991). Periodic floods are important for creating perennial refugia and providing connectivity between habitats for the dispersal of fish and their eggs in prairie stream networks (see Section 4.7.3.3; Labbe and Fausch, 2000; Franssen et al., 2006).

4.7.2.5. *Human Alterations*

Human alterations to prairie river networks have affected physical, chemical, and biological connectivity in these systems both directly and indirectly. Crop and livestock agriculture are predominant land uses in the Great Plains (Galat et al., 2005; Matthews et al., 2005) and represent major nonpoint sources of nutrients, sediment, and pesticides (Battaglin et al., 2003; US EPA, 2006; Alexander et al., 2008). Livestock concentrate in and near streams for shade, food, and water, leading to bank erosion, increased soil bulk density, sedimentation, and elevated fecal bacteria concentrations (Armour et al., 1991; Strand and Merritt, 1999).

To support these agricultural enterprises, water has been diverted from channels, mined from regional aquifers, and stored in reservoirs. Groundwater withdrawals in the Great Plains are the highest in the United States (Sophocleous, 2010), causing many once perennial river segments to regularly dry out completely during summer months, particularly in the drier western portions of the Great Plains (Cross and Moss, 1987; Ferrington, 1993; Falke et al., 2011). Nearly all river networks in prairie regions have been altered by impoundments for irrigation storage and flood control, from small farm ponds in headwaters to large reservoirs on river mainstems (Smith et al., 2002; Galat et al., 2005; Matthews et al., 2005). Decline in flood magnitude, altered flow timing, and reduced flow variability and turbidity are evident in many prairie rivers compared to historically documented conditions (e.g., Cross and Moss, 1987; Hadley et al., 1987; Galat and Lipkin, 2000). Reductions in peak discharge derived from prairie streams have contributed to the narrowing of the region's once broad and shallow river channels (e.g., Friedman et al., 1998; Wohl et al., 2009). Dynamic mosaics of sand bars common in most prairie rivers have become stabilized and coalesced islands. The establishment of trees along prairie river riparian zones was limited by floods prior to settlement, but now dense zones of native and invasive trees and shrubs further reduce flows through high evapotranspiration (Johnson, 1994; Dahm et al., 2002).

4.7.3. Evidence

4.7.3.1. *Physical Connections*

4.7.3.1.1. *Water*

As in other river systems, water is the primary medium by which materials are transported from streams to rivers in prairie networks. Floods are common in Great Plains streams (e.g., Fausch and Bramblett, 1991; Hill et al., 1992; Fritz and Dodds, 2005), and propagation of these floods from streams to downstream rivers demonstrates hydrologic connectivity. Fritz and Dodds (2004, 2005) characterized the hydrology of intermittent streams draining native tallgrass prairie in a study that coincided with the highest flow on record (on May 13, 1995, with a return interval of at least 50 years). Kings Creek and one of its headwater streams (N01B) are both headwater streams draining into the Kansas River, downstream of the USGS gaging station at Fort Riley and upstream from the confluence of the Big Blue and Kansas Rivers and the USGS gaging station at Wamego (see Figure 4-6). The peak flow rising and descending limbs were very rapid at Kings Creek and N01B compared to those recorded for the Kansas River at Wamego, where the peak arrived approximately 12 hours later (see Figure 4-7).

Hydrographs for the upstream Fort Riley gage on the Kansas River and the Big Blue River indicate that the May 13, 1995 peak at the downstream Wamego gage was associated with floods propagating from Kings Creek and other small streams (see Figure 4-7). The subsequent peak at the Wamego gage that occurred five days later was associated with a storm falling mainly on portions of the Kansas River basin upstream of the Fort Riley gage, which elicited only a slight increase in discharge at Kings Creek and N01B (see Figure 4-7).

Figure 4-6. Map showing the location of Kings Creek and N01B, intermittent tributaries to the Kansas River.

A flood occurring June 14−20, 1965 on the Platte River (Colorado and Nebraska) is among the largest U.S. floods in recorded history, with a recurrence interval of 900 to 1,600 years (Matthai, 1969). This flood originated from runoff of intense rainfall (360 mm in 4 hours) over headwater portions of the drainage south of Denver, CO. Normal annual precipitation for this area is approximately 400 mm. Flows in Plum Creek, one of the intermittent headwater streams to the Platte River that received the heaviest rains, rose from $<5\ m^3\ s^{-1}$ to $4{,}360\ m^3\ s^{-1}$ in only 40 minutes. Under the Federal Flood Control Act of 1944, detention impoundments were extensively constructed on headwater streams in the Great Plains to retard flooding in downstream rivers (Schoof et al., 1978; Van Haveren, 1986). Headwater impoundments reduced runoff to the Washita River in Oklahoma by 36%, but channel dredging

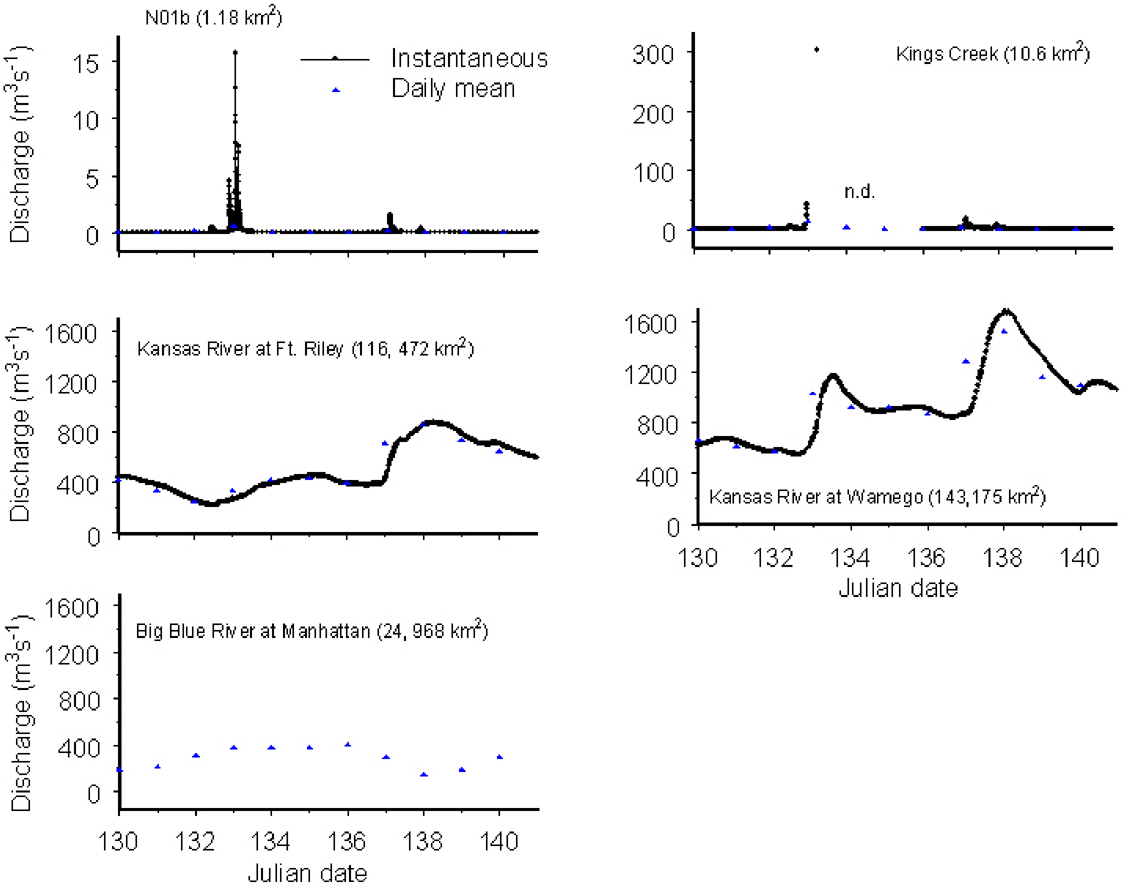

Figure 4-7. Hydrographs (instantaneous and daily mean) showing propagation of the 13 May 1995 (Julian data 133) flood downstream from headwater sites (N01B and Kings Creek) to the Kansas River at Wamego. Also shown are hydrographs from upstream gages on the Kansas River at Fort Riley and the Big Blue River (see Figure 4-6 for all site locations). Instantaneous data were not available at Kings Creek immediately following the flood because of damage to the USGS gage and were not available from Big Blue River. The peak instantaneous discharge for Kings Creek was estimated by USGS.

of streams offset these reductions by increasing flow from groundwater and reducing transmission loss (Schoof et al., 1978).

Machavaram et al. (2006) examined hydrologic connectivity between intermittent prairie streams, a headwater pond, and a perennial stream reach approximately 10 km downstream using chemical and isotopic tracers in a southeastern Kansas system. They found that, following precipitation, 20% of downstream water originated from the upstream pond, which was fed by ephemeral and intermittent streams; elevated oxygen stable isotope tracer associated with the pond water took 26−31 hours to reach the downstream site (Machavaram et al., 2006). Streams connected to lakes and wetlands contributed proportionally more flow to a southeastern Minnesota river in summer, when other water sources were minimal, than in spring (Lenhart et al., 2010). Flow from these streams has a delayed or lagged release because of storage in lakes and wetlands, and stream flow backed up because of high mainstem flows (Lenhart et al., 2010).

4.7.3.1.2. *Temperature (heat energy)*

Water temperatures represent a substantial stress to biotic communities in Great Plains rivers (see Section 4.7.3.3). Rivers to the north experience cold winters, and those to the south and west experience hot summers. Streams, particularly those strongly connected to more stable groundwater, can provide thermal refugia for avoiding temporary hypothermic and hyperthermic stress (see Section 4.7.3.3.2). Wide, shallow channels with little overhead canopy can result in high water temperatures under summer low flows. Over a 1-km reach of the South Canadian River in Oklahoma, summer (August 18−19, 1976) maximum mainstem water temperatures were 36−37°C, with cooler water (32−35°C) in backwater pools and a tributary stream (Matthews and Zimmerman, 1990). Mean water temperatures of seven streams immediately upstream from confluences with the Missouri River (at the Kansas-Missouri border) did not differ from water temperatures in the mainstem river, 200−300 m downstream of the confluences, except during March when streams were warmer than the river (Braaten and Guy, 1999). Mean water temperature was determined to be homogeneous with no relationship between drainage area and water temperature across two agriculturally dominated drainages in Illinois, where most flow was derived from surface and shallow subsurface runoff (agricultural tiles) rather than deeper groundwater (Wiley et al., 1990).

4.7.3.1.3. *Sediment*

Great Plains rivers are naturally turbid (Jewell, 1927; Cross and Moss, 1987; Huntzinger, 1995), with suspended sediment derived from the fine soils through which these river networks flow. Turbidity and suspended sediment concentration increase in prairie networks with increasing discharge and drainage area (Hill and Gardner, 1987b; Wiley et al., 1990; Lenhart et al., 2010), and can vary seasonally (Lenhart et al., 2010). Seasonal turbidity levels at tributary mouths and adjacent mainstem reaches, however, were not related across seven Missouri River confluences in Kansas and Missouri (Braaten and Guy, 1999), suggesting that these streams did not influence river turbidity at baseflow conditions. In contrast to other studies in the prairie region, no relationship was found between suspended particle concentration and stream size among 22 sites ranging in land use and network position (second- to eighth-order) in the Kansas

River basin (Whiles and Dodds, 2002). A significant positive relationship did exist when the authors excluded suburban sites and sites influenced by impoundments. Concentrations of suspended fine inorganic and organic matter were highest in the smallest stream draining suburban land use, whereas a comparably small stream draining native tallgrass prairie had among the lowest concentrations (Whiles and Dodds, 2002).

The downstream transport of metal-contaminated sediment was documented from mine tailings adjacent to a South Dakota headwater stream down through the river network to a reservoir approximately 200 km downstream, at the confluence of the Cheyenne and Missouri Rivers (Horowitz et al., 1988; Marron, 1989). The total amount of mine tailings transported from the headwater stream to downstream waters and adjacent floodplains over a 100-year span was estimated to be approximately 100 million metric tons (Marron, 1989). Contributions from streams to large rivers can therefore depend on the quantities available for transport from headwater streams from surrounding land uses.

4.7.3.2. *Chemical Connections*

4.7.3.2.1. *Nutrients and other chemicals*

Studies show that chemical constituents are exported from small prairie streams (Dodds et al., 1996a) and these chemical connections, or the downstream, flow-associated transport of nutrients, ions, dissolved and particulate organic matter, and other substances along prairie stream drainage networks, can significantly influence downstream water quality (Kemp and Dodds, 2002; Dodds et al., 2004; Dodds and Oakes, 2006).

Small prairie streams also can be important in preventing downstream nutrient transport. Studies conducted in Kings Creek, a stream draining a 1,060-ha tallgrass prairie catchment in Kansas, indicate that small prairie streams are highly nitrogen retentive (Tate, 1990; Dodds et al., 1996a; Dodds et al., 2000). For example, Dodds et al. (1996a) found that nitrogen transport through four second- and third-order streams in the Kings Creek watershed ranged from 0.01 to 6.0% of the total nitrogen supplied by precipitation, the balance being retained by the stream system. Similar patterns of nutrient retention have been demonstrated at larger spatial scales, as well. Alexander (2000; 2008) modeled the contribution of different-sized streams and rivers (including prairie streams) to nutrient loading in the Gulf of Mexico. They found that large rivers deliver more of their nitrogen and phosphorus loads to the Gulf of Mexico than small streams (Alexander et al., 2008), largely due to increased instream nutrient uptake and removal by small streams (Alexander et al., 2000). Despite their relative retentiveness, however, small streams do make substantial contributions to downstream nutrient loading due to their large numbers, with small to mid-sized streams in the western regions of the Mississippi River basin (which includes the Great Plains) delivering approximately 25−50% of their nitrogen loads to the Gulf (Alexander et al., 2008).

Correlations between water quality and upstream land use also indicate that prairie stream headwaters affect downstream reaches. Dodds and Oakes (2006, 2008) examined relationships between water quality and watershed land use at different spatial scales, along one fifth-order prairie stream network (2006) and across 68 small prairie streams (2008) in eastern Kansas. In the single drainage study, they found that concentrations of total nitrogen and nitrate were significantly related to riparian cover in the 2 km upstream of sampling sites, even when controlled for catchment land cover at each site (Dodds and Oakes, 2006). In the cross-drainage study, riparian cover along first-order streams was more closely correlated with total nitrogen, nitrate, ammonium, total phosphorus, atrazine, dissolved oxygen, and fecal coliform concentrations than riparian cover 2 or 4 km immediately upstream of sites across the 68 drainages (Dodds and Oakes, 2008). Nutrients are elevated in most prairie streams and rivers and nutrient concentrations in these systems are related to nonpoint land uses (Dodds and Oakes, 2004). These, along with widespread nature of headwater streams in river networks, are highly indicative that streams have strong chemical connection, functioning as important links between the surrounding lands to downstream waters.

Because prairie streams frequently experience intermittent flow, their influence on downstream waters is often discharge-dependent and temporally variable. For example, nitrate concentrations tend to be higher in intermittent prairie streams immediately after flows resume, versus when flow recedes (Tate, 1990). In addition, nitrogen uptake lengths (Dodds et al., 2000) and total phosphorus loads (Banner et al., 2009) increase with discharge. The effect of precipitation-driven flows on downstream water quality can depend on the relative contributions of surface water delivered from upstream channels and groundwater. Prairie streams typically are tied closely to groundwater sources (see Section 4.7.2.2), so the influence of headwaters can be especially pronounced during periods of high precipitation. Kemp and Dodds (2001) found that nitrate concentrations in fourth- and fifth-order lowland prairie reaches were lowest during periods of high precipitation, when more low-nitrate water was delivered downstream from second- and third-order reaches and high-nitrate groundwater influences were minimized.

4.7.3.2.2. *Dissolved and particulate organic matter*

Differences in DOC inputs along the prairie stream longitudinal gradient provide further indirect evidence of chemical connections between prairie stream headwaters and downstream reaches. McArthur et al. (1985b) isolated bacteria from stream sediments of grassland reaches and gallery forest reaches of a prairie stream and exposed them to leachates derived from grasses and bur oak (a common gallery forest species). Grassland bacteria only grew when provided with grass leachates as a carbon source, whereas gallery forest bacteria grew when provided with either grass or bur oak leachates. This finding suggests that either (1) grass-derived DOC-consuming bacteria are transported downstream and then coexist with bacteria consuming forest-derived DOC, or (2) grass-derived DOC is transported downstream, and local bacterial communities have adapted to use more refractory DOC exported from upstream reaches (McArthur et al., 1985b).

Studies measuring POM exported from low-order prairie stream reaches show significant temporal and spatial variability. For example, Golladay (1997) documented little POM export from a third-order prairie stream in Kansas, whereas two prairie streams in Texas had much higher rates of POM transport (Hill and Gardner, 1987b). In part these differences might reflect variability between stormflow and baseflow sampling, as organic matter concentrations can be positively correlated with stream discharge (Hill and Gardner, 1987b; Golladay, 1997). Whiles and Dodds (2002) examined seston (suspended fine particles) dynamics along the Kansas River drainage network (second- to eighth-order), and found that seston concentrations showed a significant positive relationship with stream size, increasing approximately 17-fold along the longitudinal gradient. This increase in seston was correlated with an increase in the taxa richness of filter-feeding invertebrates (Whiles and Dodds, 2002), illustrating that detrital transport along the stream gradient can influence invertebrate assemblages, which is a basic tenet of the River Continuum Concept (Vannote et al., 1980).

Stagliano and Whiles (2002) found that the standing stock of FPOM in a perennial reach of a tallgrass prairie stream was insufficient to support the annual secondary production (i.e., the rate of heterotrophic biomass formation) of collector-gatherers (Cummins and Klug, 1979), the dominant group of macroinvertebrates feeding on deposited FPOM. The replenishment of FPOM standing stocks, at least in part from upstream sources via algal senescence, the transport and settlement of suspended POM, and the breakdown and transport of coarse POM, likely accounted for this apparent imbalance: turnover of FPOM standing stocks was estimated to occur every 20 days (Stagliano and Whiles, 2002). Whiting et al. (2011) examined organic matter dynamics and trophic structure along a tallgrass prairie stream network (first- to fifth-order). They found that collector-filterers (macroinvertebrates that feed upon suspended POM; Cummins and Klug, 1979) in upstream reaches consumed <1% of suspended POM flux; gatherers that feed upon fine and very fine POM dominated secondary production in downstream reaches; and predators in downstream forested reaches consumed 107% of locally derived macroinvertebrate production. Predators in the upstream and middle reaches consumed 65% and 74% of available macroinvertebrate production, respectively. These findings support the idea that downstream secondary production depends in part on the export of energy sources (i.e., particulate organic matter and invertebrates) from upstream reaches.

As discussed earlier (see Section 4.7.2.4), prairie stream headwaters typically are open-canopied systems that receive little organic matter from terrestrial inputs, relative to forested headwaters (Jewell, 1927). Given the importance of autochthonous production in these systems, the fact that algal-based contributions to prairie stream seston can be significant (Swanson and Bachmann, 1976; Hill and Gardner, 1987b; Lenhart et al., 2010) is not surprising. In four Iowa streams, export of chlorophyll *a* (a measure of algal biomass) was positively correlated with upstream channel bottom area, suggesting that downstream suspended algae originated as benthic algae in upstream portions of the network (Swanson and Bachmann, 1976). This downstream transport of algae can also provide colonists for downstream reaches after flooding or drying of stream channels. For example, Dodds et al. (1996b) examined the recovery of periphyton biomass upon channel rewetting in an intermittent prairie stream. Within 2 weeks, chlorophyll had returned to maximum levels on rocks placed in the stream, even when they had been treated and scrubbed to remove desiccation-resistant propagules; this finding suggests that algal colonists in this stream were transported downstream from permanent upstream pools (Dodds et al., 1996b).

Coarse particulate organic matter can connect prairie stream headwaters to downstream reaches. Johnson and Covich (1997) examined detrital inputs along a second- to fifth-order prairie stream network in Oklahoma. They found that leaves in the stream originated from farther upstream than expected, with the percentage of whole leaves at a site best explained by riparian forest cover in reaches 500 and 1,000 m upstream. The percentage of leaf fragments >1 mm was best explained by downstream distance along the stream network (Johnson and Covich, 1997), suggesting increased processing and fragmentation of leaves as they move down the longitudinal gradient.

4.7.3.3. *Biological Connections*

4.7.3.3.1. *Invertebrates*

Existing evidence for invertebrate-mediated biological connectivity along prairie stream networks mainly comes from studies of invertebrate assemblage recovery following flooding and drying in small prairie streams. Recovery from these disturbances tends to be relatively rapid, with substantial gains in invertebrate taxa richness and density observed within days to weeks (Miller and Golladay, 1996; Hax and Golladay, 1998; Fritz and Dodds, 2004), suggesting that these reaches are quickly repopulated by invertebrate drift from upstream sources, aerially dispersing adults, or disturbance-resistant survivors.

Fritz and Dodds (2002, 2004, 2005) examined postflooding and postdrying recovery of invertebrates in small intermittent and perennial prairie streams along an approximately 5-km

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stretch of Kings Creek in Kansas. They found that initial recovery of invertebrate taxa richness in intermittent reaches, and taxa richness of invertebrate drift and aerially colonizing insects, were negatively related to distance from upstream perennial water (Fritz and Dodds, 2002, 2004). Distance from upstream refugia, however, was not a significant predictor of invertebrate diversity measures across annual time scales (Fritz and Dodds, 2005); they speculated that movement of water along the entire stream network (i.e., maintenance of hydrologic connectivity) makes proximity to colonists less important over longer time scales. These findings suggest that recovery from disturbance in these systems depends on biological connectivity via both downstream drift of colonizers and downstream (and potentially upstream) movement of aerially dispersing, egg-depositing adults (Miller and Golladay, 1996; Dodds et al., 2004).

4.7.3.3.2. ***Fishes***

Research on prairie stream fish assemblages provides perhaps the strongest and most well studied evidence of biological connections throughout these networks. Much of this evidence focuses on two related aspects of the ecology of prairie stream fish: the dispersal and recruitment of pelagic-spawning prairie stream fish and the recovery of fish assemblages after disturbance, especially flooding and drying.

Many prairie stream fish broadcast spawn nonadhesive, semibuoyant eggs, which develop (typically hatching within 1 to 2 days) as they are transported downstream with water flow (Cross and Moss, 1987; Fausch and Bestgen, 1997; Platania and Altenbach, 1998; Durham and Wilde, 2006). The distance these eggs travel downstream depends on discharge and several other factors (e.g., development time); Platania and Altenbach (1998) estimated, however, that unimpeded eggs could travel as far as 144 km before hatching, and another 216 km as developing protolarvae (i.e., the swim-up stage), illustrating that downstream transport of these drifting organisms can be extensive. Without adequate water flow along sufficient lengths of the stream network, eggs can drop out of suspension before hatching (Platania and Altenbach, 1998; Durham and Wilde, 2006). Based on historical and contemporary fish surveys, eight species of pelagic-spawning cyprinids require a minimum length of greater than approximately 100 km (ranging from 103 to 297 km, depending on the species) of undisrupted stream channel (e.g., channels with no impoundments and no drying associated with human withdrawal) to support persistent populations (Perkins and Gido, 2011).

This pelagic-spawning reproductive strategy also necessitates upstream movement by adult fish, if populations are to be maintained in small prairie streams (Fausch and Bestgen, 1997; Durham and Wilde, 2008). Prairie stream fishes generally are highly vagile, with adults capable of long-distance migrations. For example, individuals of one species of prairie fish

(*Hybognathus placitus*) in the South Canadian River, NM were observed to move approximately 250 m upstream over a 15-minute period, illustrating that prairie fishes can move substantial distances over relatively short periods (Fausch and Bestgen, 1997).

The effect that impoundment of prairie streams and rivers has had on the region's native fish assemblages highlights the importance of hydrologic connectivity in these systems. Many studies have documented statistically significant associations between impoundment of prairie streams and loss of native fishes (e.g., Winston et al., 1991; Luttrell et al., 1999; Schrank et al., 2001; Falke and Gido, 2006; Matthews and Marsh-Matthews, 2007). For example, Schrank et al. (2001) found that, across 26 streams in the Flint Hills region of Kansas, sites from which Topeka shiners (*Notropis topeka*) had been extirpated had significantly more small impoundments on them and higher largemouth bass (*Micropterus salmoides*) catch-per-unit-effort than sites at which the shiners were extant. Fewer studies have specifically examined the mechanisms by which impoundments affect these changes, although impoundments likely disrupt both the downstream transport of developing eggs and larvae (Platania and Altenbach, 1998) and the upstream and downstream movement of adult fish.

Because many small prairie streams have intermittent flow, maintenance of fish populations often depends on dispersal out of intermittent reaches before drying occurs and recolonization of these habitats once water flow resumes—both of which require hydrologic connectivity along the stream network. Many fishes also require different habitats during different life stages, further necessitating hydrologic connectivity across these areas (Labbe and Fausch, 2000; Falke et al., 2010).

For dispersal and recolonization to occur, fishes must be able to access refuge habitats under adverse conditions, and then expand into newly habitable areas once adverse conditions abate. Small, spring-fed prairie streams serve as key refuges for endemic prairie fishes (Hoagstrom et al., 2010), because they are groundwater-fed and maintain permanent pools that can provide habitat during periods of channel drying (Wohl et al., 2009). This groundwater influence also allows these spring-fed streams to provide refuge from adverse temperatures. For example, a spring-fed stream in Missouri had more stable temperatures than the mainstem river, with cooler summer and warmer winter temperatures; in winter, fish from the mainstem river moved into this habitat, where their food availability, growth, and average egg size were greater than those of fish that stayed in the mainstem (Peterson and Rabeni, 1996).

During and after floods, juvenile and adult fishes can move upstream or downstream (or get displaced downstream) into newly available habitat (Fritz et al., 2002; Franssen et al., 2006). Once channels are rewetted, prairie stream fishes can move quickly into these previously unoccupied habitats (Harrell et al., 1967; Fritz et al., 2002; Franssen et al., 2006). For example, Harrell et al. (1967) examined fish response to channel drying in third- to sixth-order reaches of

Otter Creek, an intermittent prairie stream in north-central Oklahoma, and found that most fish species collected after 8 months of flow prior to channel drying were already present three days after channel rewetting (Harrell et al., 1967). After a flood in an intermittent prairie stream in Kansas, fish dispersed into the headwaters from a perennial reach approximately 5 km downstream (Franssen et al., 2006).

4.7.4. Prairie Streams: Synthesis and Implications

Prairie streams typically represent a collection of spring-fed, perennial pools and reaches, embedded within larger, intermittently flowing segments (Labbe and Fausch, 2000). Due to the region's geographic location, substantial interannual variation in rainfall exists. Expansion (flooding) and contraction (drying) of these systems, particularly in terms of summer rainfall deficit (Borchert, 1950), determine the timing of hydrologic connectivity at any given time. Because of this temporal variability, connectivity in prairie river networks must be considered over relatively long time scales (multiple years).

- Studies have demonstrated significant physical, chemical, and biological connections from prairie headwater streams to larger rivers, despite extensive alteration of historical prairie regions by agriculture, water impoundment, water withdrawals, and other human activities (Matthews and Robinson, 1998; Dodds et al., 2004), and the challenges these alterations create for assessing connectivity.

- The most compelling evidence for connectivity along prairie river networks comes from examples of streams as sources of water via flood propagation (e.g., Matthai, 1969; Fritz and Dodds, 2004, 2005), sources of contaminated sediment transport (Horowitz et al., 1988; Marron, 1989), sites of nutrient lags and transformation (e.g., Dodds et al., 1996a; Alexander et al., 2008), the downstream transport of prairie fish eggs and larvae (e.g., Platania and Altenbach, 1998; Perkins and Gido, 2011), and refugia for prairie fishes (e.g., Fausch and Bestgen, 1997; Franssen et al., 2006).

- Impoundments for irrigation storage and flood control have altered flood magnitude, altered flow timing, and reduced flow variability and turbidity across the prairie regions (e.g., Cross and Moss, 1987; Hadley et al., 1987; Galat and Lipkin, 2000). The effect that impoundment of prairie streams and rivers has had on the regions' native fish assemblages highlights the importance of hydrologic connectivity in these systems. Maintenance of fish populations often depends on dispersal out of intermittent reaches before drying occurs and recolonization of these habitats once water flow resumes—both of which require hydrologic connectivity along the stream network—and many fishes also require different habitats during different life stages (Labbe and Fausch, 2000; Falke et al., 2010).

4.8. CASE STUDY: SOUTHWESTERN INTERMITTENT AND EPHEMERAL STREAMS

4.8.1. Abstract

Ephemeral and intermittent streams are abundant in the arid and semiarid landscapes of the West, and particularly the Southwest (see Figure 4-8). These areas are characterized by low and highly variable precipitation where potential evapotranspiration exceeds precipitation. In Arizona, 94% of tributary streams to major rivers are intermittent or ephemeral based on the National Hydrography Dataset (NHD, 2008). The heavily studied Upper San Pedro Basin in southeastern Arizona is discussed in detail as it provides a well understood example of the hydrologic behavior and connectivity of rivers common to the southwestern United States where ephemeral and intermittent tributaries comprise the majority of the basin’s stream reaches. Flows and floods from ephemeral and intermittent tributary streams are also a major driver of the dynamic hydrology of the limited number of perennial reaches existing in the Southwest. They also supply water to mainstem alluvial aquifers and regional groundwater aquifers. Both alluvial and regional aquifers, in turn, supply baseflow to perennial mainstem stream reaches over extended periods (sometimes months) when little or no precipitation occurs. It is this baseflow and shallow groundwater that supports the limited, naturally occurring, vibrant riparian communities in the region. In addition, ephemeral streams export sediment, which contributes to shaping the fluvial geomorphology and alluvial aquifers of streams in the regions (Shaw and Cooper, 2008), as well as nutrients, which contribute to river productivity. Several studies found that native fishes and invertebrates are well adapted to the variable flow regimes common in rivers of the Southwest and are heavily influenced by ephemeral tributary streams (Turner and List, 2007).

4.8.2. Introduction

This section addresses the hydrologic and ecological influence of ephemeral and intermittent streams on perennial or intermittent rivers in the arid and semiarid southwestern United States with particularly emphasis on Arizona and New Mexico. The structure of this section differs slightly from the prairie stream case study (see Section 4.7) because of the uniquely thorough understanding of one particular southwestern river system, the San Pedro River, which has been the subject of a long-term research program (Goodrich et al., 2000; Stromberg and Tellman, 2009). Hence, evidence for the function and connectivity of ephemeral and intermittent tributaries to the San Pedro River is described in detail, and its application to other river systems in the Southwest is subsequently explored.

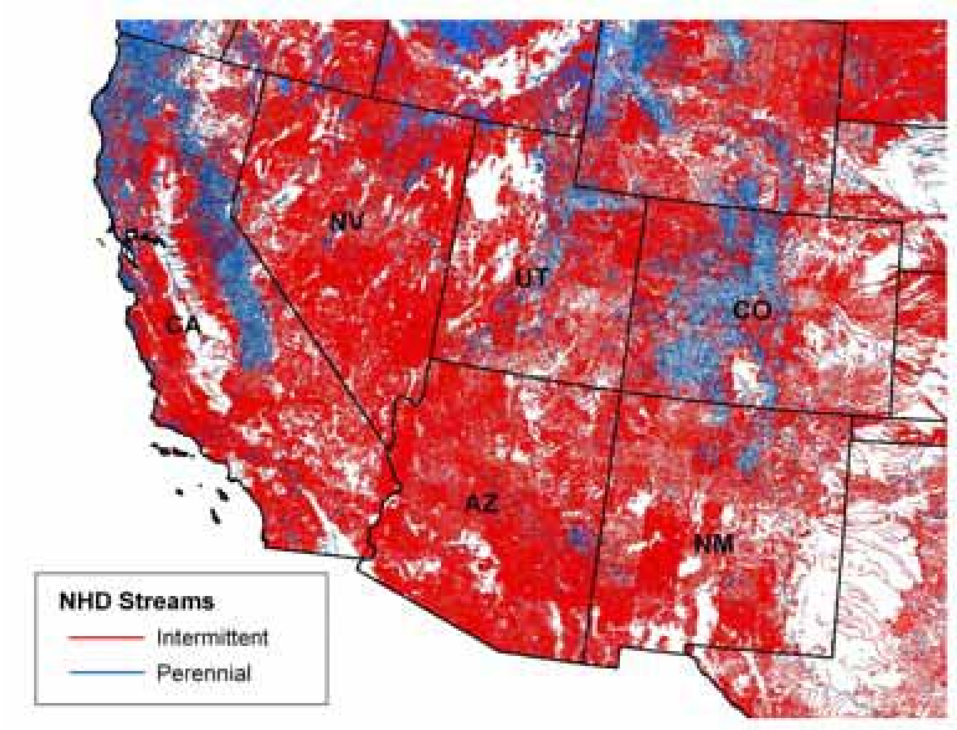


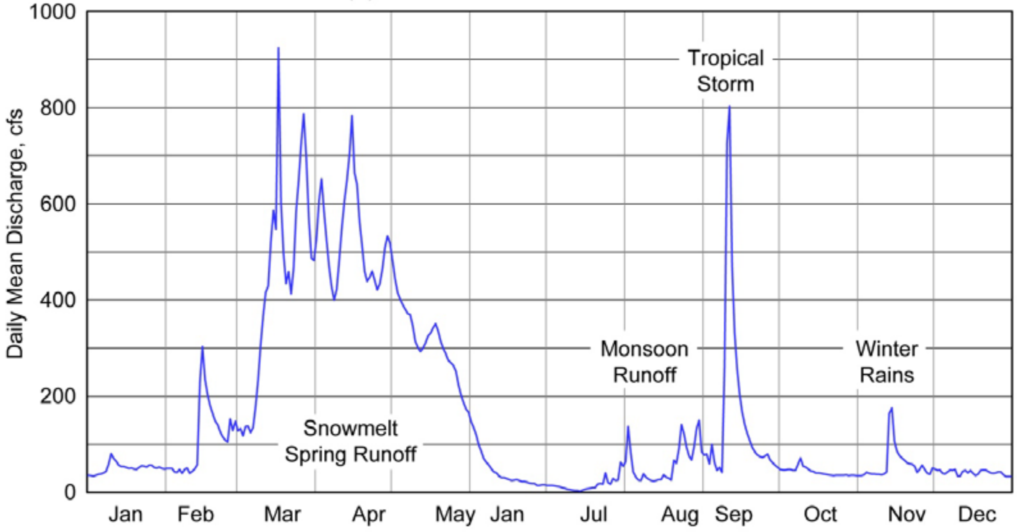
Figure 4-8. Geographic distribution of intermittent (includes ephemeral) and perennial streams in the southwestern states, illustrated using the National Hydrography Dataset (NHD) stream map (http://nhd.usgs.gov/). Note that the NHD may not accurately reflect the total extent of ephemeral or intermittent streams, as it does not include stream segments less than one mile in length, combines intermittent and ephemeral streams, and is based on 1:100,000 scale topographic maps.

4.8.3. Southwestern Rivers

Understanding the unique characteristics of southwestern American rivers is necessary to evaluate the influence of ephemeral and intermittent streams on these rivers (Levick et al., 2008). Southwestern rivers differ in many ways from rivers in the humid eastern United States or in the Midwest and West. Southwestern rivers typically can be divided into two main parts, particularly in the basin and range geologic province. One part comprises rivers in the mountainous upper basins that receive higher precipitation, often as snow, and the second part comprises those rivers located in arid or semiarid plateau regions and plains dominated by ephemeral streams (Blinn and Poff, 2005). For example, more than 80% of the Gila River corridor in New Mexico and Arizona meanders through desert scrublands. Precipitation is seasonal. In summer, precipitation is strongly influenced by atmospheric moisture flowing from the Gulf of Mexico and the Gulf of California (Mexican monsoon), where local heating triggers high-intensity air-mass thunderstorms (summer monsoon). In fall, tropical depressions, often remnants of hurricanes, can bring infrequent but long-duration rainfall events; such storms are responsible for many of the larger floods in the region (Webb and Betancourt, 1992). Cyclonic storms from the Pacific Ocean, resulting in large frontal systems, dominate winter precipitation in the form of snow in higher elevations and typically as low-intensity rainfall in lower elevations (Blinn and Poff, 2005). Figure 4-9 illustrates the 2003 calendar year hydrograph from the White River near the Fort Apache USGS gaging station (upper) in east central Arizona, and the San Pedro River near Tombstone, in southeast Arizona (lower). Although the two gaging stations differ in elevation by less than 200 m, the watershed contributing to the White River is substantially larger and higher in elevation than the San Pedro watershed, resulting in long-duration spring runoff from snowmelt. Monsoon-generated, short-duration runoff dominates the San Pedro watershed but monsoonal influence also is apparent in the White River hydrograph. Runoff generated from late monsoon precipitation in September caused a major increase in discharge in the White River and a minor increase in the San Pedro. Most perennial and intermittent rivers in the Southwest are groundwater-dependent, flowing primarily in a baseflow regime and supported by discharge from a connected regional and/or alluvial aquifer. As discussed in more detail below, part of baseflow also is sustained or augmented by slow drainage of a shallow alluvial aquifer from past flooding. In arid and semiarid regions, the riparian areas that perennial and intermittent streams support occupy a small percentage of the overall landscape but they harbor disproportionately greater percentage of the biodiversity than the areas surrounding them (Goodrich et al., 2000; Stromberg et al., 2005). Reservoir construction, irrigation withdrawals, and groundwater pumping have converted many historical, perennially flowing reaches into intermittently flowing reaches (Blinn and Poff, 2005).

Dominant hydrologic flowpaths vary with location within southwestern river basins. After climate and weather, recharge and infiltration mechanisms are the next most important factors determining the occurrence of ephemeral, intermittent, and perennial streams. Recharge over longer time scales (months to centuries) is essential to replenishing regional groundwater and near-stream alluvial aquifers, which in turn are essential to maintaining baseflow in perennial streams. Primary recharge mechanisms include mountain block recharge, mountain front recharge, diffuse hillslope or interchannel recharge, and ephemeral channel recharge. Key advances brought forth in a recent synthesis of research on groundwater recharge in the southwest and western United States include: (1) desert vegetation effectively eliminates diffuse recharge in most areas of the basin floor; (2) ephemeral channel recharge can be very important in wet years and greatly dominates recharge in basin-floor environments; and (3) environmental tracers are now available to “fingerprint the sources and amounts of groundwater recharge at the basin scale” (Phillips et al., 2004).

(a) WHITE RIVER NEAR FORT APACHE



(b) SAN PEDRO RIVER NEAR TOMBSTONE

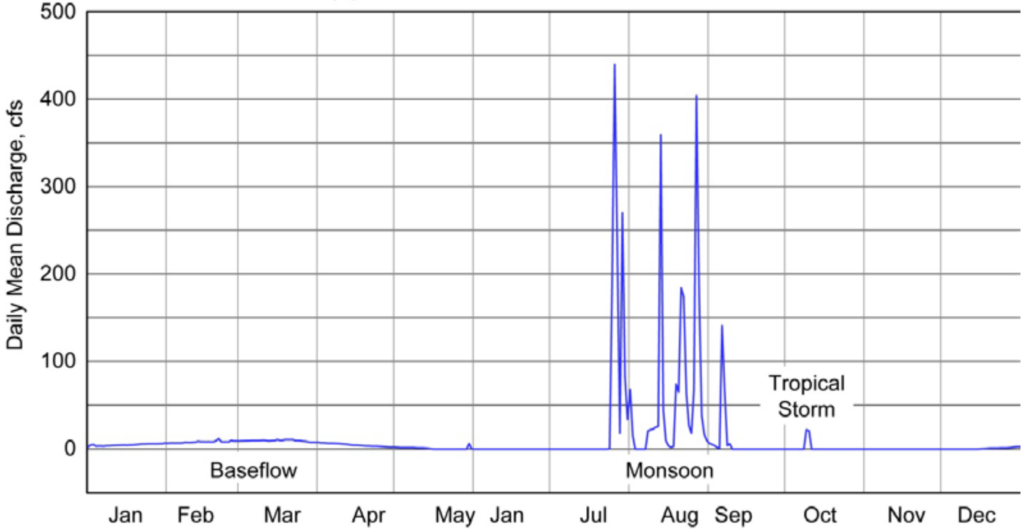


Figure 4-9. 2003 calendar year hydrographs from (a) the White River near Fort Apache, Arizona and (b) the San Pedro River near Tombstone, AZ.

Mountains with deeper soils or those consisting of fractured rock will have higher infiltration capacities, less frequent occurrences of overland flow, and serve as recharge areas for regional groundwater (Wilson and Guan, 2004; Blasch and Bryson, 2007; Wahi et al., 2008). Mountains with shallow soils and more consolidated rock will shed streamflow and shallow groundwater off the mountain block onto the valley, which often consists of deep alluvium, particularly in the basin and range geologic province. This is where mountain front recharge occurs. High-elevation perennial streams often become intermittent or ephemeral at this transition, with their downstream disappearance of surface flow dependent on the flow rates coming off the mountain block and the permeability of the valley alluvium into which they enter. During periods of high flow, they can reconnect with other perennial stream reaches maintained by groundwater flow (Blinn and Poff, 2005; Blasch and Bryson, 2007; Yuan and Miyamoto, 2008).

Runoff generation in arid and semiarid valley floors and lowlands is dominated by the infiltration excess mechanism where precipitation rates exceed infiltration rates. In the arid and semiarid Southwest, this situation typically is triggered by high-intensity convective thunderstorms. Generally, such storms are relatively short in duration, resulting in ephemeral flows with short runoff duration (Goodrich et al., 1997). As water flows down dry ephemeral channels, it infiltrates into the channel bottom and sides (i.e., channel transmission losses occur) where channel substrate is porous. If restricting soil or geologic layers underlying the channel do not substantially inhibit downward motion, channel transmission losses will recharge either the regional or alluvial groundwater (Tang et al., 2001; Constantz et al., 2002; Harrington et al., 2002; Coes and Pool, 2005; Vivoni et al., 2006; Blasch and Bryson, 2007). In this influent stream environment typical of many southwestern streams, the volume of transmission water losses in ephemeral channels increases as watershed size increases, resulting in a losing stream environment as opposed to a gaining stream environment encountered in wetter hydroclimatic regimes (Goodrich et al., 1997). As noted above and discussed in Phillips et al. (2004), these ephemeral tributary channels are the dominant source of recharge in valley floors, and at the basin scale they can provide substantial recharge during wet years. Typically, as stream drainage area increases, the alluvium under and adjacent to streams begins to serve as important shallow aquifers that receive and store streamflow infiltration during hydrologic events and sustain baseflow and riparian communities between storms (Stromberg et al., 2005; Dickinson et al., 2010).

The magnitude of aquifer recharge has high temporal variability in the Southwest. Winter precipitation, which has a predominant effect on mountain block and mountain front recharge in the Arizona-New Mexico portion of the Southwest, is correlated with El Niño/Southern Oscillation (Woolhiser et al., 1993) at interannual time scales. Over decadal climate cycles, winter precipitation is also related to the Pacific Decadal Oscillation (Pool, 2005). The magnitude of ephemeral channel recharge varies widely from year to year, depending on the strength of the monsoon season (Goodrich et al., 2004) and the occurrence of relatively infrequent prolonged precipitation events resulting from tropical depressions. Floods and large runoff events caused by any of these mechanisms can have a long-lasting influence (6 to 10 months) on baseflow of southwestern rivers by recharging near-stream alluvial aquifers and thereby sustaining streamflow as they drain (Brooks and Lemon, 2007).

4.8.4. San Pedro River

4.8.4.1. *Basin Characteristics*

Because of a rich research and long-term monitoring history, the San Pedro Basin and River in southeastern Arizona represents an excellent case study of the hydrologic behavior and connectivity of southwestern rivers (Goodrich et al., 2000; Stromberg and Tellman, 2009; Brookshire et al., 2010). The San Pedro River originates in Mexico, flowing undammed north to its confluence with the Gila River. The San Pedro Basin is comprised of 49% nonperennial (includes ephemeral and intermittent), 31% perennial, and 20% artificial path (human canals or diversions) reaches in the U.S. portion of the basin as derived from the USGS NHD[1]. However, the most recent wet-dry, ground-based mapping of reaches in the San Pedro conducted by The Nature Conservancy in June 2012, historically the time of lowest streamflow, found only 29% of the reaches surveyed in the basin were wet, including the portion in Mexico (http://azconservation.org/downloads/category/san_pedro_river). It is the only unimpounded significant river in Arizona and is the last remaining stream in southern Arizona that has long perennial reaches (Kennedy and Gungle, 2010; see Figure 4-10). Most tributaries to the river are ephemeral at their confluence with the mainstem. The river basin, located in the Basin and Range Province, has a valley that is generally 30−50 km wide, comprising sedimentary fill deposits, and slopes upward from the river to mountains with elevation ranging from 2,000 to 2,900 m.

Annual precipitation within the basin ranges from 300 to 750 mm with highest amounts occurring in the mountains. Vegetation includes desert scrub, grasslands, oak woodland savannah, mesquite woodland, riparian forest, coniferous forest, and agriculture (Kepner et al., 2000; Kepner et al., 2004). Brush and grasses typical of southwest semiarid landscapes (Goodrich et al., 1997) dominate the valley floor vegetation.

At the U.S. Department of Agriculture, Agricultural Research Service (USDA-ARS) Walnut Gulch Experimental Watershed (WGEW**—**a sub watershed of the San Pedro near Tombstone, Arizona), approximately two-thirds of annual precipitation on the watershed occurs as high-intensity, convective thunderstorms of limited aerial extent (Goodrich et al., 1997). Winter rains (and occasional snows) are generally low-intensity events associated with slow-moving cold fronts and are typically of greater aerial extent than summer rains. Runoff on the lower elevation WGEW is generated almost exclusively from convective storms during the

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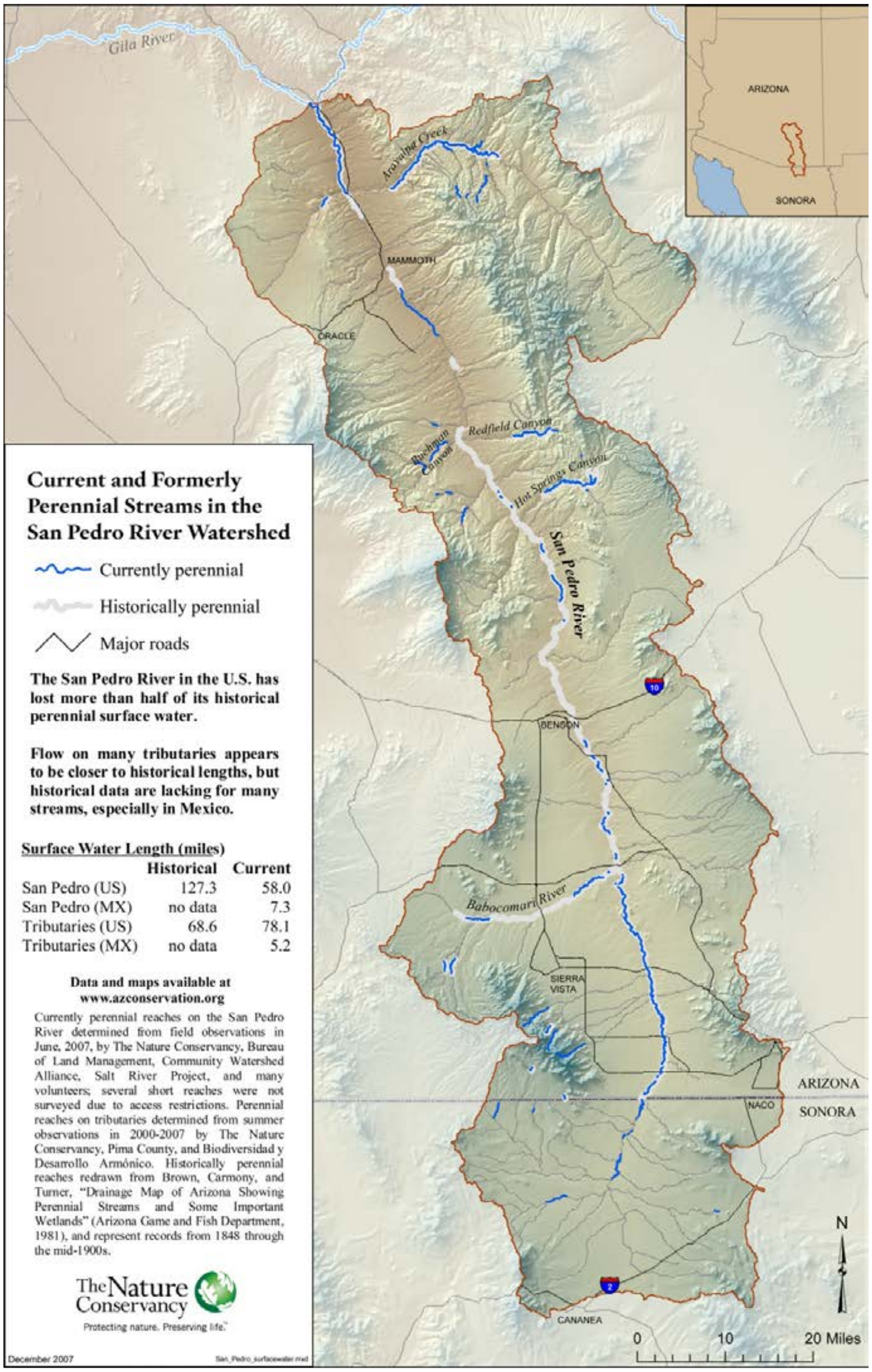
[1] Based on USGS National Hydrography Dataset (NHD) stream map (http://nhd.usgs.gov/). Note that the NHD may not accurately reflect the total extent of ephemeral or intermittent streams, as it does not include stream segments less than one mile in length, combines intermittent and ephemeral streams, and is based on 1:100,000 scale topographic maps.



Current and Formerly Perennial Streams in the San Pedro River Watershed

The San Pedro River in the U.S. has lost more than half of its historical perennial surface water.

Flow on many tributaries appears to be closer to historical lengths, but historical data are lacking for many streams, especially in Mexico.

Surface Water Length (miles)

	Historical	Current
San Pedro (US)	127.3	58.0
San Pedro (MX)	no data	7.3
Tributaries (US)	68.6	78.1
Tributaries (MX)	no data	5.2

Data and maps available at www.azconservation.org

Currently perennial reaches on the San Pedro River determined from field observations in June, 2007, by The Nature Conservancy, Bureau of Land Management, Community Watershed Alliance, Salt River Project, and many volunteers; several short reaches were not surveyed due to access restrictions. Perennial reaches on tributaries determined from summer observations in 2000-2007 by The Nature Conservancy, Pima County, and Biodiversidad y Desarrollo Armónico. Historically perennial reaches redrawn from Brown, Carmony, and Turner, "Drainage Map of Arizona Showing Perennial Streams and Some Important Wetlands" (Arizona Game and Fish Department, 1981), and represent records from 1848 through the mid-1900s.

The Nature Conservancy
Protecting nature. Preserving life.

Figure 4-10. San Pedro River basin map showing major physiographic features and current and historical perennial reaches.

From Levick et al. (2008), courtesy of The Nature Conservancy, Arizona. Available online at *http://azconservation.org/map_gallery/current_and_formerly_perennial_san_pedro_river_surface_water*.

summer monsoon season via infiltration excess that produces overland flow. The hydrogeology of the San Pedro River basin is typical of many alluvial basins in the Southwest (Dickinson et al., 2010). Groundwater flows through the basin-fill aquifer (regional aquifer) from recharge areas near the mountains and beneath ephemeral tributaries to perennial reaches of the San Pedro River (Wahi et al., 2008; Dickinson et al., 2010). A narrow band of highly permeable stream alluvium is incised into the basin-fill along the major stream channels (see Figure 4-11). The stream and floodplain alluvium is an important alluvial aquifer that receives discharge from the basin-fill aquifer and streamflow via streambank infiltration occurring during high stream stages.

This bank and alluvial aquifer storage supports riparian vegetation during periods lacking runoff (Dickinson et al., 2010). The San Pedro River network with associated shallow alluvial aquifers (mainstem and portions of some tributaries) support extensive riparian vegetation communities (Stromberg et al., 2005) that provide habitat for more than 350 species of birds, 80 species of mammals, and 40 species of reptiles and amphibians (Kennedy and Gungle, 2010). Alluvial aquifers are also zones of extensive hyporheic exchange (Stanford and Ward, 1988; Fernald et al., 2001).

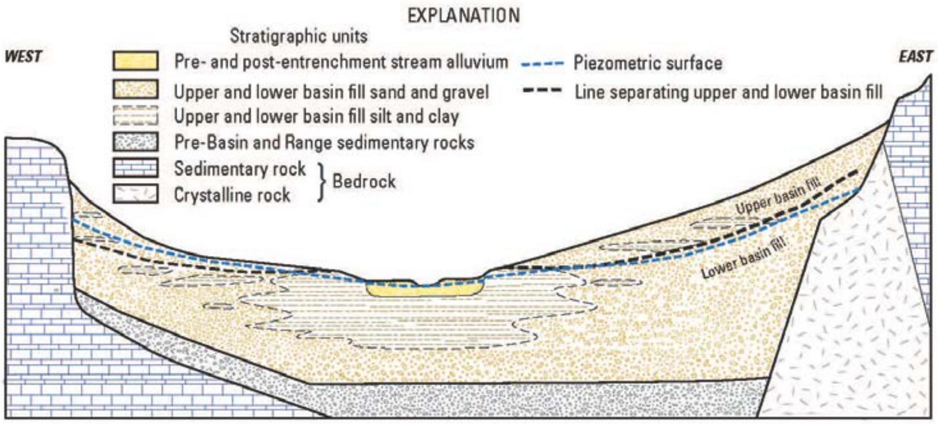


Figure 4-11. Generalized east-west section and stratigraphic units in the middle San Pedro watershed.

From Dickinson et al. (2010).

4.8.4.2. *Ephemeral Stream Connections to and Influence on the San Pedro River.*

Overland runoff generation and associated ephemeral streamflow is common in San Pedro tributary streams. Goodrich et al. (1997) examined hundreds of hydrologic events in different-sized catchments at the USDA-ARS WGEW and found that the relationship between watershed area and runoff volume was increasingly nonlinear as drainage area increased. The authors found a critical threshold watershed area of approximately 36−60 ha, at which runoff responses became much less linear and channel transmission losses increased more rapidly with increasing watershed area. This relationship is very different from commonly observed relationships in humid streams of the East, where runoff is generally proportional to watershed area (see Section 4.3.1). Two reasons were given for this variability in runoff produced per unit watershed area: (1) the spatial variability and limited spatial extent of runoff producing precipitation, and (2) the loss of runoff water by infiltration into the bed of ephemeral channels (transmission losses). Figure 4-12 illustrates this process. During a major rainstorm on 27 August, 1982, most of the precipitation occurred in the upper watershed. As overland flow occurred and became concentrated in the ephemeral tributary network, streamflow dramatically diminished as the runoff hydrograph traveled downstream through the channel network.

There is strong evidence that transmission losses in ephemeral tributary streams recharge alluvial and regional aquifers (Goodrich et al., 1997; Callegary et al., 2007). Using three fundamental approaches to estimate ephemeral channel recharge (1—closing the water balance for the channel reach, 2—measuring changes in groundwater volume directly [well levels] or indirectly [microgravity], and 3—using geochemical tracers), Goodrich et al. (2004) estimated that during the relatively wet 1999 and 2000 monsoon seasons, regional aquifer groundwater recharge from ephemeral streams ranged from approximately 15 to 40% of total average annual recharge as estimated from a calibrated regional groundwater model (Pool and Dickinson, 2007). During the dry monsoon seasons of 2001 and 2002, limited ephemeral runoff and stream channel infiltration occurred, but no discernible deep aquifer recharge was detected.

The influence of stormflows from ephemeral tributary streams extends to the San Pedro River mainstem. As stormflow is exported from the tributaries to the mainstem and water moves downstream, transmission losses and bank recharge occur within the mainstem river itself and supply water to the alluvial aquifer of the mainstem (Kennedy and Gungle, 2010). Using geochemical tracers (chloride, sulfate, and stable isotopes of hydrogen and oxygen in water), Baillie et al. (2007) found two mains sources of water in the alluvial aquifer for the upper San Pedro River: (1) regional groundwater recharged along the Huachuca Mountains (mountain block, mountain front) to the west, and (2) local recharge from monsoon floodwaters. Alluvial groundwater composition varied between gaining and losing reaches. Locally recharged floodwater comprised 60 to 85% of the alluvial groundwater in losing reaches but only 10 to 40% in gaining reaches. Baseflow also contained a significant component of monsoon floodwater throughout the year, from 80% in upstream reaches to 55% after passing through several gaining reaches.

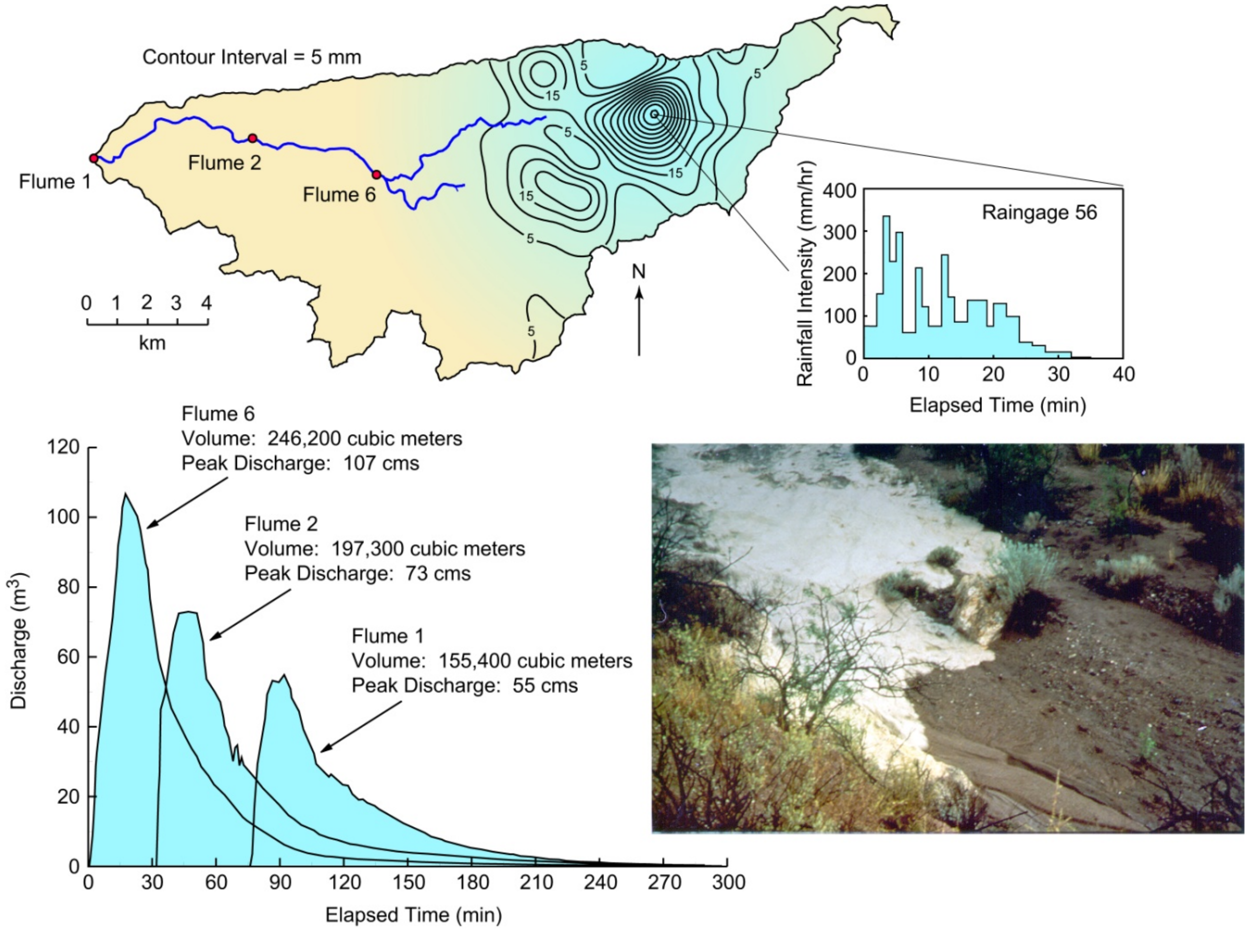


Figure 4-12. Spatial and temporal distribution of precipitation and discharge at nested flumes at Walnut Gulch Experimental Watershed for rainstorm on August 27, 1982.

Photograph shows ephemeral streamflow in a Walnut Gulch ephemeral stream.
From Levick et al. (2008).

Ephemeral tributary stormflows are also sources of sediment and alluvium for the main San Pedro River. Only the largest, less frequent events can flush sediment completely through ephemeral tributaries (Lane et al., 1997). For example, in an arid watershed in Israel, Lekach et al. (1992) found that more than 90% of the bedload yield originated from the mid-catchment channels during larger runoff events. Ephemeral tributary stormflows and their associated sediment loads influence the character of river floodplains and alluvial aquifers (Nanson and Croke, 1992; Shaw and Cooper, 2008).

Extensive riparian plant communities along the mainstem San Pedro River depend on the availability of water in the alluvial aquifer along the river, including water derived from ephemeral stream stormflows (Stromberg et al., 2005; Baillie et al., 2007). These riparian areas, in turn, strongly influence river attributes through stream shading, channel stabilization, nutrient cycling, inputs of invertebrates and other organisms, and inputs of detritus, wood, and other materials (Gregory et al., 1991; National Research Council, 2002; Naiman et al., 2005).

The nutrient and biogeochemical status of the San Pedro River is heavily influenced by ephemeral tributary stormflow inputs. Brooks and Lemon (2007) performed synoptic sampling on a 95-km reach of the San Pedro River to identify the effects of regional hydrology and land use on dissolved carbon and nitrogen concentrations. They found that, during the summer monsoon season, baseflow increased 5- to 10-fold, and dissolved organic matter and inorganic nitrogen increased 2- to 10-fold. The fluorescence index of water samples indicated a large input of terrestrial solutes with the onset of monsoon runoff inflows, and both chloride and oxygen isotope tracer values indicated that streamwater and alluvial groundwater were well mixed along the entire 95-km reach. Meixner et al. (2007) used chloride tracer samples and mixing analyses to examine sources of San Pedro River water during six summer floods in 2001 (wet year) and 2002 (dry year). Results of mixing models indicated that both a groundwater-soil water end-member and a precipitation end-member (indicative of overland flow) contributed to the floods. The highest percentage of groundwater-soil water in the flood flow (46%) occurred during an early 2001 flood and the lowest during large monsoon floods of 2002. They noted that groundwater probably made lower contributions than soil water to streamflow, because high river stage during flood events created hydraulic gradients from the river to alluvial groundwater in the riparian area (water moved from the river to alluvial groundwater via bank storage, see Figure 3-13B). During the first floods of each year, nitrate and dissolved organic carbon increased dramatically in the river, whereas dissolved organic nitrogen did not exhibit increases in 2001 but did in 2002. During floods, nitrate-nitrogen (NO_3-N) concentrations in river water were 0.2–0.5 mg NO_3-N L^{-1} higher in 2002 than during 2001. This result was consistent with higher observed nitrate-nitrogen concentrations in soil water of the riparian zone (alluvial aquifer) in 2002 than in 2001.

In summary, ephemeral tributary streams have strong physical and chemical connections to the San Pedro River. The river ecosystem, including its abiotic and biotic components, depends on the influences exerted by the ephemeral tributary streams on the river environment.

4.8.5. Other Southwestern Rivers

4.8.5.1. *Physical Connections*

Hydrologic behavior and river system connectivity similar to the San Pedro River have been observed in other southwestern rivers, increasing confidence that the observations made within the San Pedro are applicable to other southwestern river systems.

Plummer et al. (2004) found that the Rio Grande in New Mexico has two primary sources of regional groundwater: (1) recharge from mountains and (2) seepage from the Rio Grande and Rio Puerco, and from Abo and Tijera Arroyos (arroyos are ephemeral streams). Vivoni et al. (2006) observed groundwater recharge processes in the Rio Puerco, a tributary river to the Rio Grande, and in the Rio Grande itself. They note that a summer monsoon rainstorm produced a flood event on the Rio Puerco that, in turn, generated a pulse of floodwaters along a losing reach of the Rio Grande (see Figure 4-2). Forty-nine percent (49%) of flood volume was lost to the shallow alluvial aquifer of the Rio Grande. Loss of river water to the alluvial aquifer was observed to decrease with distance down the river reach.

The Pecos River basin in eastern New Mexico and western Texas comprises part of southern Rocky Mountains in the north to grasslands, irrigated farmlands, deserts, and deep canyons in the southern lower reaches of the river (Yuan and Miyamoto, 2008). Precipitation occurs as snow in the mountains and summer monsoonal rainfall in the lower river valley. Based on hydrogen and oxygen isotope composition of river water, Yuan and Miyamoto (2008) separated the river basin into three subbasins: (1) the upper basin, (2) the middle basin, and (3) the lower basin. Snowmelt dominates the mountainous upper basin. The river in the topographically gentle middle basin had mixed sources of water. Thirty-three percent (33%) of river water was lost through evaporation occurring in the streams channels and irrigated fields of the middle basin. Similar to the San Pedro River, up to 85% of streamflow in the lower basin was estimated to derive from local freshwater sources, mainly monsoonal rainfall. This finding is consistent with significant contributions of flow from ephemeral tributary streams.

Shaw and Cooper (2008) studied the 14 ephemeral stream reaches in the Little Colorado River Basin in northeast Arizona. As derived from the USGS National Hydrography Dataset, this basin contains a higher percentage of ephemeral and intermittent stream reaches (70%) as compared to 54% of such reaches in the Upper San Pedro. Shaw and Cooper (2008) related watershed characteristics of the Little Colorado to downstream reaches and the riparian plant communities of those reaches. They found that as the watershed area draining to the studied reaches increased, the overall basin channel slope deceased which resulted in less erosive capacity due to channel transmission losses as well as a decrease in the variability of alluvial groundwater in these channels. This resulted in “decreased disturbance potential and increased moisture availability in the downstream direction,” and these reaches had a greater abundance of obligate riparian vegetation. Shaw and Cooper (2008) went on to develop a stream classification system that related the functional linkages between contributing upstream watersheds, stream reaches, and riparian plant ecology. Type I stream reaches have relatively small drainage areas (less than 10 km^2), which have the greatest disturbance potential with in-channel and near-channel plants resembling those of surrounding upland species. Between 10 and 100 km^2, Type II streams exhibit "more moderate shear stresses and more persistent alluvial groundwater" with riparian vegetation that is a mixture of upland and riparian species. At larger areas (greater than 100 km^2), Type III reaches are "controlled mainly by upstream hydro-climatic conditions" with wetland tree and shrub communities. Shaw and Cooper (2008) concluded that the connection of streamflow and groundwater regimes to riparian vegetation in the larger Type III watersheds, draining greater than 100 km^2, to upstream reaches far removed from larger regional floodplain rivers "… were driven by climatic patterns from distant portions of the upper watershed and were relatively insensitive to local rainfall." This finding reinforces the fact that stream-reach characteristics are influenced and connected, often episodically, to distant portions of the contributing watershed.

4.8.5.2. *Fish and Aquatic Insects*

Stanley et al. (1997) provide an excellent overview of the expansion and contraction of flowing waters within southwestern streams in response to variable precipitation events. This phenomenon commonly results in reaches of streams or rivers that have flow or residual pools with water surrounded by reaches without water. This phenomenon is common in dryland rivers across the globe (Arthington et al., 2005; Bunn et al., 2006). The isolated pools often serve as refuges for fish to survive in intermittent streams during dry periods (Labbe and Fausch, 2000).

As discussed in the previous section, the interplay between stormflow from ephemeral tributary streams, water from alluvial aquifers, and water from regional groundwater control the distribution and timing of flowing water in southwestern rivers. Native fish species of southwestern streams and rivers are adapted to these dynamic environments (John, 1964; Meffe, 1984). Rinne and Miller (2006) compared fish assemblage data in river networks for two southwestern rivers, the Gila River (New Mexico and Arizona) and the Verde River (Arizona) over 7 to 12 years. They included river hydrology and geomorphology data in their analysis and found that variable streamflows and higher flow volumes favor native fish species over nonnatives. They also noted that the presence of unconstrained alluvial valley river reaches with shallow pools favored native fish. Furthermore, when humans alter the hydrologic dynamics of ephemeral and intermittent tributaries such that flows connecting them to the river network are more frequent or more consistent, nonnative fish can invade (Turner and List, 2007). Recent nonnative invasion and a corresponding decline in native fish species diversity was observed in the lower reaches of the Aravaipa Creek, a tributary of the San Pedro River, which historically was rarely connected to the mainstem (Eby et al., 2003).

Lytle et al. (2008) found a similar adaptation strategy in populations of an aquatic insect (*Abedus herberti*) occupying sites along a natural gradient of disturbance predictability. In their study, predictability was defined as the ability of a signal or cue (rainfall) to cause a disturbance.

In this case, the disturbance was a flash flood. Using signal detection theory, they found that for 13 of 15 insect populations, the observed insect response times "were an optimal compromise between the competing risks of abandoning versus remaining in the stream, mediated by the rainfall-flood correlation of the local environment." They concluded that these aquatic insect populations are able to evolve in their responses to changes in the flow disturbance regime, providing evidence that these aquatic populations can adapt to "among-stream differences in flow regime."

4.8.6. Southwestern Intermittent and Ephemeral Streams: Synthesis and Implications

Rivers of the arid and semiarid Southwest are products of a highly variable and dynamic environment. Even before groundwater pumping dewatered numerous river reaches, southwestern rivers commonly had distributions of reaches with perennial, intermittent, and ephemeral streamflow conditions. Many tributary streams to southwestern rivers are ephemeral, but they exert strong influences on the structure and function of the rivers. Some of the major ways in which ephemeral streams are connected with and influence rivers are as follows:

- Flows from ephemeral streams are a major driver of the dynamic hydrology of southwestern rivers. Ephemeral tributary streamflows are especially important drivers of downstream floods during monsoon seasons.

- Mainstem river native fishes and invertebrates are adapted to the variable flow regimes that ephemeral tributary streams strongly influence. Ephemeral flows prevent or mitigate invasion by introduced species.

- Ephemeral tributary streams supply water to mainstem river alluvial aquifers; these alluvial aquifers aid in sustaining river baseflows.

- Ephemeral streams export sediment to rivers during major hydrologic events; the sediment contributes to materials that comprise alluvial aquifers and shape the fluvial geomorphology of rivers.

- Ephemeral tributaries export nutrients to the mainstream rivers during hydrologic flow events; nutrients occur in many forms and are contributors to the productivity of rivers.

- Water, sediment, and nutrients exported to the river from ephemeral tributaries support mainstem river riparian communities; the riparian communities profoundly influence river attributes through shading and allochthonous inputs of organic matter, detritus, wood, and invertebrates to the river.

- Regional groundwater aquifers are in part recharged through infiltration of water to the streambed of ephemeral stream channels during wet years; the regional aquifer supplies a varying but critical portion of baseflow for perennial river reaches.

5. WETLANDS: PHYSICAL, CHEMICAL, AND BIOLOGICAL CONNECTIONS TO RIVERS

5.1. ABSTRACT

Wetlands are transitional ecosystems that occur between terrestrial and aquatic systems. They are inundated or saturated by water at a frequency and duration sufficient to support hydrophytic vegetation and development of hydric soils. The effects of wetlands on rivers and other downstream waters depend on functions within the wetlands and connectivity between wetlands and downstream waters. Riparian/floodplain wetlands can be hydrologically connected to streams and rivers through unidirectional flows of surface water and groundwater from upgradient areas (e.g., hillslopes and adjacent uplands). In addition, riparian/floodplain wetlands have bidirectional connections to streams and rivers through lateral movement of water between the channel and riparian areas. Connections between riparian/floodplain wetlands and streams or rivers can be permanent, can occur frequently (e.g., if the wetland is located within the mean high-water mark), or can occur infrequently (e.g., if the wetland occurs near the edge of the floodplain). Even riparian/floodplain wetlands that rarely flood can have important, long-lasting effects on streams and rivers. Riparian/floodplain wetlands can reduce flood peaks by storing floodwaters, remove large amounts of sediment and nutrients from upland areas, influence stream geomorphology by providing woody debris and sediment, and regulate stream temperature. Riparian/floodplain wetlands also are sources of food for stream and river invertebrates and serve as rearing habitat for fish.

Wetlands in unidirectional landscape settings lack bidirectional connections with channels. However, these settings have the potential for unidirectional hydrologic flows from wetlands to the river network through surface water or groundwater. Unidirectional wetlands can attenuate floods through depressional storage and can recharge groundwater and thereby contribute to baseflow. These wetlands can affect nutrient delivery and improve water quality by functioning as sources (e.g., dissolved organic carbon) and as sinks for nutrients (e.g., nitrogen), metals, and pesticides. Unidirectional wetlands can also provide habitat or serve as sources of colonists for biological communities in downstream waters, through movement of amphibians, reptiles, birds, and mammals. The extent to which unidirectional wetlands perform these functions depends on their hydrologic and biological connectivity with downstream waters. Unidirectional wetlands occur on a hydrologic gradient, from wetlands with permanent connections with perennial channels, to geographically isolated wetlands with groundwater or occasional surface water connections, to highly isolated wetlands with minimal hydrologic connection to the river network (but which could include surface and subsurface connections to other wetlands). Unidirectional wetlands that are connected to the river network through a

channel (i.e., wetlands that serve as stream origins) will have an impact on downstream waters, regardless of whether the outflow is permanent, intermittent, or ephemeral. For unidirectional wetlands that do not connect to the river network through a stream channel (i.e., geographically isolated wetlands and wetlands that spill into losing streams that are completely disconnected from the river network), the type and degree of connectivity with downstream waters will vary with position in the watershed and over time. The literature we reviewed does not provide sufficient information to evaluate or generalize about the degree of connectivity (absolute or relative) or the downstream effects of wetlands in unidirectional landscape settings. However, evaluations of individual wetlands or groups of wetlands could be possible through case-by-case analysis. We can conclude, however, that:

1. A wetland having a surface water outflow to a stream network (e.g., a wetland that serves as a stream origin) is connected to the stream network and has an impact on downstream waters.
2. Many unidirectional wetlands interact with groundwater, which can travel long distances and affect downstream waters.
3. Even hydrologically isolated wetlands can influence downstream rivers by preventing water and other materials from entering the river network.
4. Within a watershed or region, wetlands and open-waters that are closer to rivers and streams will have a higher probability of being connected than more distant areas, assuming that conditions governing type and quantity of flows (e.g., slope, soil, and aquifer permeability) are similar.

5.2. INTRODUCTION

This chapter provides detailed information, based on a review of the pertinent peer-reviewed literature, on how wetlands connect to and influence streams and rivers. In particular, we address two questions (see Section 2.1): (1) What are the connections to and effects of riparian and floodplain wetlands and other waters (e.g., oxbow lakes) on downstream waters? (2) What are the connections to and effects of unidirectional wetlands on downstream waters?

In Chapter 3, we provided definitions for wetlands, gave a rationale for distinguishing between wetlands in bidirectional and unidirectional settings, and discussed general hydrologic and biological mechanisms by which wetlands can connect to and affect streams and rivers. Given that streams and rivers are the endpoints of interest, we limit our discussion of bidirectional wetlands to those occurring in riparian and floodplain settings. Below, we provide a detailed review of the contributions of riparian/floodplain wetlands (see Section 5.3) and unidirectional wetlands (see Section 5.4) to rivers, followed by conclusions concerning these wetlands and their effects on rivers (see Section 5.5). Examples of some of the functions discussed in these two sections are found in Table 5-1. The chapter ends with four case studies on specific types of wetlands or lentic waters representing different landscape settings and geographic regions: oxbow lakes (see Section 5.6), Carolina and Delmarva bays (see Section 5.7), prairie potholes (see Section 5.8), and vernal pools (see Section 5.9).

Most of the literature that we evaluate in this chapter does not specify the type or size of the stream or river (or other water body) that the wetland(s) are connected to or influence. If available, we note this information, but in many cases we can only discuss generic connections to streams, rivers, or downstream waters. However, given that rivers are connected to all upstream components of the river network, including streams (see Chapter 3), and the functional relationships between streams and rivers (see Chapter 4), we consider any evidence of connectivity with a stream (other than losing streams that are completely disconnected from the river network) to be evidence of connectivity with the river and other downstream waters.

5.3. RIPARIAN AND FLOODPLAIN WETLANDS

As previously defined in the conceptual framework (see Section 3.2.1), riparian and floodplain wetlands are locations within bidirectional settings in riparian areas and floodplains (see Figures 3-2 and 3-3), respectively, that meet the Cowardin et al. (1979) definition of having wetland hydrology, hydrophytic vegetation, or hydric soils. The terms “riparian wetland” and “floodplain wetland” frequently describe the same geographic area. Because riparian areas and floodplains also contain upland areas, some riparian/floodplain wetlands are geographically isolated (i.e., completely surrounded by upland).

Although ample literature is available on riparian and floodplain wetlands—especially bottomland hardwood and swamp wetlands—most papers on riparian areas and floodplains do not specify whether the area is a wetland. This lack of specification occurs because riparian areas and floodplains also are studied by stream ecologists and hydrologists who might not focus on whether their study site meets the Cowardin et al. (1979) definition of a wetland. This situation creates a dilemma, because limiting our literature review to papers that explicitly describe the area as a wetland would exclude a major portion of this body of literature and greatly restrict our discussion of wetland science. Alternatively, if we include papers that do not explicitly classify the area as a wetland, we could mistakenly incorporate results that are relevant only to upland riparian areas. Our response to this dilemma was to survey the riparian literature broadly and include any results and conclusions that we judged were pertinent to

Table 5-1. Examples of mechanisms by which riparian/floodplain wetlands and wetlands in unidirectional settings influence downstream waters, by functional type. See relevant section numbers in parentheses for greater detail. Note that there is not always a clear distinction between types of functions, e.g., denitrification could be considered a sink or transformation function

Source Function
• Riparian/floodplain wetlands and unidirectional wetlands connected to the stream network by channelized flow—ranging from ephemeral to permanent—are sources of downstream water (5.3.1.1, 5.4.2.1, 5.6.3.1, 5.7.2.3, 5.8.3.1).
• Wetlands that serve as origins for streams (e.g., seeps) can be sources of groundwater discharge, contributing to stream baseflow (5.2.3, 5.4.2.1).
• Unidirectional wetlands lacking a channel outlet can be sources of water via overland flow to the stream network if wetland storage capacity is exceeded (5.4.2.1, 5.9.3.1, 5.8.3.1). They can also provide water via subsurface drains (“tile drains”) or surface ditches (5.4.2.1, 5.7.3.1, 5.8.3.1).
• Riparian/floodplain wetlands and unidirectional wetlands can be sources of nutrients and sediments to downstream waters (5.3.2, 5.4.3, 5.7.3.2, 5.8.3.2).
• Riparian areas are a source of allochthonous inputs, the primary energy input into the food webs of small forested streams (5.3.2.4). They are also sources of woody debris that can affect stream morphology and flow regime, and provide habitat for aquatic organisms (5.3.1.2).
• Riparian areas and unidirectional wetlands can be sources of dissolved organic matter utilized by aquatic food webs, with additional potential effects on pH and mercury concentrations of downstream waters (5.3.2.1, 5.3.2.6, 5.3.3.1, 5.4.3).
• Riparian/floodplain wetlands and unidirectional wetlands can be sources of organisms, including plants, invertebrates, amphibians, reptiles, and fish, to downstream waters transported via passive or active dispersal (5.3.3, 5.4.4, 5.6.3.3, 5.8.3.3, 5.9.3.2).
• Riparian/floodplain wetlands can provide feeding habitat for riverine organisms, such as fish, during periods of overbank flow (5.3.3.2, 5.6.3.3).
Sink Function
• Riparian/floodplain wetlands and unidirectional wetlands can be sinks for water by intercepting overland or subsurface flow, if available water storage capacity of the wetlands is not exceeded. This can reduce or attenuate flow to downstream waters and flooding (5.3.1.1, 5.4.2.3, 5.8.3.1).
• Riparian areas and unidirectional wetlands can be sinks for sediment and chemical contaminants, such as pesticides, metals, mercury and excess nutrients carried by overland or subsurface flow, potentially reducing loading to downstream waters (5.3.1.2, 5.3.2, 5.3.2.6, 5.4.3.2).
• Riparian areas can be sinks for water, sediment, pesticides, and nutrients from overbank flow events, reducing or attenuating downstream peak flows and materials entrained in the water column (5.3.1.1, 5.3.2, 5.6.3.2). They can also be sinks for seeds and plant fragments deposited via overbank flow (5.3.3.1).
• Riparian/floodplain wetlands and unidirectional wetlands can be sinks for nitrogen by converting nitrogen to molecular nitrogen through denitrification, which is then lost to the atmosphere (5.3.2.2, 5.4.3.2).

Table 5-1. Examples of mechanisms by which riparian/floodplain wetlands and wetlands in unidirectional settings influence downstream waters, by functional type. See relevant section numbers in parentheses for greater detail. Note that there is not always a clear distinction between types of functions, e.g., denitrification could be considered a sink or transformation function (continued)

Refuge Function
• Riparian/floodplain wetlands and unidirectional wetlands can provide refuge for fish, aquatic insects, or other lotic organisms, from predators or other environmental stressors, facilitating individual or population survival (5.3.3.2, 5.4.4).
• Riparian/floodplain wetlands and unidirectional wetlands can provide refuge during certain life stages for lotic organisms. For example, they are breeding sites for frogs and other amphibians that reside in streams as adults (5.4.4, 5.7.3.3, 5.9.3.2; see Table 5-2), and unidirectional wetlands are additionally nesting and nursery sites for American alligators that otherwise primarily reside in streams (5.4.4).
Transformation Function
• Microbial communities in riparian/floodplain wetlands and unidirectional wetlands can transform elemental mercury to methylmercury prior to entering a stream. Methylmercury is a particularly toxic and mobile form that bioaccumulates in aquatic food webs (5.3.2.6, 5.4.3.1).
• Riparian/floodplain wetlands and unidirectional wetlands can transform nitrate to molecular nitrogen through denitrification (5.3.2.2, 5.4.3.2).
Lag Function
• Riparian/floodplain wetlands can temporarily store water following overbank flow, which then can move back to the stream over time as baseflow (5.3.1.1).
• Riparian/floodplain wetlands and unidirectional wetlands can contribute to groundwater recharge under low water table conditions, which ultimately contributes to baseflow (5.4.2.2, 5.4.2.3 5.8.3.1).
• Unidirectional wetlands can increase the time for stream discharge to rise and fall in response to a precipitation event due to wetland storage capacity (5.4.2.3).

riparian/floodplain wetlands. This judgment was based, in part, on: (1) the processes described in the conceptual framework (see Sections 3.2.2 and 3.2.3); (2) whether the information applies to all riparian areas, regardless of whether they are wetlands or uplands (e.g., all riparian areas are subject to periodic overbank flooding); and (3) an understanding of the specific processes. For example, riparian studies of denitrification are likely to be either in a wetland or applicable to riparian/floodplain wetlands, because the alternating oxidation/reduction conditions required for denitrification are present in wetlands. Therefore, in our assessment of evidence regarding the connectivity and effects of riparian areas and floodplains, we have concluded based on these judgments that the processes and functions discussed are provided by water bodies within those areas.

As addressed in Chapter 3, much of the theory developed to explain how riverine systems work has focused on linkages between system components (e.g., Vannote et al., 1980; Newbold et al., 1982a; Newbold et al., 1982b; Junk et al., 1989; Ward, 1989; Benda et al., 2004; Thorp et al., 2006). Indeed, central tenets of stream hydrology and ecology are the intimate connectivity between a river and its riparian area/floodplain, and the substantial influence this bidirectional exchange has on the hydrology, chemistry and biology of the river system (Junk et al., 1989; Tockner et al., 2000; Naiman et al., 2005). For instance, the Flood Pulse Concept, first articulated by Junk et al. (1989) and extended by Tockner et al. (2000), is a fundamental paradigm in riverine ecology, depicting the lateral expansion and contraction of the river in its floodplain and the resulting exchange of matter and organisms. Many fish populations, for example, are adapted to use floodplain habitat for feeding and spawning during high water (Junk et al., 1989; Bayley, 1991; Pezold, 1998). Riparian/floodplain wetlands are widely recognized as having frequent connections to streams and rivers and significant influence on water, sediment, and solute fluxes to streams (Naiman et al., 2005; Vidon et al., 2010) and are similarly affected by material and energy fluxes from streams. For instance, the restoration of 70 km of the Kissimmee River channel in Florida includes reestablishing the links between the river and >100 km^2 of river and floodplain habitats, with a focus on restoring interactions between hydrology, nutrients, dissolved and particulate organic matter, and wetland vegetation (Dahm et al., 1995). Dahm et al. (1995) expect over 11,000 ha of wetland scrub habitat to be restored from current pasture/upland scrub/human-influenced habitats based on reestablishing the hydrology of the system. Riparian/floodplain wetlands also influence streams as an area of nutrient and sediment deposition, and by shading, stabilizing streambanks, and providing habitat for diverse organisms (Naiman et al., 2005; Vidon et al., 2010). This section provides further details on the connections between riparian wetlands and streams and rivers, and the resulting effects.

5.3.1. The Physical Influence of Riparian Areas on Streams

5.3.1.1. *Hydrology*

Riparian areas have a diverse set of hydrologic inputs and outputs that connects them to streams and rivers (see Figure 3-6A). These inputs and outputs are described in Section 3.2 and reviewed by various authors (National Research Council, 2002; Naiman et al., 2005; Vidon et al., 2010). Many studies document that riparian floodplains help attenuate flood pulses in streams, by both capturing water from overland flow and storing excess water from streams. Bullock and Acreman (2003) reviewed the wetland literature and reported that floodplain wetlands reduced or delayed floods in 23 of 28 studies. Walton et al. (1996) found that peak discharges between upstream and downstream water gages on the Cache River in Arkansas were reduced 10−20%, primarily due to floodplain water storage. A study by Gamble et al. (2007) reported that 12 floodplain wetlands in Ohio stored an average of 3,654 $m^3\ ha^{-1}$ of water. They further developed equations relating volume to area and depth for more than 650 regional wetlands and reported that these systems could store approximately 1−2% of the daily flow of larger streams and approximately 40% of the daily flow of small streams (Gamble et al., 2007). As streamflow decreases after hydrologic events, the water temporarily stored in riparian areas can flow back into the channel, supporting stream baseflow (Whiting and Pomeranets, 1997; Chen and Chen, 2003). Although not all riparian/floodplain wetlands store the same amount of water, almost all of them have the potential to perform this function. In addition to the water storage capacity of floodplain and riparian wetlands, riparian vegetation also can influence water levels in the stream by capturing and transpiring water. Phreatophytes (plants that obtain their water from the saturated zone) can intercept groundwater and overland flow before it enters a stream and decrease stream flow by directly taking up stream water through their roots. Meybloom (1964) studied two streams in the Prairie region of the United States to understand how associated floodplain vegetation affects streamflow fluctuations. When the two streams decreased in flow, the floodplain vegetation accounted for 20 and 100% of this reduction (Meyboom, 1964).

5.3.1.2. *Geomorphology (Sediment-Vegetation Interactions)*

Overland flow from uplands can be ponded by infiltrate riparian areas, thereby retaining sediment from uplands before it reaches the stream. Riparian areas can also promote sediment removal in water from overbank flow events. As discussed in Section 4.3.2, sediment is important to streams and rivers because it strongly influences stream energy dissipation and channel morphology; sediment movement creates point bars, meanders, channel cutting, and other channel patterns, which are constantly changing (Ward, 1998; Ward et al., 2002).

Wetlands in riparian areas and floodplains serve as important depositional environments for sediment carried by overland flow from erosion of adjacent uplands (Boto and Patrick, 1979; Whigham et al., 1988). Riparian areas retain portions of this sediment before it enters the stream, especially if the overland flow enters the riparian area as sheetflow runoff rather than as channelized flow, due to the greater volume of water exposed to riparian-wetland soils and vegetation surfaces (Dabney et al., 1995; Meyer et al., 1995; Naiman and Decamps, 1997; National Research Council, 2002; Naiman et al., 2005). Riparian open-waters (e.g., oxbows) as well as wetlands are effective at retaining eroded clays, silts, and sands that would otherwise enter stream channels (Cooper et al., 1987; Heimann and Roell, 2000). Riparian areas were shown to remove 80−90% of sediments leaving agricultural fields in North Carolina (Cooper et al., 1987; Daniels and Gilliam, 1996; Naiman and Decamps, 1997). Grassy riparian areas alone can trap more than 50% of sediments from uplands when overland water flows are less than 5 cm deep (Dillaha et al., 1989; Magette et al., 1989; Naiman and Decamps, 1997). Thus, riparian areas can buffer stream channels against excessive sediment input.

Riparian areas can be both sinks and sources for sediments in streams. When streams flood their banks, increased surface contact and friction decrease the flow velocity. The slower moving water has a diminished capacity for keeping material in the water column in suspension, which causes the sediments to deposit. Heavy particles such as sand are the first to be removed (National Research Council, 2002; Naiman et al., 2005), whereas finer particles such as clays and silts are lighter and take longer to deposit. In southeastern coastal plain systems, sediment deposition rates from the stream to the floodplain are high because of frequent overbank flow and relatively high sediment loads of the rivers (Hupp, 2000).

Conversely, riparian areas can also be a source of sediment to the stream, particularly through stream bank erosion. Although stream bank erosion is a natural process, it can be accelerated through vegetational changes, since root tensile strength of riparian vegetation reinforces the soil (Naiman and Decamps, 1997; Burt et al., 2002). Streambanks that are devoid of vegetation are often highly susceptible to channel widening (Hupp et al., 1995; Naiman and Decamps, 1997). A study of 748 bends in four southern British Columbia streams, for example, reported that bank erosion was 30 times more prevalent on nonvegetated versus vegetated banks (Beeson and Doyle, 1995). In a comparison of row-crop agriculture, grazing, and forested riparian areas in central Iowa, the forested areas exhibited significantly reduced streambank erosion rates (Zaimes et al., 2004). Certain riparian wetland vegetation types, such as black willow (*Salix nigra*), maintain bank integrity and decrease erosion so well that they are used in river restoration and bank stabilization projects (Pezeshki et al., 2007). Thus, the riparian vegetation community is integral to stream geomorphology and erosion control.

Riparian vegetation also shapes stream geomorphology through inputs of woody debris or logs, which in turn shape stream channels. Woody debris can enter streams through tree mortality, bank undercutting, windthrow, wildfire, floods, landslides, and debris flows (Gurnell et al., 2002; Reeves et al., 2003). Gurnell et al. (2002) reported that the amount of wood deposited into streams can range from 12 to 40 t km^{-1} yr^{-1}, depending on the type of stream and nearby vegetation. As discussed in Section 4.3.3, woody debris can alter stream channels, trap sediments, and form new aquatic habitat (Anderson and Sedell, 1979; Harmon et al., 1986; Nakamura and Swanson, 1993; Abbe and Montgomery, 1996; Naiman and Decamps, 1997; Gurnell et al., 2002).

5.3.1.3. *Temperature and Sunlight*

Riparian areas can modify stream temperatures, and particularly in forested areas, the amount of light available for photosynthesis. Surface water temperatures are often highly related to groundwater and riparian soils. Excepting groundwater flowpaths discharging directly to the stream, groundwater often moves through the alluvium of the riparian area, exchanging heat and equalizing its temperature prior to reaching the stream (Brosofske et al., 1997; Naiman and Decamps, 1997; Poole and Berman, 2001; Naiman et al., 2005). Additionally, riparian areas play a major role in modifying stream temperatures when vegetation shades the stream (Barton et al., 1985; Gregory et al., 1991; Blann et al., 2002). Dense, overhanging vegetation greatly reduces the intensity of light, whereas open canopies allow light to penetrate (Gregory et al., 1991). This radiant energy, or lack thereof, has a strong influence on stream temperature (Barton et al., 1985; Gregory et al., 1991; Blann et al., 2002). The maximum temperature of a stream in Oregon, for example, was 7°C higher in a reach where the riparian vegetation was removed compared to its temperature when it was forested. Fifteen years of regrowth in the harvested area was required for the stream temperature to return to preharvest levels (Johnson and Jones, 2000).

By affecting stream temperatures, shading by riparian vegetation can alter fish growth, activity and mortality, while also influencing their prey species (Beschta et al., 1987). Higher temperatures, for example, can lead to greater stream invertebrate biomass (Beschta et al., 1987). The net temperature effect on fish growth, however, depends upon the balance between food availability and higher metabolic rates (Beschta et al., 1987). Riparian vegetation enhancement can be used by managers to promote fish habitat for certain desired species. Blann et al. (2002) investigated the degree to which different types of riparian vegetation could increase shade, reduce stream temperatures, and promote habitat for brook trout (*Salvelinus fontinalis*) in Minnesota. The researchers concluded that both forested and herbaceous riparian vegetation shaded the stream and buffered stream temperature, and could aid in creating appropriate coldwater trout habitat (Blann et al., 2002).

Shading of the stream by riparian vegetation also has a direct influence on the instream net primary productivity (NPP) of aquatic plants and other photosynthetic organisms, such as algae, by altering light availability (Gregory et al., 1991). Net primary production is greatest in open reaches and is significantly less in reaches that are forested and shaded (Gregory et al., 1991). For example, Gregory et al. (1991) reported that net primary production in open streams in Oregon averaged 210 mg carbon (C) m^{-2} d^{-1}, whereas forested reaches of streams with deciduous vegetation averaged 58 mg C m^{-2} d^{-1}. Reduced net primary production leads to lower densities of herbivores in streams (Hawkins and Sedell, 1981; Gregory et al., 1991). Shading can be limiting to streams (Hill and Knight, 1988; Gregory et al., 1991), but it can also be beneficial by reducing excessive algal production in nutrient-enriched waters. Algae can lead to excessive biological oxygen demand and turbidity and can decrease water quality in downstream systems (Volkmar and Dahlgren, 2006).

5.3.2. The Chemical-Nutrient Influence of Riparian Areas on Streams

Wetlands have been described as depositional areas in an eroding landscape (Brittain and Eikeland, 1988). Pollutants and materials relevant to discussions on water quality—such as nutrients, pesticides, and metals—enter wetlands (e.g., Tiner, 2003c; Comer et al., 2005) through flow pathways that include dry and wet (e.g., rain, snow) atmospheric deposition; point sources such as outfalls, pipes, and ditches; and nonpoint sources, such as runoff from agricultural and urban fields and lawns, drift spray, and diffuse near-surface water inputs (Nixon and Lee, 1986; Whigham and Jordan, 2003; Whitmire and Hamilton, 2008). For riparian/floodplain wetlands, transport from upstream reaches or through the hyporheic zone (see Figure 3-6) is another important source of these substances. Such materials can then be sequestered via sorption (adsorption and absorption) or sedimentation processes, assimilated into the flora and fauna, transformed into other compounds, or lost to the atmosphere through transformational processes (Nixon and Lee, 1986; Johnston, 1991; Mitsch and Gosselink, 2007). These processes include conversion between particulate and dissolved forms of compounds via biologically mediated degradation (e.g., Bärlocher et al., 1978) and reduction-oxidation (redox) reactions (Nixon and Lee, 1986; Reddy and DeLaune, 2008). Redox reactions play an essential role in microbial respiration and are critical to both defining wetland systems and understanding transformational processes that are mediated by microbes (Boon, 2006; Reddy and DeLaune, 2008).

5.3.2.1. *Hyporheic/Soil Processing of Nutrients*

Riparian areas connect upland and aquatic environments through both surface and subsurface hydrologic flowpaths (Naiman et al., 2005; see Figure 3-6). Riparian areas act as buffers that are among the most effective tools for mitigating nonpoint source pollution (Knight et al., 2010). These areas are uniquely situated in watersheds to receive and process waters that pass through the root zone before reaching streams (Gregory et al., 1991). Deep groundwater hydrologic flowpaths (see Figure 3-5) that enter a river or stream below the active riparian root zone are not affected by these processes. The focus of this section, however, is on surface and shallow subsurface flows; deep groundwater flow paths are not addressed here.

Riparian areas can have significant impacts on nutrients and other exports from watersheds (Gregory et al., 1991) and can be considered areas of major nutrient transformation as subsurface waters move through them (Dahm et al., 1998). Riparian areas remove nutrients such as nitrogen and phosphorus from water as it flows from uplands to streams (Lowrance et al., 1997; Dosskey, 2001; Mayer et al., 2007). The ability of a riparian area to act as either source or sink of nitrogen, phosphorus, organic matter, pesticides, and mercury is largely controlled by the substance's concentration in riparian soils (Gregory et al., 1991), soil redox conditions, and hydrology (Vidon et al., 2010). For example, riparian plant communities can release seasonal pulses of dissolved leachates derived from stream litter (Fisher and Likens, 1973). Riparian areas are therefore central to watershed water quality management (Burt, 1997; Lowrance et al., 1997).

5.3.2.2. *Nitrogen*

Riparian areas can remove dissolved nitrogen in subsurface flowpaths that would otherwise flow into streams (Vidon et al., 2010). Removal occurs via plant uptake and microbial transformations (i.e., assimilative uptake, assimilatory nitrate reduction to ammonium, and dissimilatory nitrate reduction to ammonium or nitrogen gases such as dinitrogen, nitric oxide, and nitrous oxide via denitrification). Indeed, a study has demonstrated that intact riparian and hyporheic zones are critical in decreasing the amount of dissolved inorganic nitrogen that finds it way from headwaters to larger, downstream waterways (Triska et al., 2007). Riparian areas are often responsible for the removal of more than half of the nitrogen from surface and shallow subsurface water transporting ammonium and nitrate through the rhizosphere (Vidon et al., 2010). However, leaching from nitrogen-fixing plants (e.g., red alder, *Alnus rubra*) in riparian systems can also be a major source of nitrogen to stream systems (Compton et al., 2003).

Denitrification potential in surface and shallow subsurface flows is not homogenous across the riparian area, and increases greatly in the presence of organic carbon or anoxic conditions which create denitrification "hot spots" (Vidon et al., 2010). Therefore, for riparian areas to appreciably increase nitrogen removal, flowpaths that convey nitrate-rich water into such denitrification "hot spots" must be present (Vidon et al., 2010).

Some studies have examined denitrification potential in riparian surface soils 0−20 cm in depth (Vidon et al., 2010). The highest denitrification potentials occur where high organic matter levels, denitrifying microbes, and saturated soil conditions are present (Vidon et al., 2010). Rates of denitrification have been shown to be greater in riparian soils nearer to streams (Gregory et al., 1991). High soil moisture and deposited organic matter enhance microbial activity, thereby tending to increase denitrification (Vidon et al., 2010).

As subsurface flow passes through riparian areas, vegetative demand for dissolved nutrients also can reduce nutrient loads (Vidon et al., 2010). More than three-quarters of the dissolved nitrate transported from agricultural fields to a Maryland river (Vidon et al., 2010) were removed by riparian forests. Nitrate N was removed at a rate of 45 kg ha^{-1} yr^{-1} as subsurface flow moved from agricultural fields through riparian zones to nearby streams (Peterjohn and Correll, 1984). In the coastal plains of Georgia, riparian forests retained more than 65% of the nitrogen and 30% of the phosphorus contributed from nearby agriculture (Vidon et al., 2010). In southern Pennsylvania, a forested riparian area had a subsurface NO_3^- budget with an average removal of 90 kg NO_3^- ha^{-1} yr^{-1}, which was 26% of the total nitrate input (Newbold et al., 2010).

5.3.2.3. *Phosphorus*

The movement and uptake of phosphorus in riparian areas are a result of the coincidence of phosphorus sources, hydrology, and biogeochemistry (Vidon et al., 2010), with interactions between groundwater and surface waters driving the biogeochemical processes (Hoffmann et al., 2009). Therefore, phosphorus loss and retention in riparian areas are related to the flowpath of the water through the riparian area to the stream (e.g., overland flow of water from adjacent agricultural fields, river water inundation of floodplain riparian areas). Flowpath dictates the confluence and interaction of phosphorus with minerals that drive biogeochemical cycling of phosphorus in riparian areas (Hoffmann et al., 2009). The physical processes of sedimentation and plant uptake are active in these flowpaths and can account for particulate P retention rates as high as 128 kg P ha^{-1} yr^{-1} and 15 kg P ha^{-1} yr^{-1}, respectively (Hoffmann et al., 2009). Retention of dissolved phosphorus in riparian areas is more modest, with values often reported as being less than 0.5 kg P ha^{-1} yr^{-1}. Studies show, however, significantly higher numbers for the release of dissolved phosphorus at up to 8 kg P ha^{-1} yr^{-1} (Hoffmann et al., 2009).

Although riparian soils generally act as sources of phosphorus when soils are anoxic or when mineral dissolution releases phosphorus (Baldwin and Mitchell, 2000; Chacon et al., 2008), riparian areas act as phosphorus sinks in oxic soils (Carlyle and Hill, 2001). Portions of riparian areas where agricultural sediments are deposited are phosphorus sources to streams if the phosphorus is desorbed and leached but can be sinks by adsorbing dissolved phosphorus if sediment phosphorus concentrations are low (Dillaha and Inamdar, 1997; Sharpley and Rekolainen, 1997). Riparian areas can also act as phosphorus sinks when upland surface runoff travels through the riparian area or where phosphorus in fine-grained sediment is deposited overbank onto the riparian area (Dillaha and Inamdar, 1997). These sediments, however, can become sources of phosphorus if they are later saturated with water and iron and manganese are reductively dissolved during anoxic conditions, thus causing them to desorb phosphorus (Reddy and DeLaune, 2008).

5.3.2.4. *Carbon and Allochthonous Inputs*

Both production and consumption of organic and inorganic carbon occur in riparian areas. In areas with reducing conditions, microbes generally oxidize organic carbon and reduce available electron acceptors, releasing carbon dioxide gas and making the soils more alkaline (Vidon et al., 2010). This process can result in chemical gradients in which electron acceptor concentrations decrease and alkalinity increases along subsurface flowpaths (Burns, 1996; Cirmo et al., 2000; Bailey Boomer and Bedford, 2008). Riparian areas, especially those in low-lying flatlands, tend to have low subsurface flow velocities resulting in anoxic conditions, shallow water tables, and slow organic matter decomposition, as is often seen in riparian wetlands. This is why riparian areas are active areas for biogeochemical transformations (Vidon et al., 2010).

Allochthonous inputs to streams in riparian areas are critical to aquatic food webs, particularly in headwater catchments (reviewed in Tank et al., 2010). Allochthonous inputs are terrestrial organic materials that enter the stream through vegetation litter (i.e., woody debris, leaves, and partially decomposed plant parts), erosion, and hydrologic flows (Wetzel, 1992). In small forested watersheds, overhanging trees provide organic matter inputs, while simultaneously reducing photosynthesis by autotrophic organisms (Vannote et al., 1980). This dual effect makes allochthonous inputs the primary source of energy flow into the food web of these streams. For example, in a New Hampshire stream the surrounding forest supplied more than 98% of the organic matter (Gregory et al., 1991). Organic matter inputs are important because they impact food availability to aquatic organisms by releasing organic carbon and nitrogen into streams (Wetzel and Manny, 1972; Mulholland and Hill, 1997). For instance, in a small headwater stream near Louisville, KY, macroinvertebrate communities, which are critical food sources for fish (Wallace and Webster, 1996), relied almost exclusively on leaf inputs (Minshall, 1967). Excluding litter from the riparian area changed the food web structure of a North Carolina stream (Wallace et al., 1997) and decreased its dissolved organic carbon concentrations and loadings (Meyer et al., 1998). In addition to the impacts of total inputs, the composition and timing of allochthonous inputs, largely determined by riparian plant species composition, can also influence instream decomposition and aquatic invertebrates (Cummins et al., 1989; Swan and Palmer, 2006).

Downstream, much less of the stream is directly influenced by streamside vegetation, decreasing the relative importance of allochthonous inputs while concomitantly increasing the importance of instream photosynthesis (Vannote et al., 1980). The macroinvertebrate community responds to this shift in input types. For example, macroinvertebrate shredders that use large inputs, such as leaves, become less prevalent as streams increase in size. Besides changing longitudinally with stream size, riparian allochthonous inputs also can vary seasonally, with a large pulse occurring in deciduous forests during autumn leaf fall.

5.3.2.5. *Pesticides*

The roots in riparian areas can be important for the removal of pesticides from shallow subsurface flow, because the labile organic matter and organic residues that accumulate near roots can increase microbial biomass and activity (Vidon et al., 2010). Pesticides and their metabolites can be mineralized and adsorbed where there is high surface area contact and sufficient contact time with roots (Krutz et al., 2006). A study of the pesticides alachlor and atrazine in a riparian area notes the importance of plant uptake in the fate of these pesticides, and suggests that vegetated buffer zones help to protect water supplies (Paterson and Schnoor, 1992). Studies examining specific pesticides—for example, isoproturon (Benoit et al., 1999), metolachlor (Staddon et al., 2001), and atrazine (Mudd et al., 1995)—found that the presence of vegetation, associated root zones, and accumulated organic matter increased the removal of those pesticides (Vidon et al., 2010). Pesticide-degrading microbial populations increase after repeated chemical applications (Gonod et al., 2006), suggesting that riparian areas can become better at degrading pesticides that enter these zones (Vidon et al., 2010). In addition, microbial biomass has been shown to be positively correlated with the loss of the herbicides 2,4-D (2,4-dichlorophenoxyacetic acid) and dicamba, suggesting a relationship between the amount of microbial biomass in the soil and the capacity of an ecosystem to degrade pesticides (Voos and Groffman, 1996).

5.3.2.6. *Mercury*

Mercury enters the global atmosphere primarily through waste incineration and coal combustion. It can directly enter wetland systems or can be deposited on terrestrial areas and then transported into riparian areas and wetlands via rainfall and runoff (St. Louis et al., 1994). Riparian soils and wetlands are important both for mercury mobilization (Mierle and Ingram, 1991; Driscoll et al., 1995) and the production of methylmercury (MeHg), a particularly toxic and mobile form of the element. Mercury methylation occurs in the presence of anoxic, saturated soils high in organic matter, mercury-methylating microbes, and mercury from either atmospheric deposition or soils (St. Louis et al., 1996). The redox conditions found in the presence of a fluctuating water table are thought to be a strong driver of mercury methylation (Heyes et al., 2000; Branfireun and Roulet, 2002; Branfireun, 2004). Export of mercury and methylmercury can expose organisms in downstream aquatic ecosystems to potential toxicity (Thurman, 1985; Driscoll et al., 1995). Mercury bioaccumulates in fish, and consumption of fish is the main human pathway for exposure to mercury (Rypel et al., 2008).

The source-sink dynamics of riparian areas with respect to mercury are complex. Because soils accumulate mercury, they buffer aquatic ecosystems against the full impact of this pollutant (Aastrup et al., 1991). However, because some of this mercury and methylmercury moves from soils to surface waters, riparian areas may also be a source of the mercury that ends up in the aquatic food web.

5.3.3. Biological Connections Between Riparian Areas and Streams

The dynamic nature of river systems is most apparent in riparian areas, where a shifting landscape mosaic supports diverse communities of aquatic, amphibious, and terrestrial species adapted to periodic or episodic inundation of riparian areas and floodplains (Robinson et al., 2002). In unregulated rivers, floodplain inundation greatly increases the area and diversity of aquatic habitats (Junk et al., 1989; Tockner et al., 2000). It also allows rapid cycling of nutrients imported from river channels (see Section 5.3.2), resulting in high primary productivity of plants and algae (Junk et al., 1989; Tockner et al., 1999). The combination of diverse habitat types and abundant food resources makes floodplains important foraging, hunting, and breeding sites for fish (Copp, 1989), aquatic life stages of amphibians (Richardson et al., 2005), and aquatic invertebrates (Smock et al., 1992; Smock, 1994). Many of these organisms have growth stages or reproductive cycles timed to coincide with seasonal hydrologic connectivity between rivers and floodplains. Thus, lateral fluctuations in hydrologic connectivity can increase overall levels of species productivity and biodiversity in river systems (Junk et al., 1989). Here, we review examples of adaptation to and exploitation of riparian habitats by aquatic species of plants, fish, mammals, and invertebrates.

5.3.3.1. *Vascular Plants and Phytoplankton*

Channels, riparian wetlands, and floodplain wetlands provide habitat for aquatic vegetation, emergent vegetation, and phytoplankton. When seeds, plant fragments, or whole organisms move back and forth between riparian/floodplain wetlands and the river network (via water, wind, or animal dispersal), these areas become biologically connected. Species can disperse via overbank flow between channels and riparian/floodplain wetlands (e.g., Schneider and Sharitz, 1988; Middleton, 2000; Nilsson et al., 2010). Seeds from vegetation within the channel or that have been mobilized from upstream riparian/floodplain wetlands can be deposited on bordering or downstream riparian areas and floodplains (Nilsson et al., 2010), much like sediment and in many cases with sediment (Gurnell, 2007; Gurnell et al., 2008). For instance, in the southwestern United States, soil seed banks of wetland plants can be established or replenished in floodplains when those areas are connected to a stream channel by overbank flow (Boudell and Stromberg, 2008). In another example, 41% of plant species whose seeds deposited on riparian areas during winter flood flow in two United Kingdom rivers were wetland or aquatic plants (Gurnell et al., 2008). Overland flow or flooding can also dislodge viable plant fragments in riparian/floodplain wetlands, which then get transported back down the river network. Fragments of seep monkeyflower (*Mimulus guttatus*) are easily dislodged by the typically high flow velocities along riparian areas, and fragments can survive and reestablish downstream at rates above 90% (Truscott et al., 2006).

Floodplains can function as sinks for seeds and plant fragments. For example, in a forested floodplain wetland in Illinois, many bald cypress (*Taxodium distichum*) seeds dispersed by the river network were deposited but did not germinate (Middleton, 2000). Alternatively, establishment and reproduction of refuge floodplain populations can become important wetland seed sources for the river network, especially if catastrophic flooding scours vegetation and seed banks that can exist on streambeds (Gurnell et al., 2008).

Hydrologic connectivity between channels and riparian/floodplain wetlands can significantly enhance riparian vegetation diversity (Jansson et al., 2005) and determine floodplain wetland community structure (Boschilia et al., 2008). In the case of nonnative species, however, connectivity can facilitate invasion, resulting in changes in riparian vegetation community structure. In an intermittent stream in Illinois, tubers of the nonnative Chinese yam (*Dioscorea oppositifolia*) were dispersed via stormflow and overbank flow and became established along a narrow upstream riparian area and wider channel and floodplain more than 1 km downstream; the presence of the nonnative plant significantly reduced native plant cover (Thomas et al., 2006). Vegetation community composition, in turn, can affect the function of riparian areas as nutrient sources or sinks to the river network (e.g., see Sections 5.3.2.2 and 5.3.2.4). Invasion by nonnative riparian plants also can result in altered stream invertebrate diversity among other effects (Lecerf et al., 2007).

Seeds of aquatic and riparian plants also can be actively dispersed by animals that consume them. For instance, seeds of the aquatic emergent bur-reed (*Sparganium emersum*) were found to be ingested and viably excreted by common carp (*Cyprinus carpio*; Pollux et al., 2007), which elsewhere have been observed using channel and floodplain wetland habitat (King et al., 2003). Absent hydrologic connections, riparian floodplain and wetland vegetation can disperse and exchange seeds via terrestrial animal vectors and the wind. Animals that travel overland can also disperse ingested seeds or seeds adhering to fur or limbs between riparian/floodplain wetlands and the river network (see Section 5.3.3.2 for discussion of animal movement). Many macrophyte species have evolved for dispersal by wind, including some of the most invasive in North America, cattail (*Typha spp.*) and reed canary grass (*Phalaris arundinacea*; Barrat-Segretain, 1996; Soons, 2006 and references therein). Given the proximity of riparian/floodplain wetlands and the river network itself, dispersal of pollen and seeds between these habitats could be quite frequent. For instance, seeds of some 20 species found in floodplain wetlands in bald cypress swamps in Illinois were caught in aerial seed traps, and dispersal of three species averaged more than100 seeds m^{-2} yr^{-1} (Middleton, 2000).

Phytoplankton also moves via water between floodplain wetlands and the river network. A river with overbank flow can homogenize the phytoplankton communities in floodplain wetlands separated by more than 5 km (Angeler et al., 2010), and phytoplankton communities in river networks can be bolstered by high productivity conditions in temporarily connected floodplain wetlands. For example, a portion of flow from California's Sacramento River is seasonally diverted from the main channel into the Yolo Bypass, an adjacent 240-km^2 floodplain. From January to June 2003, 14 and 31% of total diatom and total green algae biomass, respectively, was produced in the floodplain (Lehman et al., 2008). This considerable contribution of carbon to the aquatic food chain, which ultimately supports downstream fisheries, resulted from the high net primary productivity of the floodplain. This observation is particularly impressive because the median flow through the floodplain during the period of measurement (23 m s^{-1}) was just 3% of the median flow through the main channel. Considered collectively, these studies indicate that riparian/floodplain wetlands can be both sources and sinks for phytoplankton and water-, animal- and wind-dispersed vascular plants with respect to the river network.

5.3.3.2. *Vertebrates*

Animals, including many fish and mammals, move between riparian/floodplain wetlands and the river network. When hydrologically connected, there is strong and abundant evidence that fish can move between the main river channel and riparian/floodplain wetlands that, in some cases, are seasonal or temporary. Such wetlands provide refuge, feeding, and rearing habitat for many fish species and function as sources by augmenting recruitment to the river network; examples include fish taxa in forested floodplain wetlands of the southeastern and southwestern United States and salmonids of the northwestern United States such as Coho salmon (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*; e.g., Wharton et al., 1982; Matheney and Rabeni, 1995; Pease et al., 2006; Henning et al., 2007; Jeffres et al., 2008). In one section of the mainstem Rio Grande in New Mexico, over 90% of the larval and juvenile fish of six different captured species were from riparian areas with zero water velocity (backwaters, former side channels, and isolated pools; Pease et al., 2006). Oxbow lakes are also important habitats for fish feeding and rearing. Based on a 5-year study of fish in oxbow lakes, Shoup and Wahl (2009) concluded that the entire floodplain should be considered a single functioning unit that supports the overall biological integrity of a river (see also Section 5.6). The use of riparian/floodplain wetlands by fish depends on many factors intrinsic to the particular river system (e.g., periodicity and duration of floodplain inundation) and the characteristics of the resident or migratory fish community (King et al., 2003).

Fish also move between lacustrine wetlands (wetlands associated with lakes) and large lakes when hydrologic connections exist. Fish communities in the Great Lakes and their surrounding wetlands become more homogenous when surface connections between the wetlands and lake are present. Fish use these wetlands for refuge from predators and as rearing habitat (Jude and Pappas, 1992). River-dwelling mammals also move between rivers and riparian/floodplain wetlands, including river otters, which have been observed using wetlands extensively as latrines (Newman and Griffin, 1994). Thus, animal movement, especially fish, connects riparian/floodplain wetlands to the river network and supplies streams and rivers with a source of biological materials.

In addition to acting as sources, sinks, and refuges for individual species of organisms, riparian/floodplain wetlands can improve the overall health of biological communities. For example, a positive relationship between wetland cover and an index of biological integrity for fish communities in rivers was observed in 23 sites at several small catchments of the River Raisin in Michigan (Roth et al., 1996).

Besides providing a form of biological connectivity that can link riparian/floodplain wetlands and downstream waters, vertebrates in riparian areas can affect stream characteristics and influence various forms of connectivity. Perhaps the most familiar example of this is the beaver (*Castor canadensis*). Although it would seem that beaver damming should reduce hydrologic connectivity through impoundment, their influence can be more complex. For example, a study by Westbrook et al. (2006) found that beaver dams in the Colorado River affected depth, extent, and duration of inundation resulting from a 10-year flood event. In addition, beaver dams attenuated declines in water tables during drier summer periods in 25% of their 58-ha study area. However, they concluded that the main hydrologic effects occurred downstream, rather than near the dam (Westbrook et al., 2006). The hydraulic head generated by the dam raised the water level above adjacent banks, resulting in lateral and downstream spreading of flows during high- and low-flow periods; these effects extended over hundreds of meters. For example, mottled soils occurred throughout the study area, suggesting that the dams caused waterlogged soils for extended periods of time. Increased overbank flooding increases hydrologic connectivity between riparian areas and streams. In contrast, when dams were absent, flooding was limited to the area immediately adjacent to the stream channel. Beaver dams can also affect stream biogeochemistry. For example, beaver dams modify nutrient cycling and decomposition dynamics and can affect downstream transport of materials (Naiman et al., 1988), e.g., they can serve as a source of methylmercury (Roy et al., 2009). Beaver dams can also have an effect on fish species, such as coho salmon (Pollock et al., 2004).

In addition to their own direct effects, vertebrates can indirectly affect hydrologic connectivity through cascading effects on riparian plant communities. Beschta and Ripple

(2012) provide evidence from analyses at three western National Parks for a trophic cascades model where large predators can affect the morphology of river channels through intermediate effects on ungulate browsers and riparian plant community structure. For example, extirpation of wolves (*Canis lupus)* at Yellowstone National Park by the mid-1920s led to an increase in elk (*Cervus canadensis*) numbers. This caused suppression and mortality of riparian willow (*Salix spp.*) communities, ultimately resulting in changes to stream morphology such as bank erosion, decreased sinuousity, increased active channel width, and increased amount of unvegetated alluvium (Beschta and Ripple, 2012). Based on results from the three National Parks and other sites, Beschta and Ripple (2012) concluded that the removal of apex predators due to extirpation increased ungulate herbivory which altered riparian plant communities, thereby increasing bank erosion that led to either widening of the active channel or channel incision. This, in turn, reduced the frequency of overbank flows, which decreases hydrologic connectivity between the riparian area and downstream waters.

5.3.3.3. *Invertebrates*

Stream macroinvertebrates (e.g., insects, crayfish, mollusks) and microinvertebrates (e.g., daphnia, copepods, rotifers, gastropods) colonize nutrient-rich riparian areas and floodplains in large numbers during seasonal or episodic immersion by rivers and streams (Junk et al., 1989; Ilg et al., 2008). Macroinvertebrates and microinvertebrates (also called meiofauna) are the intermediate link between primary producers (e.g., algae), detritus pools (e.g., leaf litter), and predators (e.g., fish, amphibians) in river food webs (Malmqvist, 2002; Woodward and Hildrew, 2002; Stead et al., 2005; Woodford and McIntosh, 2010). The distribution of invertebrate populations in dynamic river systems is governed by the location of resources required for different needs and life stages, and invertebrates actively disperse to find and exploit resources wherever they become available (Malmqvist, 2002). As with vascular plants, hydrologic connectivity between channels and riparian/floodplain wetlands can significantly influence macroinvertebrate community structure in riparian areas (Paillex et al., 2009).

Invertebrates have evolved two basic strategies to exploit habitats adjacent to streams and rivers: (1) rapid colonization of flooded areas and short life cycles that complete before floodplains dry down again, or (2) use of aquatic refugia or dormant life stages to persist in permanent waters, the hyporheic zone, or floodplain soils between inundations (Tronstad et al., 2007). To evaluate the relative importance of each strategy in the same river system, Jenkins and Boulton (2003) compared the abundance and species composition of microinvertebrates emerging from floodplain sediments to those transported by floodwater from instream habitats at reach and catchment scales. Initially, most colonizers of newly flooded riparian habitats came from distant upstream reaches of the river network, washed downstream by floodwaters. After a few days, however, species hatching from eggs diapausing in soils greatly increased the diversity and size of the river/floodplain community. This study illustrates two important points about biological connectivity of river/riparian habitats:

1. Stream invertebrate communities are made up of species adapted to different stresses in their environment (in this case, resilient species adapted to high flows and resistant species adapted to desiccation).
2. Floods that periodically connect different parts of the river network generate potential for gene flow across time and space by mixing individuals from different locations (e.g., upstream/downstream, channel/floodplain) and different years (e.g., eggs that might have diapaused for tens or even hundreds of years).

The findings by Jenkins and Boulton (2003), that resting egg banks in riparian soils are important to the persistence of aquatic species and the composition of river communities, were validated in a separate study by Frisch and Threlkeld (2005), who compared flood-pulse colonization from a field study with laboratory hatching of copepod microcrustaceans from egg banks of inundated soils in Mississippi. The laboratory samples showed that in the absence of hydrologic connections, egg banks were sufficient for persistence of copepod populations; the field samples showed that when hydrologic connections were present, water dispersal and hatching from dormant stages were both important colonization pathways for copepods. In a perched floodplain in Missouri, Fisher and Willis (2000) showed that flood-pulsed movement of water and organisms between river channels and floodplains was bidirectional. Adaptations by stream-dwelling invertebrates to variable moisture conditions, and rapid two-way dispersal to exploit temporary or seasonal hydrologic connections, are strong evidence of long-term biological connectivity between rivers and riparian areas.

Invertebrates that disperse by aerial means take advantage of flooded riparian habitats as well. Tronstad et al. (2007) investigated aerial colonization of floodplains by insects during multiple flood pulses having different inundation periods in an unregulated river in Alabama's coastal plain. Floating colonization trays placed in floodplain waters in June, August, November, and April were colonized by at least 41 genera in 21 families across 7 orders of flight-capable insects. Insect densities varied across the period and reached a maximum in August of about 80,000 individuals m^{-2}, most of which were seeking mates or oviposition sites rather than foraging or hunting. High densities (21,291 individuals m^{-2}) of passively dispersing (e.g., via wind or animal vectors) microcrustaceans also were observed. Vanschoenwinkel et al. (2009) erected nine windsocks (sampling devices for aerially dispersing organisms) near temporary rock pools for 1 month, during which 850 viable propagules (dormant eggs, larvae, and adults) from 17 invertebrate taxa were collected. Results from these studies illustrate that aerial dispersal from multiple taxonomic orders and phyla is a significant source of stream invertebrate colonists in newly inundated floodplain habitats.

5.4. UNIDIRECTIONAL WETLANDS

5.4.1. Introduction

This section focuses on the connections and influence of unidirectional wetlands (defined in Section 3.2.1) on downstream waters. Brinson (1993), in his hydrogeomorphic classification system, categorized wetlands according to four geomorphic settings. This was subsequently expanded to the following seven classes by Smith et al. (1995): riverine, depressional, slope, mineral soil flats, organic soil flats, estuarine fringe, and lacustrine fringe. Unidirectional wetlands consist of certain depressional, slope, and flats wetlands (though some of these wetlands can occur in bidirectional wetland settings; see Section 3.2.1). Depressional wetlands occur, as their name suggests, in topographic depressions and may or may not have a surface water inlet or outlet. Common types of depressional wetlands include kettles, potholes, vernal pools, and Carolina bays (Brinson, 1993). Slope wetlands (also known as seeps) are located in breaks of slopes and are sites of groundwater discharge (Hall et al., 2001a; O'Driscoll and DeWalle, 2010). Slope wetlands include fens, which typically are groundwater driven and have diffuse outputs (Brinson, 1993; Bedford and Godwin, 2003). Mineral soil flats commonly occur on interfluves, relic lake bottoms, or large floodplain terraces. Water sources in mineral soil flats are dominated by precipitation, with little groundwater input. Wet pine flatwoods and large playas are examples of this wetland type. Unidirectional wetlands also include organic soil flats. These contain extensive peatlands, or peat bogs, which are dominated by the accumulation of partially decayed organic matter (Mitsch and Gosselink, 2007). Water inputs to bogs are generally dominated by precipitation, and these wetlands can connect to downstream waters via a channel outlet or diffuse overland flow (Brinson, 1993). Bogs are generally more acidic than fens (Bedford and Godwin, 2003). Depressional, slope, or flats wetlands can also serve as stream origins (see Section 3.2.1; Figure 3-18A).

Below, we examine the physical (see Section 5.4.2), water quality (see Section 5.4.3), and biological (see Section 5.4.4) effects of unidirectional wetlands on rivers and other downstream waters. We then briefly consider the issue of geographic isolation in unidirectional wetlands (see Section 5.4.5).

5.4.2. The Physical Influence of Unidirectional Wetlands on Streams

Section 3.4.1 provided a general description of how unidirectional wetlands can connect to downstream waters via surface and groundwater flow (see Figure 3-18). In this section, we give further details on these connections and discuss how such connections impact streamflow.

5.4.2.1. *Surface Water Connections*

Unidirectional wetlands can be connected by perennial surface flows to river networks. For example, seeps are likely to have perennial connections to streams that provide important sources of baseflow, particularly during summer (Morley et al., 2011). In a study in Maine, seeps were found to provide 40−80% of streamwater during baseflow periods (Morley et al., 2011). In other cases, surface connections between unidirectional wetlands and streams can be intermittent or ephemeral. Rains et al. (2006; 2008) showed that California vernal pools, situated on both clay and hardpan soils, connected with streams through channels containing transient water flow. The series of vernal pools on the clay soils were filled with water for 200 days of the year, and water spilled from these wetlands through the ephemeral channel for 60% of those days (Rains et al., 2008). Drainage of wetlands via ditching can also produce surface water outflows from depressional wetlands directly to streams (see Section 3.4.4).

Even unidirectional wetlands that are considered to be geographically isolated (i.e., completely surrounded by uplands), can have surface water outflows that connect them to other water bodies (see Figure 3-18B). Tiner (2003c) identifies vernal pools as one of ten types of geographically isolated wetlands. Yet, as just discussed, the studies by Rains et al. (2006; 2008) indicate that vernal pools can be connected by channels. As another example, a recent study of depressional wetlands in the Texas Gulf Coast area showed that, although classified as geographically isolated, these wetlands are actually connected to adjacent waterways via intermittent streams (Wilcox et al., 2011). During a study period of almost 4 years, nearly 20% of the precipitation that fell on a wetland complex flowed as surface runoff through the stream to an adjacent water body, the Armand Bayou (Wilcox et al., 2011). In the intermontane West, evidence suggests that depressional wetlands can connect to one another via temporary overland or shallow groundwater flows (Cook and Hauer, 2007). In the prairie pothole region, temporary overland connectivity between potholes has been observed in wet years. In 1996, during heavy spring rains, an estimated 28% of the wetlands in the study area had surface water connections to at least one other wetland (Leibowitz and Vining, 2003). Although these latter studies focused on wetland-to-wetland connections, the findings illustrate (1) the potential for geographically isolated wetlands to exhibit temporary surface water connections with other water bodies, and

(2) that interacting wetland complexes may be best understood as a functional unit (see also Section 5.4.5).

5.4.2.2. *Groundwater Connections*

In addition to surface water connections, groundwater flow can connect unidirectional wetlands with other water bodies, potentially over great distances (see Figures 3-5 and 3-18C). Many studies have shown that unidirectional wetlands can connect to groundwater, either by receiving groundwater discharge (flow of groundwater to the wetland), contributing to groundwater recharge (flow of water from the wetland to the groundwater), or both (e.g., Lide et al., 1995; Devito et al., 1996; Matheney and Gerla, 1996; Rosenberry and Winter, 1997; Pyzoha et al., 2008). For example, a 1989 study of four North Dakota prairie pothole wetlands by Arndt and Richardson (1989) clearly demonstrated groundwater connections as one wetland recharged groundwater, one was a flow-through wetland, and one was a discharge system. Hunt et al. (Hunt et al., 2006) found that benthic invertebrate communities were correlated with amounts of groundwater discharge to stream-wetland complexes in northern Wisconsin. Using stable hydrogen and oxygen isotopes in water, Matheney and Gerla (1996) concluded that, although most of the water in a depressional prairie wetland came from precipitation, groundwater connections accounted for the high salinity of the wetland soil. The high salinity is indicative of net groundwater discharge to the wetland (Brinson, 1993). A literature survey by Bullock and Acreman (2003) found 69 studies making reference to groundwater recharge from wetlands; of these, 32 studies observed groundwater recharge from a wetland, whereas 18 studies did not.

Groundwater flow-through wetlands are sites of both groundwater discharge and recharge, in essence a surface expression of the groundwater system (Richardson et al., 1992; Kehew et al., 1998; Ferone and Devito, 2004). In these wetlands, groundwater discharge generally flows into the wetland on one side or area, and flows back into the groundwater on the other side or area of the wetland. This dynamic has been shown in many locations, including: prairie potholes (Richardson et al., 1992), wetlands in glacially formed landscapes in southwest Michigan (Kehew et al., 1998), Alaskan ponds (Rains, 2011), and small Wisconsin lakes (Born et al., 1979). The lakes and wetlands of the Nebraska Sand Hills are also predominantly flow-through and an expression of a large regional groundwater system (Winter, 1999). The chemistry of the transiting, shallow groundwater is affected by the flow-through wetland. Kehew et al. (1998) found a wetland of this type diluted nitrogen concentrations in the groundwater of an agricultural watershed.

Whether a wetland recharges groundwater, is a site of groundwater discharge, or both, is determined by topography, geology, soil features, and seasonal position of the water table relative to the wetland. Shedlock et al. (1993), for instance, concluded that groundwater discharged into a bog along Lake Michigan via a breach in the sediments underlying the wetland. In dry periods when water tables are low, water tends to move out of wetlands into the groundwater, while in wetter periods with higher water tables, water can flow in the opposite direction from shallow groundwater into the wetlands (Phillips and Shedlock, 1993; Pyzoha et al., 2008). Lide et al. (1995) observed both groundwater flow into and from a Carolina bay wetland, with discharge to the wetland when the water table was high and recharge to the groundwater when the water table was low. This exchange and temporary storage of water represents a lag function that can make wetlands particularly important for groundwater recharge during dry periods. Rosenberry and Winter (1997) indicated that groundwater discharge to a wetland often alternates with flow from the wetland to groundwater, and the direction of flow is controlled by the balance of recent precipitation with current evapotranspiration demands.

The magnitude and transit time of groundwater flow from a wetland to other surface waters depends on the intervening distance and the properties of the rock or unconsolidated sediments between the water bodies (i.e., the hydraulic conductivity of the material). In some carbonate or volcanic rocks, for example, groundwater can flow relatively freely through large openings; while in unconsolidated material—such as gravel, sand, silt, or clay—the spaces between particles determine the time required for water to flow a given distance (Winter and LaBaugh, 2003). In porous material, such as gravel, water can travel a distance of a kilometer in a few days; in fine-textured materials, such as silt or clay, hundreds to thousands of years might be required for a single parcel of water to travel the same distance (Winter and LaBaugh, 2003).

In agricultural regions, the transit time of subsurface flows can be substantially decreased by artificial subsurface drainage pipes, known as tile drains (Schiller et al., 2012); see Section 3.4.4). Wetlands in these areas are sometimes fitted with inlets that connect directly to tile drains, quickly moving temporarily ponded water through the subsurface and to outlets which discharge directly to ditches or streams (Tomer et al., 2010).

In summary, unidirectional wetlands can have a range of hydrologic connectivity with other waters (see Figure 3-18). Unidirectional wetlands can be connected by permanent, intermittent, or ephemeral surface flows through swales or channels, or be connected to other water bodies via shallow or deep groundwater flows. Conversely, a wetland can be isolated hydrologically if it lacks surface water and groundwater connections entirely and evapotranspiration is the dominant form of water loss. A wetland can also be hydrologically isolated from streams and rivers if it recharges a groundwater aquifer that does not feed surface waters. Wetlands that lack surface connectivity in a particular season or year can be connected, nevertheless, in wetter seasons or years. A wetland that serves as the origin of a stream will have a permanent or temporary surface water connection with a stream network through a stream channel, unless the wetland feeds a losing stream that is completely disconnected from the river network.

5.4.2.3. *Effects of Unidirectional Wetlands on Streamflow*

Unidirectional wetlands can affect streamflow by altering baseflow or stormflow (see Section 3.2.2; Figure 3-8) through several mechanisms, including surface storage and groundwater recharge. Wetlands effectively store water because the entire aboveground portion of the wetland basin is available for water storage, in contrast to upland areas where soil particles or rock reduce water storage volume for a given volume of that soil or rock (i.e., the specific yield; Johnson, 1967). Large-scale studies have shown that wetlands, by storing water, reduce peak streamflows, and thus, downstream flooding. Hubbard and Linder (1986), for example, calculated the water retention capacity of more than 200 closed depressional prairie potholes in northeastern South Dakota. They observed that a large amount of snowmelt and precipitation could be cumulatively held by many small wetlands, reducing the potential for flooding at downstream locations. Similarly, a USGS study in the prairie pothole region found that wetlands—including both depressional and nondepressional types—stored about 11−20% of the precipitation that fell in a given watershed, and that storage could be increased by wetland restoration (Gleason et al., 2007). Vining (2002) concluded that wetland storage in the Starkweather Coulee subbasin of North Dakota likely resulted in decreased streamflow.

Regression equations developed to predict peak flows during flooding events generally use lake and wetland storage areas as variables. Utilizing this approach for Wisconsin watersheds, Novitzki (1979) estimated that peak flood flows were only 20% as large in watersheds with 40% lake and wetland area relative to watersheds without lakes or wetlands. Likewise, peak streamflows were shown to be negatively correlated with lake and wetland storage in Minnesota (Jacques and Lorenz, 1988), although a later study found peak flows to be correlated with lake storage only and not wetland storage (Lorenz et al., 2010).

The ability of wetlands to reduce flooding via storage varies with topography, wetland type, antecedent moisture conditions, and available water storage capacity. Using stable hydrogen and oxygen isotopes of water, McEachern et al. (2006) found that snowmelt in boreal forests was discharged rapidly in a sloped catchment. In contrast, in a lowland catchment much of the snowmelt was stored by wetlands, particularly by bogs with stream channel outlets. In northern Canada, stream runoff was positively correlated with slope and the presence of channel fens, but negatively correlated with lowland depressional bogs (Quinton et al., 2003). In a Light Detection and Ranging (LiDAR)-based assessment of depressional wetlands in Florida, Lane and D’Amico (2010) found an average potential wetland water storage capacity of 1,619 m^3 ha^{-1}, with values ranging from 1,283 m^3 ha^{-1} for palustrine scrub-shrub wetlands to 2,906 m^3 ha^{-1} for palustrine aquatic-bed wetlands. A literature review study concluded that depressional wetlands lacking a surface outlet (see Figure 3-18B, C, and D) overwhelmingly reduced or attenuated flooding, but the results were more mixed for wetlands with surface water channel connections to streams (Bullock and Acreman, 2003). Only half of the reviewed studies on wetlands that are stream origins (see Figure 3-18A) reported reduced or delayed flooding, while a substantial number of studies (27 of 66, or 41%) found that stream-origin wetlands actually increased flood peaks.

In addition to wetland-type, antecedent moisture conditions and available storage capacity also impact wetland water retention. The wetlands noted above, that serve as stream origins, likely increased flood peaks under saturated conditions, with low additional wetland water storage capacity (due to spring rains or snowmelt, for example), and thus conveyed any additional precipitation rapidly downstream (Bullock and Acreman, 2003). Similarly, Branfireun and Roulet (1998) concluded that prior saturation of upland areas immediately surrounding a wetland produced increased stormflows. This might mean that wetlands have less of an attenuating effect on larger floods because floods commonly occur during saturated conditions.

Besides affecting peak flows and downstream flooding, unidirectional wetlands can alter baseflow or stormflows during dry periods. Groundwater discharge wetlands that are connected to streams, such as fens or seeps, are important sources of baseflow (Morley et al., 2011). Moreover, wetlands can be focal points for groundwater recharge and thus may contribute to baseflow. Rains (2011), for example, found that perched- and flow-through ponds in southwest Alaska were sites of net groundwater recharge. Given the high prevalence of ponds on the landscape (Rains, 2011), these wetland types could cumulatively have a substantial effect on stream baseflow via groundwater inputs.

Other wetlands, however, may actually reduce flows during dry periods. Bullock and Acreman (2003) concluded that this was the case in two-thirds of the studies they surveyed. Antecedent moisture conditions and available wetland storage could partially explain this finding, in combination with relatively high evaporation rates from wetland-dominated landscapes (Bullock and Acreman, 2003). One study cited in their review (Boelter and Verry, 1977) noted that two storms of nearly equal volume and intensity produced different runoff responses from the same peatland. One storm occurring in the spring at a time of already high water tables led to runoff. The other, in midsummer at a time of low water tables, increased the water depth in the peatland but did not exceed the wetland's water storage capacity, precluding runoff. This mechanism has been observed in simulations of prairie pothole hydrology, in which wetlands reduced streamflow until storage capacity was exceeded (Haan and Johnson, 1968). Thus, wetlands may function as a sink in dry periods if storage capacity is not exceeded and evaporation rates surpass groundwater recharge. Where storage capacity is exceeded during storm events in otherwise dry periods, catchments containing extensive wetlands can require more time for water discharge to rise and fall in response to storm events (Lindsay et al., 2004). This finding suggests that catchments with wetlands take longer to fill and exceed water holding capacity than catchments without wetlands and so, in this case, they provide a lag function by releasing water downstream more slowly.

5.4.3. Effects of Unidirectional Wetlands on Water Quality

Unidirectional wetlands can affect water quality of rivers and other aquatic systems through processes that can be generalized as source and sink functions, often mediated by transformational processes (see Section 5.3.2 for details on specific mechanisms). In some cases, unidirectional wetlands directly modify the water quality in downstream waters through their relative lack of surface water connections; this modification is accomplished by removal, sequestration, or transformation of pollutants such as nitrogen, phosphorus, and metals through processes described by Ewel and Odum (1984), Mitsch et al. (1995), Reddy and DeLaune (2008), and Kadlec and Wallace (2009), among others. Although unidirectional wetlands can lack surface water connections to downstream waters, surface and near-surface hydrologic connections to downstream waters do occur in many unidirectional systems (Sun et al., 1995; Whigham and Jordan, 2003; Wilcox et al., 2011; see Section 3.4.2 and Figure 3-18), providing pathways for materials transformed in unidirectional wetlands (such as methylmercury or degraded organic matter) to reach and affect other aquatic systems.

Below we show that unidirectional wetlands are areas where extensive microbially mediated processes occur that can affect downstream waters. In Section 5.4.3.1, we describe how unidirectional wetlands are sources for dissolved organic matter and entrained elements like carbon, nitrogen, and phosphorus, which are important components of food chains in downstream waters. Dissolved organic matter is also shown to be important in regulating whole-lake acidity and buffering capacity. Mercury is another material affected by microbial processing in unidirectional wetlands; mercury is shown to be transported along with dissolved organic matter to downstream waters, where it can become incorporated into the food web with potentially deleterious effects. In Section 5.4.3.2, we discuss how unidirectional wetlands sequester or transform materials, thereby affecting the chemical, physical, or biological condition of downstream waters. Nitrogen, nitrate, ammonium, and phosphorus compounds are shown to be removed or assimilated—often at high rates—in unidirectional wetlands. Pesticides, metals, and other potential pollutants are also demonstrated to be sequestered or assimilated in unidirectional wetlands.

5.4.3.1. *Unidirectional Wetlands as Sources for Downstream Waters*

Like all wetlands, unidirectional wetlands contain diverse microbial populations that have adapted to hydrologic, physical, and chemical extremes (Reddy and DeLaune, 2008). Microbial populations abound in wetland systems; for instance, Boon (1991) reported that Australian wetlands contained 100 times more microbes in the water column than nearby rivers, with up to 157×10^9 cells L^{-1}. Functions that occur in unidirectional wetlands can affect streams, rivers, and lakes when compounds that are transformed in wetland environments move to downstream waters through overland flow or shallow groundwater (Winter and LaBaugh, 2003; see Section 3.2.2). Two processes that occur in unidirectional wetlands (as well as in riparian/floodplain wetlands) are useful to illustrate the influence of unidirectional wetlands on downstream waters: the methylation and transport of the bioaccumulating pollutant mercury, and the breakdown and transport of organic compounds to receiving waters.

Sulfate-reducing bacteria are primarily responsible for biological mercury methylation and thrive in peatland aerobic/anaerobic boundaries; the addition of sulfate (e.g., through atmospheric acid deposition) has been found to increase the creation of methylmercury in peatlands (Branfireun et al., 1999). Once created via microbial processes, mercury and methylmercury export to lakes is controlled by the export of organic matter, such as dissolved organic compounds and humic and fulvic acids (Linqvist et al., 1991; Mierle and Ingram, 1991; Driscoll et al., 1995). Thus, methylmercury can be translocated in basins with unidirectional wetlands through entrainment with organic matter exports, and can move through near-surface and surface flows from unidirectional peatlands to downstream waters. For instance, St. Louis et al. (1994) found that boreal forest catchments in Minnesota with unidirectional wetlands reduced total mercury concentrations, but had yields of MeHg from wetlands that were 26−79 times higher than upland areas. This yielded 1.84−5.55 mg MeHg ha^{-1} yr^{-1} to streams in the Great Lakes basin, where mercury could be incorporated into lake-wide food chains. Similarly, Porvari and Verta (2003) found that bioaccumulating MeHg export from unidirectional peatlands to downstream waters ranged from 0.03 to 3.8 ng MeHg L^{-1}, and that catchments with greater wetland abundances had greater methylmercury export.

Export of dissolved organic matter can have potentially negative effects on downstream waters because contaminants, such as MeHg and other trace metals, can be adsorbed to it (Thurman, 1985; Driscoll et al., 1995). Dissolved organic matter, however, is also an important source of energy for downstream aquatic communities (Hobbie and Wetzel, 1992; Reddy and DeLaune, 2008). Wetlands are the principal source of DOC to downstream waters in forested ecosystems (Mulholland and Kuenzler, 1979; Urban et al., 1989; Eckhardt and Moore, 1990; Koprivnjak and Moore, 1992; Kortelainen, 1993; Clair et al., 1994; Hope et al., 1994; Dillon and Molot, 1997; Gergel et al., 1999). Over prolonged periods, reductions in DOC export (e.g., through wetland conversion or degradation or alterations in hydrology) decrease the ability of downstream waters to support primary productivity, due to reduced export of entrained carbon, nitrogen, sulfur, and phosphorus (Hedin et al., 1995; Nuff and Asner, 2001). Changes in DOC export also affect the pH and buffering capacity of downstream aquatic systems (Eshelman and Hemond, 1985) and their exposure to damaging UV-B rays (Schindler and Curtis, 1997). Boreal forest basins composed of unidirectional wetlands in central Ontario were found to export between 11.4 and 31.5 kg carbon ha^{-1} yr^{-1} to downstream waters (Creed et al., 2003). Furthermore, near-surface lateral transport of DOC explained 88% of the variation in basin DOC export to lake systems where it directly affected pH and buffering capacity. Other studies have similarly shown a relationship between the proportion of wetlands in a drainage area and the average annual concentration of DOC in the receiving streams of that area, and other areas of the boreal forest/Precambrian Shield (Urban et al., 1989; Eckhardt and Moore, 1990; Koprivnjak and Moore, 1992; Clair et al., 1994; Hope et al., 1994; Dillon and Molot, 1997).

The export of dissolved organic compounds from unidirectional wetlands can also have an effect on the acidity of downstream waters. Gorham et al. (1986) addressed watershed factors associated with lake and forest acidification in Nova Scotia, Canada. In addition to atmospheric deposition of acid precipitates, they found that the ratio of unidirectional muskeg peatlands to lakes was significantly correlated with lake acidification, as muskeg wetland-dominated watersheds exported high-molecular-weight organic acids via either overland or shallow groundwater flow. Further linking unidirectional wetlands to lakes, Gorham et al. (1986) reported that even small amounts of humic DOC can greatly affect lake water pH; the pH of waters with a dissolved organic carbon value of 4.5 mg DOC L^{-1} (the log-normal mean) was 100 times more acidic than waters with a dissolved organic carbon of <1 mg DOC L^{-1} (the minimum concentration).

5.4.3.2. *Unidirectional Wetlands as Sinks and Transformers for Downstream Waters*

The wetland literature is replete with examples of wetlands improving water quality through assimilation, transformation, or sequestration of nutrients and other pollutants (e.g., Ewel and Odum, 1984; Nixon and Lee, 1986; Johnston, 1991; Mitsch and Gosselink, 2007; Reddy and DeLaune, 2008; Kadlec and Wallace, 2009). These functions can act on the large pool of pollutants that are available through nonpoint sources. Unidirectional wetland processes that affect pollutant attenuation include denitrification, ammonia volatilization, and microbial and plant biomass assimilation (Reddy and DeLaune, 2008). Other pollutants in wetland systems can be retained through sedimentation, sorption and precipitation reactions, biological uptake, and long-term storage in plant detritus (Reddy et al., 1999; Reddy and DeLaune, 2008).

Unidirectional wetlands act as sinks and transformers for various pollutants. For instance, high levels of human sewage were applied to a forested unidirectional wetland site for 4.5 years (Ewel and Odum, 1984 and chapters therein). More than 95% of the phosphorus, nitrate, ammonium, and total nitrogen (N) were removed by the wetland during the study period (Dierberg and Brezonik, 1984), and 66−86% of the nitrate removed was attributed to the process of denitrification. In another example, P retention in unidirectional marshes of the lower Lake Okeechobee basin ranged from 0.3 to 8.0 mg soluble reactive P m^{-2} d^{-1} (Dunne et al., 2006). This retention represents a sizeable amount of phosphorus removal, because only about 7% of the watershed comprised unidirectional marsh. Unidirectional wetland flats studied in Maryland and Delaware had microbially mediated denitrification enzyme activity (an indicator of potential denitrification) rates of 0.06−0.76 mg N kg^{-1} d^{-1} (Jordan et al., 2007). Because flats comprise greater than 70% of the wetland area in the basin, this value indicates a significant denitrification capacity. A unidirectional bog in Massachusetts was reported to sequester nearly 80% of the system's various nitrogen inputs, including precipitation that had a range of 1.2−1.9 mg N L^{-1} (Hemond, 1983). Prairie pothole wetlands in the upper Midwest were found to remove >80% of the nitrate load via denitrification (Moraghan, 1993). A large unidirectional prairie marsh was found to remove 86% of nitrate, 78% of ammonium, and 20% of phospate through assimilation and sedimentation, sorption, and other mechanisms (Davis et al., 1981). Geographically isolated, unidirectional wetland systems in Michigan were found to remove NO_3-N and sulfate (SO_4^{2-}) at rates of 0.04−0.55 mg NO_3-N L^{-1} ha^{-1} and 0.06−0.30 mg SO_4^{2-} L^{-1} ha^{-1}. These rates are significant, considering that nitrate-nitrogen pollution of groundwater in Michigan was reported to average 0.50 mg NO_3-N L^{-1} (Whitmire and Hamilton, 2008). Together, these studies indicate that sink removal of nutrients by unidirectional wetlands is significant and geographically widespread.

Other pollutants and compounds can be mitigated by unidirectional wetland sink and transformation processes. For instance, microbial methanogenesis was found to completely remove the pesticide atrazine from a mountainous bog in North Carolina (Kao et al., 2002). The environmental contaminants cobalt (Co) and nickel (Ni) can be phytoremediated by wetland plants common in forested unidirectional wetlands of the Southeast; plant concentrations were found to range from 1 to 530 mg Co kg^{-1} and up to 250 mg Ni kg^{-1} (Brooks et al., 1977). A bog in Massachusetts that Hemond (1980) extensively studied acted as a sink and annually stored 54 mg magnesium m^{-2}, 36 mg potassium m^{-2}, and 46 mg lead m^{-2}; the bog also provided acid-rain buffering for downstream waters. Based on the literature, Boon (2006) concluded that wetland microbial communities can mediate processes that degrade diesel fuel and other hydrocarbons, pesticides, heavy metals and metalloids, and chlorinated solvents that can pollute groundwater.

5.4.4. Biological Connections Between Unidirectional Wetlands and Streams

Movement of organisms between unidirectional wetlands and the river network is governed by many of the same factors that affect movement of organisms between riparian/floodplain wetlands and the river network (see Section 5.3.3). Unidirectional wetlands, however, are generally farther from stream channels than riparian/floodplain wetlands, which makes hydrologic connectivity much less frequent, if present at all. The distance, number, and variety of landscape barriers over which organisms must disperse also can be greater. Aquatic organisms have evolved numerous complex dispersal strategies to overcome unidirectional flows, reduced hydrologic connectivity, and increased geographic distance between habitats and spatially subdivided populations. Passive transport (wind dispersal and hitchhiking on other animals) and active movement (walking, crawling, and flying) are common modes of dispersal that can establish connectivity in the absence of hydrologic flows. Such dispersal events are often sporadic and asymmetric in unidirectional wetland landscapes, making them more difficult to observe than surface water flows. Their effects on community structure and diversity have been well documented (e.g., Wellborn et al., 1996; Snodgrass et al., 2000c); other effects (e.g., water quality, population or species persistence) are not well understood. We review the various dispersal mechanisms that operate in unidirectional wetland landscapes, with examples of aquatic and semiaquatic organisms found in both wetland and stream habitats.

Despite being nonmobile, plants have evolved many adaptations that facilitate dispersal. Considerable attention has been given to waterborne dispersal of aquatic and emergent macrophytes (Nilsson et al., 2010), which can play a role in unidirectional wetlands that are periodically connected hydrologically to river networks. In addition, significant numbers of such plants can be dispersed as seeds or pollen by wind (Soons, 2006). Wind dispersal enables colonization of geographically isolated unidirectional wetlands such as prairie potholes (Galatowitsch and van der Valk, 1996). Given that geographically isolated wetlands are surrounded by uplands, using wind as a vector carries the relatively high risk that propagules of obligate wetland plants will land in unsuitable habitat. Plants have developed colonization strategies to compensate for such risks. For example, Soons and Heil (2002) showed that producing large numbers of seeds increased colonization success of short- and long-distance dispersing grassland forbs; results from this and other studies are being applied to models of wetland dispersal and colonization (e.g., Soons, 2006). Seeds or vegetative plant parts also can hitchhike on or inside highly mobile animals. Migratory birds are known for dispersing over very large distances, and they both (1) consume and excrete viable plant seeds (Murkin and Caldwell, 2000; Amezaga et al., 2002; Figuerola and Green, 2002), and (2) move between geographically isolated wetlands and river networks, depending on temporally dynamic habitat availability (Murkin and Caldwell, 2000 and references therein; Haukos et al., 2006).

Identifying specific source and recipient populations for any organism over these distances can be challenging, but especially for plants having mobile life stages that cannot be precisely tracked. This makes it difficult to determine whether wetlands function as sources to or recipients of plant propagules from river networks. Genetic similarity between populations can provide general evidence of connectivity between unidirectional wetlands and the river network. Sawgrass (*Cladium jamaicense*) populations in Everglades wetlands showed low population genetic divergence at distances greater than 100 km; wind pollination and water dispersal of propagules through flooding likely keeps channel and wetland populations genetically similar (Ivey and Richards, 2001). Another approach that can provide evidence for dispersal is community-level surveying, which takes into account local determinants of community composition and structure. Controlling for local conditions like rainfall and soil type, a study in Connecticut (Capers et al., 2010) found that bodies of water—from small isolated wetlands to large lakes—that were located closer together had more similar plant communities. This finding suggests biological connectivity between proximal lakes and wetlands.

Fish tend to disperse between unidirectional wetlands and the river network during periodic surficial hydrologic connections or when humans create surface water connections via ditching (Snodgrass et al., 1996; Zimmer et al., 2001; Baber et al., 2002; Hanson et al., 2005; Herwig et al., 2010). Mammals that can disperse overland can also contribute to connectivity. Although muskrat territories are usually restricted (Shanks and Arthur, 1952), seasonal, climate-induced, and density-dependent longer distance dispersal between suitable river and unidirectional wetland habitat has been observed (Clark, 2000 and references therein). Mammals, including muskrats, also can act as transport vectors for hitchhikers like algae (Roscher, 1967).

Recent evidence suggests that invertebrate hitchhiking on birds and mammals is more common than previously thought (Figuerola and Green, 2002; Figuerola et al., 2005). Allen (2007) trapped zooplankton dispersing from a pond in Illinois and found that animals wider than 3 cm were the primary vector of reproductive adult zooplankton forms. These results suggest that animals moving among water bodies can be an important factor structuring unidirectional wetland invertebrate metapopulations. Frisch et al. (2007) found that diapausing invertebrate eggs that dispersed by hitchhiking on birds had higher incidences of hatching in January (59.4%) than in November (11.5%). These invertebrates included nematodes, microcrustaceans (i.e., rotifers, ostracods, copepods), and insects (i.e., tipulids, chironomids, and hemipterans). This study indicates that winter migrations of aquatic birds can be an important mechanism for spring colonization of habitats separated by hundreds or even thousands of kilometers.

Numerous flight-capable insects, including mayflies, caddisflies, diving beetles, backswimmers, whirligig beetles, water striders, water boatmen, scavenger beetles, crane flies, and nonbiting midges, use both streams and unidirectional wetlands (Williams, 1996). Aerial dispersal enables such insects to move outside the stream network to seek suitable habitat for overwintering, refuge from adverse conditions, hunting, foraging, or breeding (Williams, 1996; Bohonak and Jenkins, 2003).

Amphibians and reptiles also move between streams or rivers and unidirectional wetlands to satisfy part of their life-history requirements (see Table 5-2). For example, Subalusky et al. (2009a; 2009b) reported movement of adult female alligators (*Alligator mississippiensis*) from creeks to shallow, seasonal limesink wetlands for nesting and use of the wetlands as nurseries for juveniles. Subadults then shift to habitats within the river network through overland movements to the creek (Subalusky et al., 2009a; Subalusky et al., 2009b). Lamoureux and Madison (1999) used radio tracking to follow movements of green frogs (*Rana clamitans*) for 9 months in New York. Green frogs, which breed in wetlands and then move into terrestrial habitats, are susceptible to freezing temperatures. In late autumn, the frogs moved from upland habitats near breeding ponds to rapidly flowing streams and seeps to overwinter. Boreal toads (*Bufo boreas boreas*) disperse long distances (>1 km) in streams through home ranges (Adams et al., 2005). The American toad (*Anaxyrus* [=*Bufo*] *americanus*) and Eastern newt (*Notophthalmus viridescens*) are widespread habitat generalists that move among streams and wetlands to take advantage of both habitats, feed on aquatic invertebrate prey, and avoid predators (Babbitt et al., 2003; Green, 2005; Hunsinger and Lannoo, 2005; Petranka and Holbrook, 2006; see Table 5-2).

5.4.5. Geographic Isolation of Unidirectional Wetlands

In defining unidirectional wetlands (see Section 3.2.1), we noted that this category could include wetlands that are geographically isolated and those that are not. Further, we noted (see Section 3.4.1) that certain types of wetlands can be found with or without an outlet and occur along a gradient of hydrologic connectivity. This gradient can include unidirectional wetlands that have permanent hydrologic connections to the river network through perennial channels; wetlands that have losing streams that are completely disconnected from the river network as output channels; geographically isolated wetlands that have groundwater or occasional surface water connections; and geographically isolated wetlands that have minimal hydrologic connection to the river network (but which could include surface and subsurface connections to other wetlands). The existence of this gradient can make determining the degree to which particular unidirectional wetlands are connected to or isolated from downstream waters difficult.

A related issue is that spatial scale must be considered when determining geographic isolation. Tiner (2003c) provided examples of how a wetland that was not isolated at a local

Table 5-2. Partial list of amphibian and reptile species known to use both streams and unidirectional wetlands or other lentic waters

Common name	Scientific name	Habitat use
Green frog	*Rana clamitans*	Breeds in wetlands and pools; overwinters in streams (Lamoureux and Madison, 1999)
Leopard frog	*Rana pipiens*	Breeds in wetlands and pools; overwinters in streams (Rorabaugh, 2005)
Bullfrog	*Rana catesbeiana*	Uses seasonal pools as complementary nonbreeding habitat (Gahl et al., 2009)
Columbia spotted frog	*Rana luteventris*	Breeds in streams and wetlands; overwinters in streams (Pilliod et al., 2002)
Southern leopard frog	*Rana sphenocephala*	Breeds in shallow pools and wetlands; adults inhabit many shallow freshwater habitats, including temporary pools, cypress ponds, ponds, lakes, ditches, streams, river edges and floodplains, slightly brackish coastal wetlands (Butterfield, 2005)
Pacific chorus frog	*Pseudacris regilla*	Breeds in wetlands, ponds, temporary pools, streams, lakes, rivers, and other aquatic habitats (Rorabaugh and Lannoo, 2005)
American toad	*Anaxyrus* [=*Bufo*] *americanus*	Breeds in lakes, ponds, streams, ephemeral wetlands, prairie potholes, ditches, or floodplain pools (Green, 2005)
Fowler's toad	*Anaxyrus* [=*Bufo*] *fowleri*	Breeds in ponds, temporary pools, streams, ditches, lake shores, or shallows of rivers (Green, 2005)
Two-toed amphiuma	*Amphiuma means*	Adults inhabit a wide variety of aquatic environments, including ponds, lakes, ephemeral wetlands, wet prairies, streams, and ditches (Gibbons and Semlitsch, 1991; Johnson and Owen, 2005)
Greater siren	*Siren lacertina*	Breeds in shallow pools and streams, adults live in lakes, streams, ponds, and wetlands (Gibbons and Semlitsch, 1991; Hendricks, 2005)
Eastern newt	*Notophthalmus viridescens*	Breeds in permanent and semipermanent pools, ponds, wetlands, and low-flow areas of streams; adults live in pools, ponds, streams, and wetlands (Hunsinger and Lannoo, 2005; Timm et al., 2007)

Table 5-2. Partial list of amphibian and reptile species known to use both streams and unidirectional wetlands or other lentic waters (continued)

Yellow-bellied watersnake	*Nerodia erythrogaster flavigaster*	Hunts in temporary pools and wetlands (Roe et al., 2004; Mitchell et al., 2007)
Copper-bellied watersnake	*Nerodia erythrogaster neglecta*	Hunts in temporary pools and wetlands (Roe et al., 2004; Mitchell et al., 2007)
Spotted turtle	*Clemmys guttata*	Uses temporary wetlands for foraging, mating, basking, and aestivating (Joyal et al., 2001)
Blanding's turtle	*Emydoidea blandingii*	Uses temporary wetlands for foraging, mating, basking, and aestivating (Joyal et al., 2001)
Painted turtle	*Chrysemys picta*	Uses temporary wetlands for basking and foraging (Mitchell et al., 2007)
Snapping turtle	*Chelydra serpentina*	Uses temporary wetlands for basking and foraging (Mitchell et al., 2007)
American alligator	*Alligator mississippiensis*	Juveniles use seasonal wetlands as nurseries, subadults move back to river networks (Subalusky et al. 2009a, Subalusky et al. 2009b)

scale could be geographically isolated at a larger scale. Conversely, individual wetlands that are geographically isolated could be connected to downstream waters when considered as a complex (a group of interacting wetlands). This concept is demonstrated in a recent paper by Wilcox et al. (2011), who examined a depressional wetland complex on the Texas coastal plain. Although the wetlands are hydrologically connected to each other by shallow swales, they might be geographically isolated, because swales are often considered upland. In fact, Tiner (2003c) classifies these coastal plain wetlands as geographically isolated. At the scale of the wetland complex, however, the wetlands are connected to an adjacent waterway via an intermittent stream. During an almost 4-year study period, nearly 20% of the precipitation that fell on the wetland complex flowed as surface runoff through the channel to a nearby waterway, the Armand Bayou (Wilcox et al., 2011). Although these wetlands might be geographically isolated at the local scale, the wetland complex serves as the source of water for a headwater stream, and therefore, the complex is not geographically isolated at a larger scale.

Given this discussion, caution should be used in interpreting connectivity for wetlands that have been designated as "geographically isolated," because (1) the term can be broadly applied to a heterogeneous group of wetlands that can include wetlands that are not geographically isolated, (2) wetlands with permanent channels could be miscategorized as geographically isolated if the designation is based on maps or imagery with inadequate spatial resolution (e.g., Lang et al., 2012), obscured views, etc., and (3) wetland complexes could have connections to downstream waters through stream channels even if individual wetlands within the complex are geographically isolated. The term "geographically isolated" should be applied only to groups of wetlands if all those wetlands are, in fact, known to be geographically isolated. Further, even geographically isolated wetlands can be connected to other wetlands and downstream waters through groundwater connections, occasional spillage, or biological connections. Thus, the term "geographically isolated" should not be used to infer lack of hydrologic, chemical, or biological connectivity.

Finally, it is noted that it is precisely this isolation that is responsible for many of the services that geographically isolated wetlands provide to downstream waters. In particular, many of the sink and lag functions that are supplied by these wetlands result from their relative isolation with respect to the river network. It is the relative isolation of these wetlands, combined with their storage capacity, that allows them to store water and reduce peak streamflows and downstream flooding (Novitzki, 1979; Hubbard and Linder, 1986; Vining, 2002; Bullock and Acreman, 2003; McEachern et al., 2006; Gleason et al., 2007). For example, depressional wetlands in Florida had an average potential wetland water storage capacity of 1,619 m^3 ha^{-1} (Lane and D'Amico, 2010). These same sink and lag functions will also act on any materials associated with stored water, such as sediments and pollutants. Increased isolation can also decrease the spread of pathogens (e.g., Hess, 1996) and invasive species (e.g., Bodamer and Bossenbroek, 2008), and increase the rate of local adaptation (e.g., Fraser et al., 2011).

5.5. WETLANDS: SYNTHESIS AND IMPLICATIONS

5.5.1. Riparian and Floodplain Wetlands

Based on our review of the literature, riparian/floodplain wetlands are highly connected to streams and rivers through surface water, shallow groundwater, and biological connectivity. The effects of wetlands on streams and rivers are a function of the magnitude of floodwaters, the geomorphic structure of the floodplain, and the proximity of the channel. Although there is a gradient in the frequency of connectivity within the floodplain, even riparian/floodplain wetlands that rarely flood can be important because of long-lasting effects on streams and rivers. In fact, most of the major changes in sediment load and river channel structure—for example, movement of rivers through meander belts and creation of oxbow lakes—that are critical to maintaining the health of the river result from large floods that provide infrequent connections with more distant riparian/floodplain wetlands. Areas that are infrequently flooded by surface water also can be connected to the river more regularly through groundwater and the biota. Key conclusions from our literature review on riparian/floodplain wetlands are summarized in Table 5-3.

5.5.2. Unidirectional Wetlands

Unidirectional wetlands consist of depressional, slope, and flats wetlands that lack surface water inlets. These can include regional wetland types such as prairie potholes, playa lakes, vernal pools, and Carolina bays. Hydrologic flows through these wetlands are predominantly unidirectional, in contrast to bidirectional flows that occur in riparian/floodplain wetlands.

The literature we examined on unidirectional wetlands indicates that these systems have important hydrologic, water quality, and habitat functions that affect downstream waters and rivers if a connection exists between the wetland and downstream water (see Table 5-4). The problem, then, is to identify which unidirectional wetlands have such a connection. Answering this is difficult, because most wetland studies do not investigate their effects on downstream waters or, if they do, they rarely address connectivity explicitly.

Based on what is known about how water flows across the landscape (see Chapter 3), hydrologists and ecologists would generally agree that all unidirectional wetlands are interconnected to some degree with each other and with stream networks; this is why the water cycle environment is referred to as the hydrosphere. There also is general agreement among hydrologists and ecologists that some areas are more connected or have a greater influence than others. The purpose of this review is to determine, based on the peer-reviewed literature, the degree of connectivity and associated effects between different unidirectional wetlands and downstream waters.

Table 5-3. Key conclusions on the effects of riparian and floodplain wetlands on rivers

Physical Connectivity and Function
• Riparian areas are highly connected to streams, so much so that considering the riparian influence on streams is essential to understanding their structure and function.
• Riparian connectivity ranges from longitudinal flow and exchange in mountainous headwater streams to increasing lateral flow and exchange in river valleys and coastal terrain.
• Water storage by riparian areas, especially wetlands and lentic water bodies (such as oxbow lakes) that lack surface channel connections to stream networks, attenuate downstream flood pulses.
• Heterogeneous riparian areas that include wetlands and open-waters, remove large amounts of sediment and nutrients from upland areas before they can enter the stream network.
• Riparian areas influence stream geomorphology during periodic flooding through release of stored sediments.
• Forested riparian areas provide woody debris that helps to shape stream morphology.
• Riparian vegetation shades the stream and influences and regulates stream temperature and stream net primary productivity.
• Groundwater that flows through riparian areas and into the stream helps moderate stream temperatures.
Chemical Connectivity and Function
• Riparian areas, acting as buffers, are critical to protecting streamwater quality.
• The structure of the riparian area (e.g., vegetation, wetlands, redox potential) influences its ability to effectively increase water quality before it reaches the stream.
• The near-stream portion of a riparian area is often more important in protecting streamwater quality than is the near-field (adjacent to uplands) portion.
• Allochthonous inputs are generally most important to food webs in small headwater streams, especially in forested areas. As rivers become larger, primary production becomes increasingly important.
• Some of the best documented functions of oxbow lakes are as sinks for nutrients from upland runoff that might otherwise flow into rivers.
Biological Connectivity and Function
• Many types of organisms move between riparian/floodplain wetlands and the river network; those transported by water often move in response to flooding and those transported by other mechanisms (e.g., wind) move in response to seasonal cues or life-history stage requirements.
• Riparian/floodplain wetlands and oxbow lakes can be sources or sinks of organisms; one of the most important source functions is to provide rearing habitat for fish.
• Riparian/floodplain wetlands provide food sources for stream and river invertebrates.
• Many riparian/floodplain wetlands and open-waters (e.g., oxbow lakes) are used by fish and other organisms from the stream or river during flooding.

Table 5-4. Key conclusions on the effects of unidirectional wetlands on rivers

Physical Connectivity and Function
• The connections of unidirectional wetlands with downstream waters exist along a spectrum from truly isolated depressional wetlands, to those connected through groundwater, to those connected via intermittent or permanent surface flows.
• The degree to which outputs (or connections) are dominated by surface water vs. groundwater is controlled in part by soil permeability: Permeable soils favor groundwater outputs, while impermeable soils result in surface water outputs. Other factors, such as topographic setting, can also play a role.
• Groundwater recharge is common in unidirectional wetlands and can be particularly important sources of water to aquifers during dry periods.
• Groundwater networks extend from the local to the intermediate and regional scales, and provide a mechanism by which unidirectional wetlands can influence other water bodies over various time frames.
• Even in cases where unidirectional wetlands lack a connection to other water bodies, they can influence downstream water through water storage and mitigation of peak flows (flood reduction/attenuation).
Chemical Connectivity and Function
• Insofar as they often act as buffers between sources of pollution and riparian areas, unidirectional wetlands are a first line of defense in protecting streams from polluted waters.
• Unidirectional wetlands affect nutrient delivery and water quality.
• Unidirectional wetlands are a principal source for dissolved organic carbon (which supports primary productivity) to some downstream waters; the area of a basin with unidirectional wetlands is directly correlated to the contribution of that basin to dissolved organic carbon in downstream waters.
• Unidirectional wetlands are sources of mercury: Microbial processes in unidirectional wetlands methylate mercury, which can be translocated through near-surface and surface flows to downstream waters where it can bioaccumulate.
• Unidirectional wetlands are sinks for sediment, nutrients (including phosphorus, nitrate, and ammonium), metals (for example, nickel and cobalt), and pesticides (for example, atrazine).
• Unidirectional wetlands can remove, retain, or transform many of the nutrient inputs to which they are exposed.
Biological Connectivity and Function
• Natural periodic and permanent human-engineered surface water connections can connect biological communities in unidirectional wetlands and the river network; in addition, wind dispersal and overland movement connect these waterbody types with frequency decreasing as a function of distance and/or other landscape barriers.
• Migratory birds are vectors of plant and invertebrate movement between unidirectional wetlands and the river network, though their influence has not been fully quantified.
• Unidirectional wetlands promote biological interactions that can be important to the life history requirements of some stream species.
• Overland ("fill-and-spill") hydrologic connections can support biologic connections. For example, stream fish found in wetlands that periodically dry down indicate presence of surface flows sufficient for colonization.

Unidirectional wetlands exist on a gradient of hydrologic connectivity that can include wetlands that have permanent hydrologic connections to the river network through perennial channels; wetlands that have output channels but are isolated from the river network; geographically isolated wetlands that have local or regional groundwater or occasional surface water connections; and highly isolated wetlands that have minimal hydrologic connection to the river network (but which could include surface and subsurface connections to other wetlands).

Based on our literature review and basic hydrologic principles, we conclude that unidirectional wetlands that are connected to the river network through surface water will have an impact on downstream waters, regardless of whether the outflow is permanent, intermittent, or ephemeral. Such unidirectional wetlands include wetlands that serve as stream origins or which are connected downstream to the river network through ditches. They would also include geographically isolated wetlands (i.e., wetlands completely surrounded by uplands) that are connected downstream to the river network through upland swales. Further, while our literature review did not address other unidirectional water bodies to the same extent as wetlands, our overall conclusions apply to these water bodies (e.g., ponds and lakes that lack surface water inlets) as well, since the same principles govern hydrologic connectivity between these water bodies and downstream waters (see Chapter 3).

Unidirectional wetlands that do not connect to the river network through surface water include wetlands that spill into losing streams that are completely disconnected from the river network (i.e., the wetland exports water through an output channel but the water is completely lost before it reaches the river network due to evapotranspiration or loss to groundwater). Also included are geographically isolated wetlands that either do not spill, or spill into an upland swale that does not enter the river network. While such wetlands lack surface water connections to streams and rivers, they can be connected through local, intermediate, or regional groundwater flows or through biological movement. Connectivity between these wetlands and downstream waters will vary within a watershed as a function of local factors (e.g., position, topography, and soil characteristics; see Sections 3.4.1 and 3.4.2), some of which are identified and discussed in this section. Connectivity will also vary over time, as the river network and water table expand and contract in response to local climate.

The literature that we reviewed—which included more than 130 peer-reviewed articles on unidirectional wetlands—does not provide us sufficient information to evaluate the type or degree of connectivity (absolute or relative) or the variability in connectivity for those unidirectional wetlands that lack surface water connections to downstream waters. This lack of information applies to groups of these wetlands within a particular watershed and to comparisons between different types of regional wetlands. For example, the literature does not tell us whether connectivity between vernal pools and downstream waters is greater than connectivity between prairie potholes and downstream waters. We emphasize that this does not mean these wetlands do or do not have connectivity with downstream waters. Rather, it means that the literature we reviewed does not allow us to distinguish connectivity of these wetland types from each other. Literature that was not included in our review, such as reports from local resource agencies, could allow the connectivity of these wetlands to be further evaluated, as could analysis of existing or new data or field evaluation.

Further complicating our evaluation is the fact that some of the effects that wetlands have on downstream waters are due to their isolation, rather than their connectivity. Wetland functions that trap materials and prevent their export to downstream waters (e.g., sediment removal and water storage) result because of the wetland's ability to isolate material fluxes. Increased connectivity (e.g., due to ditching) is likely to reduce the effects of such functions on downstream waters (though functions dependent on connectivity could be increased).

Despite these limitations, we can make some conclusions: (1) Many unidirectional wetlands interact with groundwater, which can travel long distances and increases the potential for an indirect effect on downstream waters. (2) Even in cases where wetlands lack a hydrologic connection to other water bodies, they can influence downstream water through water storage and mitigation of peak flows (flood reduction/attenuation). (3) Within a watershed or region, areas that are closer to rivers and streams will have a higher probability of being connected than areas farther away, assuming that other key conditions governing type and quantity of flows (including slope, soil and aquifer permeability) are similar (see Section 3.4.1). (4) Wetland sink functions are likely to be greatest when the wetland is located downgradient from pollutant sources and upgradient from a stream or river. (5) Caution should be used in interpreting connectivity for wetlands that have been designated as geographically isolated because (a) the term can be applied broadly to a heterogeneous group of wetlands, which can include wetlands that are not geographically isolated (e.g., some vernal pools are not geographically isolated because they have output channels; see Section 5.4.2.1); (b) wetlands with permanent channels could be miscategorized as geographically isolated if the designation is based on maps or imagery with inadequate spatial resolution, obscured views, etc.; and (c) wetland complexes could have connections to downstream waters through stream channels even if individual wetlands within the complex are geographically isolated. Thus, the term "geographically isolated" should be applied only to groups of wetlands if all those wetlands are, in fact, known to be geographically isolated, something that we cannot determine based on this literature review. As previously noted, additional information that was not included in our literature review (e.g., reports from local resource agencies, analysis of existing or new data, or field evaluations) could allow some wetlands that are truly geographically isolated to be distinguished from some of those that are not. Further, even geographically isolated wetlands can be connected to other wetlands and downstream waters through groundwater connections, occasional spillage, or biological connections. Thus, the term “geographically isolated” should not be used to infer lack of hydrologic, chemical, or biological connectivity. Key conclusions from our literature review on unidirectional wetlands are summarized in Table 5-4.

5.6. CASE STUDY: OXBOW LAKES

5.6.1. Abstract

Oxbow lakes are water bodies that originate from the meanders of rivers that become cut off. They are common in the floodplains of large rivers around the world. In the following case study, we provide evidence from the peer-reviewed literature to support two conclusions: (1) oxbow lakes periodically connect to the active river channel, and (2) the connection between oxbow lakes and the active river channel provides for several ecological effects on the river ecosystem.

5.6.2. Introduction

5.6.2.1. *Origin and Description*

Oxbow lakes and ponds (hereafter referred to as oxbow lakes) originate from river meanders that are cut off from the active river channel. In floodplain rivers, natural erosion of the outer banks of curves in the active river channel leads to increased meandering over time. As these meanders grow, the active channel can come into contact with itself and cut off the curved segment of the river; this cutoff channel becomes an oxbow lake within the floodplain.

Oxbow lakes are dynamic ecosystems. Young oxbow lakes are located near the active river channel and tend to have steep banks. As oxbow lakes are subjected to flooding over time and begin to fill with sediment, they can become shallower, and eventually develop terrestrial characteristics. Continued movement and meandering of unconstrained, shallow river channels can leave some oxbow lakes at considerable distances from the active river channel (Winemiller et al., 2000). Owing to the dynamic physical processes that create and promote succession in oxbow lakes, among-lake variation often is large in terms of the character and connectivity of individual oxbow lakes within a floodplain.

Oxbow lakes are an integral element in alluvial floodplain valleys of meandering rivers around the world (Winemiller et al., 2000; Glinska-Lewczuk, 2009). Studies of these ecosystems have been conducted in river floodplains in Australia (e.g., Crook and Gillanders, 2006), Europe (e.g., Hein et al., 2003), North America (e.g., Winemiller et al., 2000; Zeug et al., 2005), and South America (e.g., da Silva et al., 2010). Due to the common origin, characteristics of, and interactions between oxbow lakes and rivers, evidence from around the world is presented here.

5.6.3. Evidence

Oxbow lakes commonly connect with the active river channel. The most evident connections are direct physical linkages, in which water movement between the active river channel and oxbow lakes is traceable. Although these physical connections are intrinsically important, they also facilitate the movement and exchange of chemical and biological material between the river and lake ecosystems.

5.6.3.1. *Physical Connections*

Physical connections between the active river channel and oxbow lakes can be through water movement as overland surface flow, subsurface flow from river infiltration, and subsurface flow from hillslope aquifers (Amoros and Bornette, 2002). In some cases, natural or constructed stream channels are present between the river and the oxbow lake. For the purpose of this report, oxbow lakes with this type of permanent physical connection are a priori considered an integrated part of the river network. Evidence presented here is largely for oxbow lakes that lack permanent physical connections to the river network; therefore, we focus on overland flow events (i.e., temporary connections occurring during high river stages and floods) and shallow groundwater flow as the dominant surface connection between ecosystems.

Regional- and local-scale climate and hydrogeologic patterns are important for understanding the dynamics of physical connectivity between oxbow lakes and active river channels. Regional differences influence the predictability of hydrologic connectivity between rivers and oxbow lakes. In temperate rivers (e.g., Brazos River, TX), surface flow connections between the river channel and oxbow lakes are likely to occur at irregular intervals, in response to flow magnitude and lake geomorphology (Humphries et al., 1999; Zeug and Winemiller, 2008). Tropical rivers, in contrast, are likely to have more regular inundation patterns associated with seasonal flooding (Junk et al., 1989; da Silva et al., 2010). The predictability of subsurface connections also can vary regionally. An isotope tracer analysis of lakes in the Old Crow Flats, Yukon Territory, Canada, indicated that oxbow lakes receive much of their water input from shallow groundwater flow during the relatively short thaw season (Turner et al., 2010). The regularity of connectivity has important implications for the exchange of chemical and biological material between oxbow lakes and the river (e.g., Junk et al., 1989; Humphries et al., 1999).

Local landscape characteristics and position of water bodies in the floodplain influence the relative contribution of surface and subsurface water movement between individual lakes and the active river channel. A study of oxbow lakes on the Loire and Allier Rivers, France, demonstrates this. Water in two oxbow lakes had different geochemical signatures, suggesting a difference between when river water was introduced to the lakes (Negrel et al., 2003). The younger oxbow lake was more connected to the surface network due to its closer proximity to the river channel and a small stream connection, while an older oxbow lake, which was more distant from the river channel, was more dependent on subsurface flow (Negrel et al., 2003).

In addition to these spatial differences, temporal differences can occur in the short-term dynamics of hydrologic connectivity. Amoros and Bornette (2002) describe a system of pulsing connectivity, where the direction of water exchange between floodplain water bodies, including oxbow lakes, and a river is related to river stage. At low water stage, floodplain water bodies might receive water from a hillslope aquifer, and water from the oxbow lake likely drains through the alluvium toward the river. In contrast, when a river has a high water stage, water is more likely to seep through the alluvium from the river to the oxbow lake. Finally, inundation would result in surface water connectivity, where river water moves overland to the oxbow lake. This pattern of pulsing connectivity is influenced by the local topography and the characteristics of the floodplain alluvium (Amoros and Bornette, 2002) and is an illustration of the expansion and contraction concepts described in the framework (see Sections 3.2 and 3.3).

Physical connectivity between oxbow lakes and the river network has direct consequences on the hydrologic dynamics of that river network. Oxbow lakes provide flood protection. Like other floodplain water bodies, they retain water. This retention lowers water velocity and can reduce the height of floodwater over adjacent terrestrial landscapes (Winemiller et al., 2000). In addition to storing floodwaters, oxbows trap sediment as the velocity of floodwaters declines during the process of retention, allowing sediment to settle out of suspension.

Human alterations of natural flow patterns in rivers can influence connectivity between oxbow lakes and the active river channel. On one hand, connectivity can be enhanced. Channels between oxbow lakes and the river channel are often constructed for their benefits to biological productivity (Glinska-Lewczuk, 2009). On the other hand, isolation might be enhanced. An analysis of sediment cores in two small oxbow lakes in the Vistula River valley, Poland, showed changes in sedimentation rate and grain size following flood dike construction along the river (Galbarczyk-Gasiorowska et al., 2009). These changes in sedimentation can alter the balance of subsurface connections. The absence of channel migration since the 1980s has restricted flooding to areas close to the main channel of the Ebro River, Spain. The effects of this diminished river-floodplain interaction (e.g., erosive floods) left two of three oxbow lakes examined relatively isolated from the river channel, with a thick layer of fine sediment and thus little connection to subsurface flows (Cabezas et al., 2009).

5.6.3.2. *Chemical Connections*

The dynamics of hydrologic connectivity are important for understanding the chemical character of oxbow lakes. Flooding of the river facilitates exchange of chemicals between the river water and the water in oxbow lakes. In some cases, these surface water exchanges act to reset the chemical environment in oxbow lakes (e.g., periodic floods introducing well-aerated water to oxbow lakes in Poland; Obolewski et al., 2009). The chemical effects of flooding are not limited to changes in the water column. For example, the isolation of oxbow lakes from the active river channel corresponded with changes in sediment chemistry, and ultimately, an acceleration of eutrophication (Galbarczyk-Gasiorowska et al., 2009).

Subsurface connections also influence oxbow lake chemistry in important ways. For example, an assessment of oxbow lakes on the River Lyna, Poland indicated that nutrient concentrations in oxbow lakes were likely influenced by a combination of river water from surface connections, groundwater seepage from the alluvial aquifer, infiltration from hillslope runoff, and inlake nutrient processing (Glinska-Lewczuk, 2009). In some cases, these other connection types can play a more important role in oxbow lake chemistry than periodic surface connections created during flood events. An examination of sediment chemistry in floodplain water bodies on the River Havel, Germany showed little impact of flooding on sediment chemistry (particulate organic matter, carbon, nitrogen, phosphorus, and iron) in oxbow lakes (Knosche, 2006). As is the case with physical connectivity, the relative importance of surface and subsurface connectivity depend on local characteristics of the floodplain ecosystem.

Alterations of natural flood dynamics affect the exchange of chemical materials between the river and oxbow lakes. Total organic carbon and total nitrogen accretion in river floodplains are important ecosystem functions of floodplain water bodies, like oxbow lakes, that might improve water quality in rivers (e.g., Mitsch, 1992). An analysis of sediment, carbon, and nitrogen accretion in oxbow lakes on the River Ebro, Spain showed lower accumulation currently (1963−2007) compared to the past (1927−1963; Cabezas et al., 2009). In this example, the reduced accumulation of carbon and nitrogen concentrations in oxbow lake sediment was related to reduced size and frequency of flood events in this floodplain ecosystem (Cabezas et al., 2009).

Importantly, oxbow lakes reduce pollution loading to the river network. Oxbow lakes can intercept nutrients from upland runoff, leaving them in the oxbow lake rather than in the river (e.g., Glinska-Lewczuk, 2009). A similar process of physical interception is observed in riparian wetlands, where wetland ecosystems have been considered habitats that might control nonpoint-source pollution of nutrients (e.g., Mitsch, 1992), sediment (e.g., Brix, 1994), or pesticides (e.g., Gregoire et al., 2009) to rivers. In addition to being areas of deposition, high mineralization rates in oxbow lakes suggest that these lakes can process and remove some nutrients in terrestrial runoff before the runoff reaches the river channel (Winemiller et al., 2000).

5.6.3.3. *Biological Connections*

Hydrologic connectivity influences the biological character of oxbow lakes and facilitates exchange of biological material between oxbow lakes and the active river channel. Evidence also suggests a temporally dynamic relationship between biological assemblages of river and oxbow lake ecosystems.

Oxbow lakes represent important areas of relatively high biological productivity in the floodplain landscape. Oxbow lakes can be a source of plankton to the active river channel (Hein et al., 2003). In contrast to terrestrial sources of carbon that often dominate the water column of rivers, plankton is more labile and easier to assimilate into aquatic food webs (Thorp and Delong, 2002; Bunn et al., 2003).

The connectivity relationship has added complexity for plankton, because oxbow lakes need to be periodically isolated from the river to establish populations of these organisms. Intermediate residence times (i.e., the amount of time a water molecule spends in a lake) of between 10 and 27 days in oxbow lakes along the River Danube resulted in the highest carbon flow between phytoplankton and zooplankton (Keckeis et al., 2003). Likewise, the time since inundation is an important factor influencing the composition of zooplankton communities. Recently inundated floodplain water bodies are dominated by rapid-colonizing rotifers, and then become dominated by cladocera as the time since inundation increases (Baranyi et al., 2002). In this study, total zooplankton biomass, crustacean biomass, and the number of crustacean species were positively related to time since inundation. These results indicate a relationship between the time since inundation and plankton assemblages, and suggest that this relationship exists because colonization and reproduction within an oxbow lake requires time without disturbance.

Although short periods of isolation are necessary for the development of within-oxbow productivity, periodic connections are important for plankton exchange between oxbow lakes and the active river channel. Exchange can occur from the river to the oxbow lake (e.g., juvenile riverine fish may feed in floodplain water bodies; Baranyi et al., 2002) or from the oxbow lake to the river (e.g., phytoplankton; Hein et al., 2003). These periodic connections between floodplain water bodies and corresponding export of labile phytoplankton from floodplain water bodies to rivers contribute to the food sources of biological assemblages in adjacent rivers (Thorp and Delong, 2002; Bunn et al., 2003; Keckeis et al., 2003).

Connectivity between oxbow lakes in the floodplain and the active river channel is important for maintaining mollusk populations in oxbow lakes. A comparison of three oxbow lakes with different levels of connectivity (lotic, semilotic, and isolated) showed the highest level of mollusk diversity in the semilotic lake (eight vs. four taxa in each of the other lakes) on the Lyna River, Poland (Obolewski et al., 2009). In this example, the occurrence of taxa was associated with physiochemical characteristics (oxygen, temperature, and phosphorus) of oxbow lakes. These findings support the idea that the degree of oxbow lake-river connectivity influences the abundance and composition of mollusk communities in floodplain water bodies, and these communities support the diversity of mollusk taxa throughout the river system (Reckendorfer et al., 2006).

Physical connectivity between oxbow lakes and the active river channel influences the composition of benthic macroinvertebrate communities in oxbow lakes. For example, hydrologic connection explained 28% of the variability in benthic invertebrate communities between sites in the active river channel, constructed oxbow lakes, and natural oxbow lakes of the Middle Ebro River, Spain (Gallardo et al., 2008). Macroinvertebrate richness and abundance increased with hydrologic connectivity (i.e., floods and flow pulses) between oxbow lakes and the river channel, and a diversity metric (Shannon index) peaked at intermediate levels of connectivity (Gallardo et al., 2008).

Oxbow lakes have food resources and habitat that often support abundant fish populations (Winemiller et al., 2000; Zeug et al., 2005; Zeug and Winemiller, 2008; Zeug et al., 2009). A comparison of fish biomass in oxbow lakes and a river channel showed that fish biomass in oxbow lakes was three times the biomass caught in rivers. Average catch per unit effort in oxbow lakes was 364.3 g per 10-m seine haul and 5,318 g m^{-1} ha^{-1} of gillnet sampling, versus 138.1 g per 10-m seine haul and 495 g m^{-1} ha^{-1} of gillnet sampling in the river (Winemiller et al., 2000). Additional studies by this research group have found similar patterns for juvenile fish (Zeug and Winemiller, 2008).

Periodic surface water connections between the river and oxbow lakes facilitate the movement of fish from the river to oxbow lakes, where riverine fish can exploit these relatively productive floodplain water bodies before moving back to the river. Dietary data provide evidence that oxbow lakes are important spawning and nursery habitats for gizzard shad in the Brazos River, TX (Zeug et al., 2009). Isotope analysis showed that gizzard shad in oxbow lakes had different isotopic signatures based on habitat type: oxbow, river, and an oxbow-river mixture (Zeug et al., 2009). Although oxbow lakes clearly provided habitat for both juvenile and adult shad, the authors did not observe oxbow-specific isotopic signatures in shad in the river channel (Zeug et al., 2009). In addition, an analysis of otolith chemical signatures by Crook and Gillanders (2006) indicates that floodplain lakes were an important source of carp recruitment to the Murray-Darling River, where floodplain lakes were estimated to be the source of 98% of the young-of-year carp for areas 140 km downstream of the floodplain lakes. In a third example, floodplain water bodies, with their diverse and productive habitats, were considered nurseries for drifting larvae of migratory fish (Meschiatti et al., 2000). Half of the migratory fish species from the Mogi-Guacu River, Brazil also were observed as juveniles in oxbow lakes along the river (24 of the 46 migratory riverine species were observed in 2 oxbow lakes), and most of the migratory fish observed in oxbow lakes were juveniles, rather than larvae or reproductively mature age classes (Meschiatti et al., 2000). This age structure suggests that the oxbow lakes were not the site of reproduction, but were important habitats for juvenile fish.

Individual fish species have specific habitat and reproductive requirements and use floodplain habitats in different ways, giving the dynamic hydrologic connectivity of oxbow lakes and the river network added significance. For example, owing to variable flow in the Rio Grande, NM, recruitment success varies between years of high (e.g., Junk et al., 1989) and low flow (e.g., Humphries et al., 1999), which contributes to overall fish diversity in the Rio Grande (Pease et al., 2006). Likewise, in a 5-year study of fish in floodplain lakes, Shoup and Wahl (2009) discuss how individual oxbow lakes had different conditions and thus varied in suitability for different fish species. In their study, interannual variability was present in oxbow lake hydrology (lake-river connectivity ranged from 0 to more than 21 weeks per year) and water chemistry, and in associated differences in fish assemblages (Shoup and Wahl, 2009). Because of the complex relationships observed in their study, Shoup and Wahl (2009) concluded that the entire floodplain should be considered a single functioning unit that supports the overall biological integrity of a river.

5.6.4. Oxbow Lakes: Synthesis and Implications

The key findings of this case study are as follows:

- Evidence indicates the presence of physical, chemical, and biological connections between oxbow lakes and the river channel. These connections are influenced by the specific local and regional characteristics of both the oxbow lakes and the river.

- Some of the best-documented observed functions of oxbow lakes are as sources or sinks for water, sinks for nutrients from upland runoff that might otherwise flow into rivers, and both sources of food and refuges for riverine biota.

- Human alteration of these connections can be detrimental to the dynamics that balance connectivity and exchange between oxbow lakes and the active river channel. Practices that alter the natural flow regime of the river (e.g., river regulation) or inhibit periodic flooding of oxbow lakes (e.g., levees) affect movement of water and sediment, the use of oxbow lakes by riverine fish, and the regional biological diversity of floodplain water bodies.

- Interannual variability in oxbow lake hydrology, water chemistry, and fish assemblages demonstrate complex relationships between rivers and floodplain

> open-waters and river systems, in which the water bodies in floodplains function as single unit supporting the overall biological integrity of the river.

Although the incidence of observed connectivity between oxbow lakes and river networks varies according to spatial, temporal, physical, and biological factors, most of the evidence examined indicates that oxbow lakes are important determinants of the physical, chemical, and biological condition and function of rivers.

5.7. CASE STUDY: CAROLINA AND DELMARVA BAYS

5.7.1. Abstract

Carolina and Delmarva bays are ponded depressional wetlands that occur along the Atlantic coastal plain from northern Florida to New Jersey. Most bays receive water through precipitation, lose water through evapotranspiration, and lack natural surface outlets. Both mineral-based and peat-based bays have shown connections to shallow groundwater. Bays typically are in proximity to each other or to permanent waters, providing the potential for surface water connections in large rain events via overland flow. Fish are reported in bays that are known to dry out, indirectly demonstrating surficial connections. Amphibians and reptiles use bays extensively for breeding and for rearing young. These animals can disperse many meters on the landscape and can colonize, or serve as a food source to, downstream waters. Similarly, bays foster abundant insects that have the potential to become part of the downstream food chain. Humans have ditched and channelized a high percentage of bays, creating new surface connections to other waters and allowing transfer of nutrients, sediment, and methylmercury.

5.7.2. Introduction

5.7.2.1. *Definition and Geographic Extent*

Carolina bays are elliptical, ponded, depressional wetlands that occur along the Atlantic coastal plain from northern Florida to New Jersey (Prouty, 1952; Williams, 1996; Hunsinger and Lannoo, 2005). They have been called geographically isolated wetlands (i.e., wetlands surrounded by uplands; Tiner, 2003c), and range in water levels from permanently inundated to frequently dry (Sharitz, 2003). Carolina bays range in size from greater than 3,600 ha to less than 1 ha and are most abundant in North Carolina and South Carolina (Sharitz and Gibbons, 1982; Sharitz, 2003). Carolina bays that are geographically specific to the Delmarva Peninsula are often referred to as Delmarva bays. Delmarva bays frequently have the same elliptical shape and orientation as other Carolina bays (Stolt and Rabenhorst, 1987a), yet some lack the shape or rim (Sharitz, 2003).

The number of Carolina bays was estimated at 500,000 in the 1950s (Prouty, 1952), but only 10,000−20,000 remained by the early 1990s (Richardson and Gibbons, 1993). Carolina and Delmarva bays have been ditched and drained for agricultural purposes (see Figure 5-1; Sharitz, 2003). A study of 2,651 Carolina bays in South Carolina found that 97% of bays larger than 0.8 ha had been disturbed by agriculture or logging (Bennett and Nelson, 1991). The northern Delmarva Peninsula has an estimated 1,500−2,500 Delmarva bays remaining (Stolt and Rabenhorst, 1987a). The true number of Carolina and Delmarva bays is likely to be underestimated, because many are too small to be mapped. The National Wetlands Inventory maps have mapping units of 0.4−1.2 ha, but the Department of Energy's Savannah River Site on the upper coastal plain of South Carolina has 371 known Carolina bays with 46% having an area of 1.2 ha or less (Sharitz, 2003).

5.7.2.2. *Geology*

The origin of Carolina and Delmarva bays is unknown, but has been attributed to meteorite impacts, substrate dissolution, and historic modification of shallow ponds through the action of waves generated by winds (Johnson, 1942; Savage, 1982; Ross, 1987; Stolt and Rabenhorst, 1987a; Grant et al., 1998). The soils of both Carolina and Delmarva bays range from mineral to organic depending on the position in the landscape, hydrologic conditions, vegetation, and disturbance (Stolt and Rabenhorst, 1987b; Sharitz, 2003). Most bays have alternating layers of sand or silt with impervious clay (Bliley and Pettry, 1979). The organic horizons in bays can range from 1 to 200 cm, with bays near the coast more likely to have the thicker peat deposits (Newman and Schalles, 1990). Despite variation in soil content, water often quickly infiltrates these soils before reaching an impervious clay layer (Sharitz, 2003).

5.7.2.3. *Hydrology*

Carolina and Delmarva bays gain water primarily from precipitation and lose water by evapotranspiration (Sharitz, 2003). Thus, these systems respond to seasonal rainfall, snowmelt, and temperature. The water levels of Carolina and Delmarva bays therefore fluctuate. The water level in a bay can change from 1−2 m above the soil surface to more than 1 m below the surface (Knight et al., 1989; Schalles and Shure, 1989; Lide et al., 1995; Sharitz, 2003). Bays often are wetter in winter and early spring, when evapotranspiration rates are low, and tend to dry down

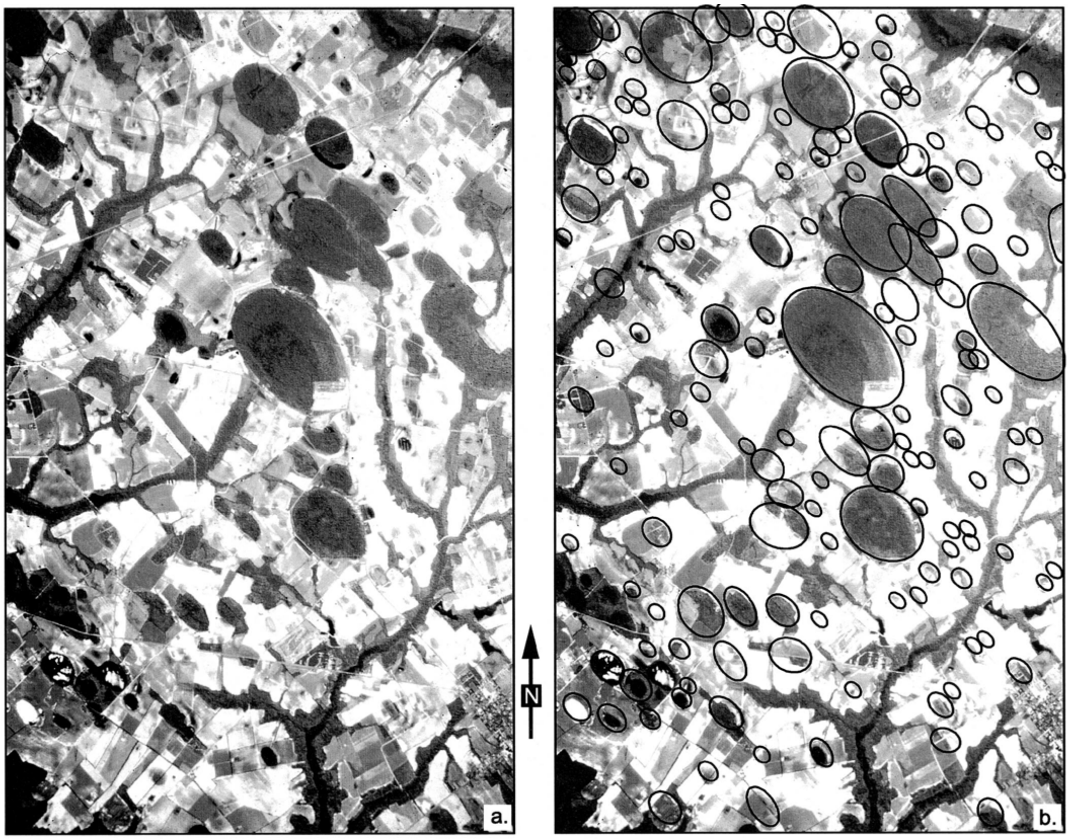


Figure 5-1. Aerial photograph of Carolina bays within a region of the upper Coastal Plain of South Carolina. (A) Infrared image showing the pattern of intact and disturbed Carolina bays within a region of the upper Coastal Plain of South Carolina (scale: 1 cm = 1.5 km), and (B) the same image with bays (or former bays that have been disturbed by agriculture) outlined.

Reprinted with permission from Sharitz (2003).

in summer when evapotranspiration rates are high. Recent work by Lang et al. (2012) using highly accurate LiDAR derived stream maps has shown that the proportion of wetlands intersected by stream channels (and thus not geographically isolated) is higher than previously thought. In an analysis of the Tuckahoe Creek watershed in the Delmarva Peninsula, the High Resolution NHD and NHD Plus were found to underestimate the number of wetlands intersected by natural stream channels by 13% and 27% respectively (Lang et al. 2012). Other hydrologic inputs into bays include artesian wells (Wells and Boyce, 1953), shallow groundwater (Phillips and Shedlock, 1993; Lide et al., 1995; Caldwell et al., 2007b), inlet channels (Sharitz, 2003), and some surface runoff during periods of high rainfall. Some bays, particularly those along the coast, can be flooded by high tides and thus are connected to coastal waters (Bliley and Pettry, 1979; Sharitz, 2003).

Despite the prevalence of clay substrates below many of these bays, some studies have found that bays exchange shallow groundwater with the surroundings (Phillips et al., 1993; Lide et al., 1995; Sun et al., 2006; Caldwell et al., 2007a; Pyzoha et al., 2008). Some Carolina bays have natural outlet channels (Sharitz, 2003), and many have human-created outlet channels (i.e., ditches) typically resulting in connections to other bays or small streams (Sharitz, 2003).

5.7.2.4. *Water Chemistry*

Water chemistry of Carolina and Delmarva bays is affected by their position on the landscape, weathering of underlying mineral substrate, accrual and decomposition of organic matter, and the degree to which surface runoff, precipitation, and groundwater influence their hydrology (Sharitz, 2003). In general, precipitation-fed wetlands are typically acidic and low in nutrients (Whigham and Jordan, 2003).

Newman and Schalles (1990) reported variable water chemistry in a study of 49 Carolina bays in North Carolina and South Carolina that spanned two transects from inland to the coast. All 49 bays were acidic (median pH = 4.6) and were classified as soft waters (median calcium = 1.69 mg Ca^{2+} L^{-1}). DOC represented 38% of the water anions (median DOC = 17.2 mg L^{-1}). Bays with thick peat layers tended to be low in nutrients, whereas bays with thin peat layers had water quality characteristics similar to local groundwater (Newman and Schalles, 1990). Phillips and Shedlock (1993) also associated bay water chemistry with shallow groundwater; their study found similarities in water chemistry between upland groundwater and the margins of three Delmarva bays. The few studies of nutrient cycling within bays indicate some have the proper wetting and drying cycles to promote denitrification (the conversion of nitrate to nitrogen gas; Groffman et al., 1992; Whigham and Jordan, 2003).

Several studies have shown that Carolina bays have the proper hydrology, organic matter content, and pH for the methylation of mercury (Snodgrass et al., 2000b; Brant et al., 2002). Mercury pollution enters water bodies from atmospheric deposition, typically in the ionic form of Hg^{2+}. Bacteria can convert Hg^{2+} to methylmercury, the bioavailable form of mercury that can accumulate in fish, birds, and other organisms. Periodic drying and flooding of Carolina bays, especially shallow ones, promotes mercury methylation and release (Snodgrass et al., 2000b). Mercury levels did not reach acute doses but pose a chronic risk to fish (Snodgrass et al., 2000b) and birds that feed on these fish (Brant et al., 2002).

5.7.2.5. *Biological Communities*

The wetting and drying cycles of Carolina and Delmarva bays promote a diverse biota, including the presence of numerous rare and endemic species (Sutter and Kral, 1994; Edwards and Weakley, 2001; Sharitz, 2003). Eleven types of vegetation communities have been described in regional surveys of Carolina bays, including species-rich herbaceous communities and cypress ponds (Bennett and Nelson, 1991; Weakley and Schafale, 1991). A seed bank study at the Savannah River Site in South Carolina reported higher diversity than any other reported freshwater wetland habitat (Kirkman and Sharitz, 1994). Researchers estimate that more than one-third of rare plant species in the Southeast occur in nonalluvial wetlands including Carolina bays (Sutter and Kral, 1994; Sharitz, 2003).

Carolina and Delmarva bays are highly valuable for providing habitat and food web support for invertebrates and vertebrates (Sharitz, 2003). For example, a Savannah River Site study of zooplankton found 44 species of cladocerans and 7 species of copepods (Mahoney et al., 1990). Another invertebrate study showed that a 1.5-ha Carolina bay contained 115 taxa of aquatic and semiaquatic insects from 29 families and 7 orders; more than 11,600 and 8,400 insects emerged from the bay in 1992 and 1993, respectively (Leeper and Taylor, 1998).

Approximately 10−21% of sampled Carolina and Delmarva bays had fish populations (Gibbons and Semlitsch, 1991; Snodgrass et al., 2000a; Sharitz, 2003). The absence of predatory fish in many bays allows abundant amphibian populations to thrive, especially those that have aquatic larval stages (Sharitz and Gibbons, 1982; Sharitz, 2003). For example, one study sampled two 1-ha bays over the course of a year and captured more than 72,000 amphibians, including 9 salamander and 16 frog species (Sharitz and Gibbons, 1982). The Savannah River Site supports 34 species of amphibians, 16 of which depend entirely on seasonal wetlands for breeding (Gibbons and Semlitsch, 1991). Several of these amphibians are endangered or threatened, including the flatwoods salamander (*Ambrystoma cingulatum*) and the gopher frog (*Rana capito*; Sharitz, 2003).

Sharitz and Gibbons (1982) also reported 6 turtle species, 9 lizard species, 19 snake species, and 13 small mammal species in bays. American alligators (*Alligator mississippiensis*) also are indigenous to southern Carolina bays (Sharitz and Gibbons, 1982). Endangered wood storks (*Mycteria americana*) nest in Carolina bays, and birds such as egrets, coots, wood ducks, and other migratory waterfowl also use Carolina and Delmarva bays (Sharitz and Gibbons, 1982).

5.7.3. Evidence of Connectivity

5.7.3.1. *Physical Connections*

There is active research on the hydrologic connectivity of Carolina and Delmarva bays to surrounding areas via groundwater flows and intermittent surface flows. A few studies have found groundwater connections or indirect evidence of surface water connections.

A study by Lide et al. (1995) found a groundwater connection to a Carolina bay. The study examined a 7-ha Carolina bay on the Savannah River Site typical of other bays in western South Carolina with loamy-sand substrate and an underlying clay layer (Lide et al., 1995). The 2-year study examined data from 38 piezometers, borehole logs, pond stage records, and weather data. They concluded that the Carolina bay was not a perched wetland, but a surface expression of the water table. Although fluctuation of pond stage was largely controlled by precipitation and evapotranspiration, nearly continuous shallow groundwater recharge was present and shallow groundwater discharge occurred periodically.

Phillips and Shedlock (1993) studied three Delmarva bays and also concluded that the bays were connected to local groundwater. They studied water table levels and chemistry in transects that ran from uplands through the Delmarva bays. Local groundwater strongly influenced the height of the water table in the Delmarva bays. The groundwater also was attributed to maintaining a low pH, contributing dissolved aluminum and lowering bicarbonate in the Delmarva bay (Phillips et al., 1993).

Another Carolina bay study in western South Carolina also found evidence for groundwater connectivity (Pyzoha et al., 2008). The more than 13-year study examined piezometer and bay water levels monthly in an 8-ha bay with sandy-loam substrate and an underlying clay layer. Researchers concluded that surface-groundwater connections were important to bay hydrology and the bay was not an isolated system. Sun et al. (2006) incorporated climate, vegetation, and soil information to model the hydrology of this bay, which confirmed that the bay was receiving groundwater discharge and recharging groundwater to lower topographic areas.

Caldwell et al. (2007b) also used a model to understand the hydrology of three Carolina bays in North Carolina and inferred groundwater connections. All three bays were larger than 100 ha, and their hydrology had not been altered by artificial drainage. Soil types were mineral on the perimeter to mostly organic in the center. The team modeled bay hydrology using climate, vegetation, soils, and hydrology data. They estimated that 10% of water inputs to the bays were surface runoff. Groundwater inflow was the source of 3−26% of water volume into the perimeter of the bays, and groundwater outflow volume (2−21%) was frequent in the center of the bays (Caldwell et al., 2007b).

In addition to groundwater, several studies infer Carolina and Delmarva bays are connected to other water bodies through surface water connections. For example, a study of Carolina bays in Virginia revealed that several of the largest bays were at sea level and bordered the Chesapeake Bay (Bliley and Pettry, 1979). Tidal marshes have encroached and entered these Carolina bays, reflecting a direct link between the Carolina bays and the estuarine environment.

Researchers have used GIS methods to determine the nearest river or tributary to Carolina bays (Sharitz, 2003). A GIS analysis at the Savannah River Site of 371 Carolina bays showed that 8% were within 50 m of a stream or tributary, and 12% were within 100 m (mapping units with a minimum resolution of 0.22 ha; Sharitz, 2003). The same methods showed that 12% of the 2,170 Delmarva bays in Maryland were within 50 m and 19% were within 100 m of streams (mapping units with a minimum resolution of 0.40 ha; Sharitz, 2003). During large storms, the bays located closest to the river network may exhibit hydrological connections via overland flow or shallow groundwater flow.

Perhaps the strongest evidence that Carolina bays are connected hydrologically to streams or estuaries is that many of these bays are ditched, creating a conveyance for surface water. These ditches commonly connect the surface water of bays to other bays that are lower on the landscape, and ultimately, to streams (Sharitz, 2003).

5.7.3.2. *Chemical Connections*

Few peer-reviewed papers examine chemical connections between Carolina and Delmarva bays and other waters. One, by Phillips et al. (1993), examined groundwater in the Delmarva Peninsula and found that the amount of nitrate in groundwater decreased with the presence of forested depressional bays. The authors speculated that the nitrate reduction was due to denitrification in the wetlands. These systems do have the appropriate wetting and drying hydrology to promote denitrification, which could reduce the amount of nitrates in both groundwater and surface waters (Groffman et al., 1992).

Carolina and Delmarva bays are frequently connected chemically to downstream waters through ditches. If the bays are sediment and nutrient sinks due to their surficial isolation, ditch connections would make them sources for these materials. For example, Bennet and Nelson (1991) reported that 71% of 2,600 bays were disturbed by agriculture. Whereas the bays might have been a nutrient sink for excess fertilizer that was in surface runoff, these nutrients could now pass through the bays and into the ditches, reaching downstream locations. Additionally, the conditions in Carolina bays have been shown to promote mercury methylation (Snodgrass et al., 2000b). If these bays connect to downstream waters via ditches, some bioavailable mercury would be expected to move to other waters.

5.7.3.3. *Biological Connections*

Carolina and Delmarva bays are “hotspots” for regional biological diversity and animal use (Sharitz, 2003), which indicates a high potential for movement between bays and other water bodies. The current published evidence for biological connections between bays and other waters is, however, limited or indirect.

The presence of fish in Carolina and Delmarva bays indirectly demonstrates that these bays are connected to other waters. For example, fish were found in 21% of 63 Carolina bays on the Savannah River Site, many of which dry out during parts of the year; fish likely colonized these bays through intermittent or permanent surface hydrologic connections (Snodgrass et al., 1996). One Carolina bay in North Carolina, Mattamuskeet Bay, has been colonized by both freshwater and estuarine fishes through four canals connecting the bay to Pamlico Sound (Rulifson and Wall, 2006).

Insect emergence from bays can affect nearby waters. Leeper and Taylor (1998) studied insects in a 1.5-ha Carolina bay and recorded 115 taxa representing 29 families. There were 39 genera of the family Chironomidae, 16 of which are known to live in both pond and stream environments (Hudson et al., 1990; Leeper and Taylor, 1998). Although Leeper and Taylor (1998) did not directly document movement, these species can hatch in Carolina bays and then become important food sources for fish in nearby streams after adult emergence and aerial dispersal. The total number of chironomids emerging from the aforementioned Carolina bay was moderate compared to other wetlands, but cumulative emergence from thousands of bays across the landscape would create a significant food source for organisms, including fish, in other nearby waters.

Carolina and Delmarva bays are immensely productive amphibian breeding habitats, and are critical for persistence of pond-breeding amphibian populations that can move to other water bodies (Sharitz and Gibbons, 1982). Gibbons et al. (2006) documented more than 360,000 juvenile amphibians, from 24 species, emigrating from one Carolina bay during a single breeding season. Greater than 95% of the biomass (about 1,330 kg) came from juveniles of the southern leopard frog (*Rana sphenocephala*), which is known to use both stream and wetland habitats (see Table 5-2). Given the finding that 12−19% of Carolina and Delmarva bays were within 100 m of a tributary (Sharitz, 2003), amphibians emigrating from these bays could transfer extremely high levels of energy and organic matter into rivers and streams. For example, a gene flow study of the wood frog (*Rana sylvatica*), also abundant in Carolina bays, determined that these frogs could move distances of more than 1,600 m (Semlitsch, 2000). About 90% of Carolina bays located in the Savannah River Site have a tributary or river within this distance (Sharitz, 2003).

5.7.4. Carolina and Delmarva Bays: Synthesis and Implications

The key findings of this case study are as follows:

- Both peat-based and mineral-based bays have been shown to have shallow groundwater inputs and outputs.

- Some Delmarva bays have surface water connections to the Chesapeake Bay, and the many bays within proximity to each other and to nearby permanent waters can be connected during high precipitation events.

- Human channeling and ditching of the bays are widespread and create surface connection to other waters.

- Fish are found in bays that periodically dry out, indirectly showing that a hydrologic connection occurred at some time.

- Dispersive amphibians and reptiles use bays for breeding or rearing young.

- The abundant insects in bays could become part of the food chain for downstream fish.

Although generally supporting the existence of or potential for connectivity between Carolina and Delmarva bays and regional rivers or estuaries, the preponderance of evidence found in the literature we reviewed for this case study is indirect. Furthermore, evidence from this literature review that these connections influence the physical, chemical, and biological conditions and functions of rivers or estuaries is circumstantial. Therefore, the literature that we reviewed does not provide sufficient information to fully evaluate the impact of Carolina and Delmarva bays on rivers and estuaries at this time.

5.8. CASE STUDY: PRAIRIE POTHOLES

5.8.1. Abstract

Prairie potholes are a complex of glacially formed wetlands, usually occurring in depressions that lack permanent natural outlets, that are found in the central United States and Canada. The vast area they occupy is variable in many aspects, including climatically, topographically, geologically, and in terms of land use and alteration, which imparts variation on the potholes themselves. Potholes demonstrate a wide range of hydrologic permanence, from holding permanent standing water to wetting only in years with high precipitation, which in turn influences the diversity and structure of their biological communities. Owing in large part to their spatial and temporal variability, individual prairie potholes span the entire continuum of connectivity to and isolation from the river network and other bodies of water. Potholes generally accumulate and retain water effectively due to the low permeability of their underlying soil, which can modulate flow characteristics of nearby streams and rivers. Potholes also can accumulate chemicals in overland flow, thereby reducing chemical loading to other bodies of water. When potholes are artificially connected to streams and lakes through drainage, isolation is eliminated and they become sources of water and chemicals. Potholes also support a community of highly mobile organisms, from plants to invertebrates to birds, that travel among potholes and that can biologically connect the entire complex to the river network.

5.8.2. Introduction

Prairie potholes are a complex of wetlands and water bodies that cover more than 700,000 km^2 of the north-central United States and southern Canada, in an area referred to as the PPR (Kantrud et al., 1989). Formed by the retreat of Pleistocene glaciers, potholes are shallow depressions underlain by low-permeability, clay-rich glacial tills that allow for the collection and temporary retention of water. Prairie potholes range widely in size from more than 200 ha to less than 0.5 ha in surface area with an average of 1 ha or less (Cowardin et al., 1981; Kahara et al., 2009). Their density across the landscape varies from region to region, from roughly 5 potholes km^{-2} in the eastern part of the region to up to 90 km^{-2} in the western part as a result of several factors, including patterns of glacial movement, topography, and climate (van der Valk and Pederson, 2003; Kahara et al., 2009).

By the 1980s, more than 50% of potholes in the region were filled, drained, or ditched, with much higher percentages lost in agriculturally intensive regions like Iowa (Dahl, 1990; see Figure 3-21). Conservation of remaining potholes and restoration of others have been prompted by various means, including the “Swampbuster” provision of the 1985 Food Security Act and the Wetland Reserve Program (administered by the U.S. Department of Agriculture National Resource Conservation Service since 1990).

5.8.2.1. *Hydrologic Dynamics*

Prairie potholes are hydrologically dynamic and heterogeneous, varying both spatially and temporally (Euliss et al., 2004). Water inflows consist largely of precipitation in the form of spring snowmelt runoff or summer rain falling directly into the depressions (Carroll et al., 2005). Some potholes also receive groundwater discharge (Winter and Rosenberry, 1998). Evapotranspiration accounts for most of the water outflow in most potholes (Carroll et al., 2005; van der Kamp and Hayashi, 2009). In some situations, water can leave the basin as overland flow (known as “fill-and-spill”) and shallow or regional groundwater recharge. Potholes with groundwater flow-through or with directional reversal of groundwater flow (discharge under some conditions and recharge under others) have also been identified (Rosenberry and Winter, 1997).

Prairie potholes experience seasonal cycles in water level. Potholes fill in the spring, typically reaching maximum water volume as melting snow, unable to infiltrate frozen upland soils, runs overland into topographically low places on the landscape. Water levels decline through the summer, although they can be maintained or increase due to summer rains (Winter and Rosenberry, 1995). Hydrologic permanence of these systems varies across prairie potholes in response to precipitation, in addition to pothole depth, underlying soil permeability, and position in relation to the water table. Temporary potholes have intermittent standing water only in periods of high precipitation. Seasonal potholes collect water in spring, but typically dry by mid-summer each year. Semipermanent potholes usually maintain standing water throughout the year and occasionally dry in years with low precipitation. Permanent potholes have standing water year-round and maintain standing water from year to year. Importantly, loss of temporary and seasonal potholes has happened at higher rates than loss of permanent pothole wetlands, because shallower, less permanent basins are easier to drain (Miller et al., 2009).

Spatial variation in precipitation affects interannual variation in water level and hydrologic permanence. The east-west gradient across much of the PPR delivers >800 mm of average precipitation to northwestern Iowa each year and <500 mm of average precipitation to most of North Dakota. These dynamics also depend on 20- to 200-year, large-scale climate cycles, including periodic flood and drought conditions (Ashworth, 1999; Leibowitz and Vining, 2003). Annual average climate and longer climate cycles profoundly affect individual pothole dynamics as well as interactions both among potholes and between potholes and broader landscape features (Winter and Rosenberry, 1998; Johnson et al., 2004). Hydrologic dynamics can have major effects on the diversity and abundance of biota (e.g., Euliss and Mushet, 2004).

In addition, topography at multiple scales, soil characteristics, and underlying geology impact pothole dynamics and interactions. Three major physiographic regions comprise the PPR from east to west: the Red River Valley, Drift Prairie, and Missouri Coteau. The Red River Valley was formerly a vast lake filled with glacial melt, and today consists of the relatively topographically flat, clay-rich till surrounding the Red River of the North. The Drift Prairie is higher in elevation than the Red River Valley, and consists of rolling, hummocky terrain formed by glacial deposits. The Missouri Coteau has the highest elevation of the region and relatively steep relief due to thick glacial debris deposits (Kantrud et al., 1989). More restricted local landform zones, various till plains in the Des Moines Lobe in Iowa and the Prairie Coteau in eastern South Dakota for example, also influence hydrologic characteristics of potholes (Miller et al., 2009).

5.8.2.2. ***Chemical Functions***

The chemical composition of prairie potholes is determined largely by the degree of connectivity with groundwater and the position of the wetland with respect to local and regional groundwater systems. Seasonal wetlands located high in the landscape tend to be less saline than the wetlands situated low in the landscape. This simplistic view is made more complex, however, by watershed characteristics, concentration of solutes by evapotranspiration, variability in groundwater and surface-water residence times, changing wetland volumes, and climatic variability. For example, LaBaugh et al. (1996) documented substantial interannual changes in dominant ionic species in response to climatic variability. These changes persisted beyond the climatic inputs, indicating that antecedent moisture conditions also influence wetland response to a changing climate.

Nutrient (including carbon, nitrogen, and phosphorus) cycling in prairie potholes is likely highly dependent on fluctuating water levels, wet-dry cycles, and resulting effects of vegetation cycling. Potholes tend to be nitrogen-limited environments, with the notable exception of potholes located on agricultural land that tend to receive runoff high in nitrate (Crumpton and Goldsborough, 1998). Denitrification that takes place in the anaerobic zone of these and other wetlands can make them good nitrogen sinks (van der Valk, 2006).

5.8.2.3. ***Ecological Characteristics***

The high spatial and temporal abiotic heterogeneity, both within an individual pothole and between potholes across the region, creates a variety of ecological niches and contributes to high biodiversity in these habitats. In response to hydrologic cycles, a semipermanent pothole can have up to four distinct, concentric zones of vegetation, ranging from floating aquatic plants to upland plants. Depending on the timing within annual or between interannual wet-dry cycles, a given pothole can have all zones or just one zone. A pothole also could be in the process of developing zones (regenerative phase) or losing zones (degenerative phase). Invasive species like reed canarygrass (*Phalaris arundinacea*) and cattail (*Typha angustifolia and T. x glauca*) have established in streams and wetlands across the region, disrupting natural pothole vegetation communities.

Perhaps the best known and well studied attribute of prairie potholes is their role as productive feeding and nesting habitat for waterfowl. Of the 34 species of duck that breed in North America, 12 are common in the region, which contributes up to 80% of the continent’s waterfowl game (Batt et al., 1989). In addition, a diverse assemblage of microorganisms, invertebrates, amphibians, reptiles, and sometimes fish, obligately or facultatively, use potholes to feed or reproduce. For example, 44 different invertebrate taxa, including nematodes, mollusks, and arthropods, were collected in Iowa potholes (Hentges and Stewart, 2010).

5.8.3. Evidence

5.8.3.1. *Physical Connections*

Because prairie potholes are small wetlands that form in depressions often lacking permanent outlets, they have been described as hydrologically isolated from each other and from other waters. In some instances this has proved true, but in others this generalization is measurably false.

One of the most noted hydrologic functions of potholes is water storage. Because most of the water outflow in potholes is via evapotranspiration, potholes can become water sinks, preventing flow to other waters in their river or terminal lake basins. Several studies have quantified the large water storage capacity of prairie pothole complexes. A conservative estimate puts the amount of precipitation that can be retained in prairie potholes on land enrolled in the federal Conservation Reserve Program and Wetland Reserve Program at more than 555 million m^3 (Gleason et al., 2008). In various subbasins across the PPR, including those that feed Devils Lake and the Red River of the North, both of which have a long history of flooding, potholes have consistently been estimated to hold tens of millions of cubic meters of water (Hubbard and Linder, 1986; Vining, 2002; Gleason et al., 2007).

Water storage by prairie potholes can affect streamflow. Simulations of the Starkweather Coulee subbasin that drains to Devils Lake indicate that streamflow declines substantially with increased wetland storage capacity. Increasing the volume of pothole storage across the subbasin by approximately 60% caused simulated total annual streamflow to decrease by 50% during a series of dry years and by 20% during wet years. The weaker effect of potholes on streamflow during wet years is likely due to high soil moisture conditions and maintenance of high water levels within potholes across years, which causes a greater proportion of runoff to reach streams relative to dry years (Vining, 2002). Similar simulation studies of watersheds in the Red River basin (one in North Dakota and one in Minnesota) produced qualitatively comparable results, suggesting that the ability of potholes to modulate streamflow can be widespread across the PPR (Vining, 2004). This work also indicates that reducing wetland water storage capacity by connecting formerly isolated potholes through ditching or drainage to the Devils Lake and Red River basins could enhance stormflow and contribute to downstream flooding. In many agricultural areas already crisscrossed by extensive surface and subsurface drainage systems (see Figure 3-21), total streamflow and baseflow are enhanced by directly connecting potholes to stream networks (Blann et al., 2009). The ensuing impacts of changing streamflow are numerous, including effects on stream geomorphology, habitat alteration, and ecological effects (reviewed in Blann et al., 2009).

Studies in some regions show a lack of association between pothole water storage and aspects of streamflow. For instance, modeling of an Iowa watershed indicated that total pothole outflow and total maximum pothole volume do not impact streamflow characteristics (Du et al., 2005). At the Minnesota watershed within the Red River basin discussed previously, simulated annual and daily streamflow decreased with increased pothole water storage capacity but peak streamflow was not reduced during a simulated flooding event, possibly due to an overwhelmed capacity of wetlands and upland soils to retain additional water (Vining, 2004). In yet another Minnesota watershed, wetland water storage provided no explanatory power in estimating peak streamflows for small streams (Lorenz et al., 2010).

The presence or absence of an effect of pothole water storage on streamflow depends on many factors, including patterns of precipitation, topography, and degree of human alteration. For instance, in parts of the PPR with low precipitation, low stream density, and little human alteration, the extreme hydrologic isolation of potholes likely results in few effects on larger waters. Neither a comprehensive examination of the downstream effects nor a systematic characterization of potholes for the factors that determine those effects has been conducted.

Surface water isolation is common for many prairie potholes under average precipitation conditions, but intense precipitation events or high cumulative precipitation over one or more seasons can result in temporary hydrologic connectivity via overland flow. These “fill-and-spill” events between potholes have been witnessed and measured in the Missouri Coteau and in the Drift Prairie zones of the PPR in North Dakota (Winter and Rosenberry, 1998; Leibowitz and Vining, 2003), and inferred using digital aerial photography (Kahara et al., 2009). All else being equal, a wetter climate such as that experienced in the southeastern part of the PPR should promote hydrologic connectivity (Johnson et al., 2005). Local topography can enhance or diminish the likelihood and frequency of temporary surface water connections. Authors have reasoned that the relatively wet and topographically low Red River Valley zone of the PPR should display greater surface water connectivity of potholes than either the Drift Prairie or Missouri Coteau zones. Furthermore, they suggest that stream density will impact the chance that pothole spillage connects to the larger river network. Thus, potholes in the Missouri Coteau, with its limited network of streams, should be more hydrologically isolated than potholes in the Red River Valley or Drift Prairie (Leibowitz and Vining, 2003).

Individual potholes range from isolated to highly connected to other potholes via shallow local and deeper regional groundwater flows. A high water table and soil pocketed with root pores or fractures from wet-dry cycles promote water movement between wetlands via shallow groundwater aquifers. In these cases, water moves most often from topographically high, recharge wetlands to low, discharge wetlands (van der Kamp and Hayashi, 2009), although a single wetland can shift from recharge to discharge in years where the water table is high (Carroll et al., 2005). Other wetlands shift multiple times from recharge to discharge conditions during a single year, which can either facilitate or prevent groundwater connections to adjacent wetlands (Rosenberry and Winter, 1997). Potholes can connect to the river network via groundwater if both are located within the zone of shallow local aquifer flows. One study in North Dakota described prairie wetlands and lakes as water sources to the topographically low James River via shallow groundwater flow (Swanson et al., 1988). Broader, regional movement of groundwater is restricted by very low permeability clay-rich tills that can keep deep groundwater recharge to only millimeters per year on average over a drainage basin (van der Kamp and Hayashi, 1998).

Human alterations of the landscape have had an impact on the connectivity of prairie potholes. Presence or absence of a crop on the upland adjacent to a wetland can alter the degree to which the wetland receives overland flow from the upland and the removal of water via transpiration that otherwise would recharge groundwater (Hayashi et al., 1998). Up to 30% of cropland in the Upper Midwest is artificially drained to increase agricultural productivity (Pavelis, 1987). Filling potholes and lowering the water table through use of field tiling for agriculture has likely increased isolation of remaining potholes by decreasing the density of depressions containing water. Extensive surface draining and ditching, however, have directly and dramatically increased connectivity between pothole basins and surface waters of the river network, converting these systems from precipitation sinks to water sources (Blann et al., 2009). Ditches create new surface water outlets from potholes, allowing collected water to flow into streams and rivers; drains fitted at the bottom of potholes connected to shallow subsurface pipes often discharge to open ditches or streams (Ginting et al., 2000).

5.8.3.2. *Chemical Connections*

The chemical connectivity of prairie potholes is largely mediated by their hydrologic connectivity. Potholes that are hydrologically isolated also tend to be chemically isolated. Unaltered potholes with no outlet can accumulate nutrients, sediment, and other chemical compounds as they collect runoff (Crumpton and Goldsborough, 1998; Donald et al., 1999). Such accumulations have measurable effects on the water quality of potholes and the resident organisms (e.g., Gleason et al., 2003). Presence of these materials in potholes is influenced by inflow, itself a function of precipitation and surrounding land use. Potholes surrounded by tilled fields with higher precipitation, for example, tend to accumulate nutrients, sediment, and pesticides (e.g., Gleason et al., 2008). Additionally, potholes within agricultural areas that have not been drained or ditched are hypothesized to be nitrogen sinks, transforming NO_3^- in the agricultural runoff they receive to nitrous oxide or nitrogen gas. Denitrification can transform up to 80% of nitrate that runs off into potholes (Crumpton and Goldsborough, 1998 and references therein).

On the other hand, potholes that are periodically hydrologically connected to other bodies of water via overland flow can transfer chemicals, such as dissolved ions (Leibowitz and Vining, 2003). Potholes modified by ditching or drainage also have increased hydrologic connectivity and, therefore, chemical connectivity to other water bodies (Whigham and Jordan, 2003). Wetlands drained for agriculture can contribute nitrogen, phosphorus, sediment, pesticides, and herbicides to the waters into which they drain (reviewed in Blann et al., 2009). For example, two wetlands in southwestern Minnesota fitted with surface drains that connected to subsurface tiles emptying into the Watonwan River (a tributary of the Minnesota River) were found to be sources of total solids and total phosphorus to the river during periods of high runoff (Ginting et al., 2000).

Although the chemical sink and periodic chemical source functions of potholes have been documented in the literature, the overall impacts of these functions on larger waters and river networks have been difficult to quantify. This inability is partly because altered and unaltered potholes are embedded in a matrix of land use and land management types, and many different parts of this complex landscape affect downstream water quality and ecological communities (Blann et al., 2009). The most fruitful future approach might be to model drainage basin sediment, nutrient, and pesticide transport under various climatic conditions, using pothole characteristics and functions as independent, explanatory variables (Gleason et al., 2008).

5.8.3.3. *Biological Connections*

Dispersal capabilities of organisms residing in potholes and features of the landscapes they must traverse help determine the strength of biological connectivity. Although some research has focused on internal seed and egg bank dynamics (e.g., van der Valk and Davis, 1978; Gleason et al., 2004), increasing evidence suggests that potholes are not biologically isolated. In fact, the observation that potholes lack an endemic aquatic and semiaquatic flora or fauna suggests that, at least over evolutionary time, potholes have been well connected biologically to communities in other ecosystems (van der Valk and Pederson, 2003).

Organisms can move into and out of potholes via wind, water, or land, either by self-propelling or hitchhiking on other mobile organisms. Many species of wetland plants and insects are dispersed on the wind (Keiper et al., 2002; Soons, 2006), including cattail (*Typha spp.*) seeds, which can disperse over huge areas (>80 ha; van Digglen, 2006) and have been found to quickly, passively colonize previously drained, restored potholes (Galatowitsch and van der Valk, 1996). Plants and invertebrates also can travel by becoming attached to or consumed and excreted by waterfowl (Amezaga et al., 2002). Seeds of up to half a dozen common pothole plants can be consumed and excreted by ducks in a viable state; because migrating waterfowl fly such long distances, the maximum dispersal distance of these hitchhiking plants is estimated to be 1,400 km (Mueller and van der Valk, 2002). Additionally, fast and efficient recolonization of species in restored potholes, including floating aquatics and emergent perennials, is likely facilitated by waterfowl movement (Aronson and Galatowitsch, 2008). Waterfowl often move between wetlands during the breeding season in search of food and cover, and some species also use habitats within the river network as wetlands dry or freeze (Pattenden and Boag, 1989; Murkin and Caldwell, 2000). Water also can provide a means for biologically connecting potholes. Fish and other organisms or parts of organisms that can be suspended in water (e.g., floating insect larvae or seeds) have been hypothesized to move between potholes during spillage events (Zimmer et al., 2001; van der Valk and Pederson, 2003; Herwig et al., 2010). Dispersal of waterborne organisms also can occur through manmade waterways (i.e., ditches) that connect potholes to stream networks (Hanson et al., 2005; Hentges and Stewart, 2010; Herwig et al., 2010). Most of these studies cite only anecdotal evidence for dispersal through ditches. Populations of aquatic plants in agricultural ditches in Europe, however, are genetically highly structured along these man-made waterways, suggesting that these watercourses determine dispersal pathways (Gornall et al., 1998).

Finally, overland dispersal of amphibians and mammals can connect potholes. Eight of twelve amphibian species were able to quickly recolonize restored potholes near source populations (Lehtinen and Galatowitsch, 2001). Although muskrat territories in the PPR are usually restricted (<100 m from the home stream or wetland), they can disperse longer distances to feed and breed in prairie wetland habitat under certain conditions (Clark, 2000 and references therein). In North Dakota, muskrats have been observed taking up residence in potholes for a series of years, as long as suitable water levels and vegetation existed, and then emigrating, presumably to more permanent and larger lakes and streams (Winter and LaBaugh, 2003). Not all wetland animals disperse widely, however. Populations of the pothole-dwelling salamander *Ambystoma tigrinum* (studied in small, nonpothole wetlands, in this case) can be genetically differentiated from each other down to 1.5 km, indicating low dispersal (Routman, 1993).

Landscape features, including distance, relief, and human alterations, can promote or restrict biological connections between wetlands and larger bodies of water. Distance is a major factor: For a given species, wetlands located closer together will exchange more organisms than wetlands that are farther apart. Therefore, landscapes in which potholes are located in relative proximity to each other and to the river network are likely to be connected more frequently and by more species. For example, restored potholes in pothole-dense areas tend to be recolonized by plants more efficiently (Mulhouse and Galatowitsch, 2003), and high pothole density promotes greater movement of waterfowl (Krapu et al., 1997). Unfortunately, quantification of biological effects of potholes on larger waters is severely limited. In most cases, studies involving biological isolation or connectivity in the PPR have focused on the potholes themselves as sources and recipients of organisms.

5.8.4. Prairie Potholes: Synthesis and Implications

The key findings for this case study are as follows:

- The degree to which prairie potholes are connected or have the potential to connect to river networks depends on many factors. These factors include distance to rivers or streams, topography, precipitation, climate cycles (seasonal and on longer time scales), biotic community composition, and artificial drainage. Within the PPR, distance to rivers and streams is strongly influenced by the three major physiographic regions (Red River Valley, Drift Prairie, and Missouri Coteau), which vary in the number of potholes and stream density (e.g., see Figures 3-20A and B).
- On a watershed scale, unaltered potholes often function as hydrologic sinks, sequestering water and reducing annual streamflow, but can become sources as they spill overland under high precipitation and/or low relief. When artificially drained or ditched, potholes can become sources of water, nutrients, sediment, and pesticides. Their roles as sinks and sources affect river geomorphology and biological communities.
- Potholes also might have direct biological effects on river networks via connectivity of resident populations, although these effects are less well known and studied.

Because of wide variation in the conditions that determine the incidence or magnitude of connections between prairie potholes and river networks, pothole complexes in some watersheds are more likely than others to have important influence on associated rivers and lakes. Given evidence in the current literature, however, when proper climatic or topographic conditions occur, or biotic communities are present that promote potential or observed connections, measurable influence on the physical, chemical, and biological condition and function of downstream waters is highly likely.

5.9. CASE STUDY: VERNAL POOLS

5.9.1. Abstract

Vernal pools are shallow, seasonal wetlands that accumulate water during colder, wetter months and gradually dry down during warmer, dryer months. Despite differences in geology, climate, and biological communities, some common findings about the hydrologic connectivity of vernal pools in different regions include evidence for temporary or permanent outlets, frequent filling and spilling of higher pools into lower elevation swales and stream channels, and conditions supporting subsurface flows through pools without perched aquifers to nearby streams. Insects and amphibians that can live in streams or permanent pools opportunistically use glaciated vernal pools as alternative breeding habitat, refuge from predators or environmental stressors, hunting or foraging habitat, or stepping-stone corridors for dispersal and migration. Nonglaciated vernal pools in western states are reservoirs of biodiversity and can be connected genetically to other locations and aquatic habitats through wind- and animal-mediated dispersal.

5.9.2. Introduction

The term vernal pool is broadly used to describe shallow, fishless pools situated on bedrock or low-permeability soils that lack continuous surface water connection to permanent water bodies but have a seasonal period of inundation on which aquatic species depend for completion of their life cycles (Zedler, 2003). This case study reviews evidence for physical and biological relationships between vernal pools and downstream waters in the western United States (western vernal pools) and glaciated areas of northeastern and midwestern states (northern vernal pools), where vernal pools are particularly abundant (Zedler, 2003).

5.9.2.1. *Geography and Geology*

5.9.2.1.1. *Western vernal pools*

Zedler (1987) used the term “vernal pool” to describe basin/swale systems in California’s Mediterranean climate that flood in winter, host diverse communities of aquatic plants and animals in early spring, transition to terrestrial ecosystems in late spring, and desiccate during hot, dry summer months. Western vernal pools are seasonal wetlands associated with topographic depressions, soils with poor drainage, mild, wet winters and hot, dry summers in western North America from southeastern Oregon to northern Baja California, Mexico (Bauder and McMillan, 1998). Locally, wetlands that fit this definition might go by other names, such as the upland playas in Oregon (Clausnitzer and Huddleston, 2002).

Historically, vernal pools covered 518 km^2, or 5−6% of the total land surface in southern California and northern Baja, but losses in that area have been substantial (Bauder and McMillan, 1998). Pools occur on impermeable or slowly permeable soils or bedrock (Smith and Verrill, 1998) that limit percolation and thus produce surficial aquifers that perch above regional groundwater aquifers. Pool-forming soil layers in this region include clay-rich soils, silica-cemented hardpans (duripans), volcanic mudflows, or bedrock (Weitkamp et al., 1996; Hobson and Dahlgren, 1998; Smith and Verrill, 1998; Rains et al., 2006). Because their hydrology and ecology are so tightly coupled with the local and regional geological processes that formed them, western vernal pools typically occur within “vernal pool landscapes” (Smith and Verrill, 1998), or complexes of pools in which swales connect pools to each other and to seasonal streams (Weitkamp et al., 1996; Rains et al., 2008).

5.9.2.1.2. *Northern vernal pools*

The geological formations underlying northern vernal pool landscapes were formed by the movement of glaciers across the northeastern and north-central states approximately 12,000 years ago. Retreating glaciers scoured basins in rock ledges and mountaintops, or left behind large pieces of ice that later collapsed to form topographic depressions containing deposits of gravel, sand, or mud (Colburn, 2004). Although not all vernal pools in these areas were formed by glaciers, the soils, geology, and evolutionary history of plants and animals in northern vernal pools have been profoundly affected by glacial events. Like western vernal pools, northern vernal pools are significantly grouped or clustered (Brooks, 2005). Grant (2005) found that pools in Massachusetts are more likely to occur in more porous substrates (alluvial, fine grained, or sand/gravel soils) than glacial till or impermeable bedrock, increasing their hydrologic connection to shallow groundwater.

Unlike western vernal pools, which typically occur in open grasslands, most northern vernal pools are detrital wetlands fully contained within forest ecosystems that depend on the pulse of organic matter from leaf fall that coincides with initial filling of temporary pools in these regions.

5.9.2.2. *Temporal Dynamics*

Zedler (1987) identified four distinct ecosystem phases in the annual hydrologic cycle of western vernal pools, which we have generalized here (with additional citations) to describe the temporal dynamics of northern vernal pools as well:

- Wetting or newly flooded phase: Rainwater, snow, runoff, or snowmelt infiltrate upper layers of permeable soil and, when topsoils are saturated, collect in pool basins formed by impervious rock, clay, or till layers (aquitards or aquicludes; Rains et al., 2008). In early spring, perennial plants sprout and stored seeds germinate in wet soils. Aquatic invertebrate communities develop from resting eggs and seed banks (Colburn, 2004).

- Aquatic phase: Soils are saturated and pools hold standing water, in many locations filled to capacity. In some western vernal pools, surface and subsurface flows from upland pools through swales feed downgradient pools, connecting pools at a site and extending the aquatic phase of the pool complex (Weitkamp et al., 1996; Hanes and Stromberg, 1998). Pools are colonized by dispersing insects and breeding amphibians.

- Terrestrial phase: Evapotranspiration rates increase and pool water recedes, although soils remain saturated. In western pools, aquatic plants flower and seed. Aquatic animals disperse or become dormant. Terrestrial plant communities persist.
- Dry phase: Pools and soils dry to moisture levels similar to uplands, and many plants senesce or die. Summer rains produce no new ponding or plant growth.

In the western United States, vernal complexes saturate and begin to pool during winter rains, reach maximum depth by early spring, and lose all standing water by late spring (Zedler, 1987). The timing of filling and drying of northern vernal pools vary, depending on pool type. Colburn (2004) proposed five hydrologic classes for northern vernal pools, based on time of filling and average duration of flooding: (1) short-cycle, spring-filling pools that stay wet for 3−4 months; (2) long-cycle, spring-filling pools that stay wet for 5−8 months; (3) short-cycle, fall-filling pools that stay wet for 7−9 months; (4) long-cycle, fall-filling pools that stay wet for 9−11 months; and (5) semipermanent pools that stay wet for 36−120 months. Many northern vernal pools do not dry down completely, but retain areas of saturated sediment or standing water in part of the basin. Such pools are considered “incompletely dry,” to differentiate them from pools that are “continuously flooded” or “dry.”

5.9.2.3. *Ecology*

Vernal pool ecosystems support large breeding populations of amphibians, aquatic invertebrates, and aquatic or semiaquatic plants, including many rare or endemic taxa (King et al., 1996; Zedler, 2003; Colburn, 2004; Calhoun and DeMaynadier, 2007). The annual cycle of basin flooding and drying plays an important role in structuring biological communities in vernal pools. The wet phase prevents establishment of upland plant species in pool basins, while the dry phase limits colonization by aquatic and semiaquatic plant and animal species that occur in permanent wetlands, ponds, or streams (Keeley and Zedler, 1998; Bauder, 2000). Despite their cyclical nature, vernal pool habitats are species rich and highly productive, in part because they provide relatively predator-free breeding habitat for invertebrates and amphibians (Keeley and Zedler, 1998; Calhoun et al., 2003). Many resident species are locally adapted to the timing and duration of inundation, soil properties, and spatial distribution of vernal pools in a specific geographic subregion. Other species that are widespread across regions and aquatic habitat types (including streams or lakes) use inundated pools periodically for refuge, reproduction, or feeding (King et al., 1996; Williams, 1996; Colburn, 2004).

5.9.3. Evidence

5.9.3.1. *Physical Connections*

Vernal pools are primarily precipitation fed and typically lack permanent inflows or outflows to streams or other water bodies. They can be temporarily connected, however, to permanent waters by surface or shallow subsurface flow (flow through) or groundwater exchange (recharge; Weitkamp et al., 1996; Brooks, 2005; Rains et al., 2008). Hydrologic connectivity is typically limited to flow through in vernal pools formed by perching layers; groundwater exchange can occur in vernal pool systems without perching layers (Brooks, 2005).

5.9.3.1.1. *Western vernal pools*

Rains et al. (2006; 2008) examined the hydrology and biogeochemistry of two vernal pool complexes in the northern end of California's Central Valley (Smith and Verrill, 1998). The 2006 study evaluates water balance and the relative importance of direct precipitation, evaporation, surface flow, and shallow subsurface flow in a hardpan vernal pool complex (Rains et al., 2006). The 2008 study contrasts the role of geology and soil type—specifically, clay-rich versus hardpan soils—in controlling vernal pool hydroperiod, hydrodynamics, and water chemistry (Rains et al., 2008). Clay-rich and hardpan complexes are common vernal pool types in California's Central Valley (Smith and Verrill, 1998). In both studies, study sites were pool complexes located in the upper portion of the watersheds. Within each complex, upland (feeder) pools were connected to lower (collector) pools by ephemeral swales, and the lowest pool was connected by swale to a seasonal stream.

Results showed that high and low pools were connected via surface flows 10−60% of the time; surface water flowed through swales connecting low-elevation pools to streams during 60% of the inundation period (see Table 5-5). Underlying geology and soil type influenced ponding rates and inundation periods: in water year 2003, pools in clay-rich soils accumulated water at the onset of rainfall and held water longer than pools in hardpan soils, which have higher soil infiltration rates (see Table 5-5; Rains et al., 2008). Horizontal subsurface flows reduced the number and volume of higher-elevation surface flows into hardpan pools, relative to the clay-rich pools. Most water discharging from the swale to the seasonal stream at the hardpan site was perched groundwater that had flowed around, rather than through, the pool basins. In both soil types, however, vernal pool basins, swales, and seasonal streams were shown to be part of a single surface water and shallow groundwater system connected to the river network when precipitation exceeds storage capacity of the system (Rains et al., 2006; Rains et al., 2008).

Table 5-5. California vernal pool inundation and hydrologic connectivity (summarized from Rains et al. (2008))

Soil; hydrology	Inundation period (days/water year[a])	Flow-through paths (pool-pool and pool-stream)	Surface flows between high and low elev. pools (days/water year[a], % of inundation period)	Surface flows between lowest elev. pool and stream network (days/water year[a], % of inundation period)
Fine-grained, clay-rich soils; perched surface-water	200−205	surface only	120 (60%)	120−123 (60%)
Coarse-grained, hardpan soils; perched surface-water and groundwater	150−154	surface and horizontal subsurface	15 (10%)	90−92 (60%)

[a] October 1 2002−September 30, 2003.

Pyke (2004) reported that a complex of 38 vernal pools north of Sacramento was filled to capacity in 10 of 11 years from November 1999 to June 2001. A direct precipitation-evaporation model for another hardpan complex near this Sacramento site found that direct precipitation could fill pools beyond capacity in most years (Hanes and Stromberg, 1998). Pools located at the lower end of a complex (and thus more likely to be directly connected to streams) can receive surface water through stepping-stone spillage in addition to direct input from precipitation; thus, they can remain wetted longer than upper pools. For example, Bauder (2005) found that "collector" pools with no outlet held water longer than headwater pools with no inlet. Collectively, these findings suggest that filling and overflow of vernal pools are not a rare phenomenon. Filling and spilling also can occur in other vernal pool types because all vernal pools are underlain by aquitards (Rains et al., 2008).

5.9.3.1.2. *Northern vernal pools*

Northern vernal pools include both perched and groundwater-connected aquifers (Brooks, 2004; Boone et al., 2006). As in western vernal pools, rainfall or snowmelt in excess of pool capacity is lost to surface runoff or subsurface flows into shallow, adjacent groundwater (Brooks, 2005). Studies of surface and subsurface inflows and outflows were not found in the literature.

Brooks (2004) reports that precipitation and potential evapotranspiration alone could not account for large observed water losses in four vernal pools he studied for 10 years. These losses could have been due to inaccurate estimates of precipitation or evapotranspiration (both of which were significantly related to water depth) or to surface overflow and soil infiltration, which were not measured. In a separate study, Boone et al. (2006) used a classic water-budget model to predict vernal pool hydroperiods in Minnesota and found that, although precipitation and evapotranspiration were good predictors of pool inundation in most cases, errors in model estimates for a few pools suggested that surface outflows or infiltration might have been occurring at some sites.

Individually small, temporary storage of heavy rainfall and snowmelt in vernal pool systems (pools plus soils) can attenuate flooding, provide a reservoir for adjacent vegetation during the spring growth period, and increase nutrient availability (Hobson and Dahlgren, 1998).

5.9.3.2. *Biological Connections*

Dispersal of vernal pool organisms can be active or passive and occurs at multiple scales: local scale (among adjacent pools), neighborhood scale (among pools in a geographic cluster or complex), or regional (outside of the complex, to other ecosystem types; Compton et al., 2007). Examples of active regional dispersal include insect flight or juvenile dispersal by amphibians. Passive transport is of particular interest for regional-scale dispersal, as it allows plants and low-vagility animals such as microcrustaceans to move over long distances. Examples of passive transport to and from unidirectional wetlands and pools include water-mediated dispersal of larvae (e.g., Hulsmans et al., 2007); transport of diapausing (dormant) eggs by waterbirds (e.g., Figuerola et al., 2005; Frisch et al., 2007) or flying insects (e.g., Van De Meutter et al., 2007); and wind-mediated dispersal of dormant eggs, larvae, and adult zooplankton from dry rock pools (Vanschoenwinkel et al., 2009).

Western vernal pools are highly productive ecosystems that have evolved in what Zedler (2003) describes as a “balance between isolation and connectedness.” Pacific vernal pool landscapes are tightly coupled with variable climate, soils, and geological formations in the western United States, producing diverse habitats for organisms with different life-history strategies (Bauder and McMillan, 1998). Seasonal wetlands in this region might have served as evolutionary refuges since Mesozoic times (King et al., 1996). As a result, present-day vernal pool communities have a large proportion of passively dispersing, endemic (i.e., restricted to small geographic area) species in genera that are widely distributed across continents and aquatic systems (King et al., 1996; Keeley and Zedler, 1998; Zedler, 2003). This apparent paradox is explained by the fact that individuals transported passively over long distances have colonized, and through time become locally adapted to, different vernal pool landscapes, creating new endemic species from the root stock of ancient lineages. As a result, Pacific vernal pools are now rich reservoirs of genetic and species diversity connected to other locations and aquatic habitats through continuing dispersal. The existence and connectivity of such reserves are especially important at a time when changing climatic conditions are likely to increase intermittency of stream flows and decrease duration of wetland inundations in other areas.

Western vernal pools also support generalist invertebrate communities, including crustaceans and insects that are widely distributed in permanent wetlands, ponds, lakes, and streams (Zedler, 1987; 2003). Invertebrates and zooplankton can be flushed from vernal pools into streams or other water bodies during periods of overflow, carried by animal vectors (including humans), or dispersed by wind. Wind-mediated dispersal can be of particular importance in seasonal wetlands: during the dry phase, dry soils containing large numbers of transportable seeds, resting eggs, cysts, diapausing larvae, and adults are picked up and blown away (Vanschoenwinkel et al., 2009). The maximum distance such propagules can travel is not known, but from currently available literature pool-pool or pool-stream transport is clearly possible, and the potential for long-distance transport also exists.

Food webs in northern vernal pools include highly fecund amphibians and insects that convert detrital organic matter inputs into biomass that subsidizes terrestrial and aquatic ecosystems in other parts of the watershed (Semlitsch and Bodie, 1998; Brooks, 2000; Gibbons et al., 2006). Northern vernal pools can provide alternative breeding habitat, refuge from predators or environmental stressors, hunting or foraging habitat, or stepping-stone corridors for dispersal and migration. For example, Gahl et al. (2009) reports that bullfrog (*Rana catesbeiana*) densities per unit wetland perimeter were greater in two small seasonal pools than in a larger, permanent breeding wetland. Regular use of seasonal pools by bullfrogs throughout this study offers compelling evidence for the role of seasonal pools as a component of their nonbreeding habitat. Spotted turtles (*Clemmys guttata*) used seasonal pools for foraging, basking, and mating at two sites in Massachusetts (Milam and Melvin, 2001). Many insects and amphibians found in streams, lakes, or riparian/floodplain wetlands are facultative users of vernal pool habitats (see Table 5-2).

5.9.4. Vernal Pools: Synthesis and Implications

The key findings from this case study are as follows:

- In the aquatic phase, some western vernal pools are filled to capacity in most years, creating conditions under which water flows from pools into swales and stream channels.

- Documented evidence of surface flows connecting western vernal pool complexes to the river network via swales and seasonal streams is available in the literature.

- Indirect evidence indicates that surface and subsurface flows connect northern pools without perched aquifers to shallow groundwater and thus to nearby streams.

- Many insects and amphibians that can live in streams or more permanent pools opportunistically use northern vernal pools as alternative breeding habitat, refuge from predators or environmental stressors, hunting or foraging habitat, or stepping-stone corridors for dispersal and migration.

- Nonglaciated vernal pools in western states have achieved a long-term "balance between isolation and connectedness" and have functioned as refuges for plant and animal diversity since the Mesozoic era. They are current reservoirs of biodiversity connected genetically to other locations and aquatic habitats through continuing dispersal.

Direct evidence supports the existence of seasonal hydrologic connections and indirect evidence supports the movement of organisms between western vernal pool complexes and streams. Indirect evidence supports the existence of hydrologic and biological connections between northern vernal pools and river networks, with potential for storing water during the wet season, and providing alternative breeding habitat or food resources for stream biota.

6. CONCLUSIONS AND DISCUSSION

6.1. MAJOR CONCLUSIONS

In summary, the major conclusions of this review are as follows:

1. The scientific literature demonstrates that streams, individually or cumulatively, exert a strong influence on the character and functioning of downstream waters. All tributary streams, including perennial, intermittent, and ephemeral streams, are physically, chemically, and biologically connected to downstream rivers via channels and associated alluvial deposits where water and other materials are concentrated, mixed, transformed, and transported. Headwater streams (headwaters) are the most abundant stream type in most river networks, and supply most of the water in rivers. In addition to water, streams transport sediment, wood, organic matter, nutrients, chemical contaminants, and many of the organisms found in rivers. Streams are biologically connected to downstream waters by the dispersal and migration of aquatic and semiaquatic organisms, including fish, amphibians, plants, microorganisms, and invertebrates, that use both up- and downstream habitats during one or more stages of their life cycles, or provide food resources to downstream communities. Physical, chemical, and biological connections between streams and downstream waters interact via processes such as nutrient spiraling, in which stream communities assimilate and chemically transform large quantities of nitrogen and other nutrients that would otherwise increase nutrient loading downstream.

2. Wetlands and open-waters in landscape settings that have bidirectional hydrologic exchanges with streams or rivers (e.g., wetlands and open-waters in riparian areas and floodplains) are physically, chemically, and biologically connected with rivers via the export of channel-forming sediment and woody debris, temporary storage of local groundwater that supports baseflow in rivers, and transport of stored organic matter. They remove and transform excess nutrients such as nitrogen and phosphorus. They provide nursery habitat for breeding fish, colonization opportunities for stream invertebrates, and maturation habitat for stream insects. Moreover, wetlands in this landscape setting serve an important role in the integrity of downstream waters because they also act as sinks by retaining floodwaters, sediment, nutrients, and contaminants that could otherwise negatively impact the condition or function of downstream waters.

3. Wetlands in landscape settings that lack bidirectional hydrologic exchanges with downstream waters (e.g., many prairie potholes, vernal pools, and playa lakes) provide numerous functions that can benefit downstream water quality and integrity. These functions include storage of floodwater; retention and transformation of nutrients, metals, and pesticides; and recharge of groundwater sources of river baseflow. The functions and effects of this diverse group of wetlands, which we refer to as “unidirectional wetlands,” affect the condition of downstream waters if there is a surface or shallow subsurface water connection to the river network. In

> unidirectional wetlands that are not connected to the river network through surface or shallow subsurface water, the type and degree of connectivity varies geographically within a watershed and over time. Because such wetlands occur on a gradient of connectivity, it is difficult to generalize about their effects on downstream waters from the currently available literature. This evaluation is further complicated by the fact that, for certain functions (e.g., sediment removal and water storage), downstream effects arise from wetland isolation, rather than connectivity. The literature we reviewed does not provide sufficient information to evaluate or generalize about the degree of connectivity (absolute or relative) or the downstream effects of wetlands in unidirectional landscape settings. However, evaluations of individual wetlands or groups of wetlands could be possible through case-by-case analysis. Further, while our review did not specifically address other unidirectional water bodies, our conclusions apply to these water bodies (e.g., ponds and lakes that lack surface water inlets) as well, since the same principles govern hydrologic connectivity between these water bodies and downstream waters.

6.2. DISCUSSION

Our review of the literature found abundant evidence for the central role of connectivity (or isolation) in maintaining the structure and function of streams, rivers, wetlands, and open-water ecosystems, including lakes, estuaries, and oceans. Most of the materials in rivers, broadly defined here as any physical, chemical, or biological entity, including water, heat energy, sediment, wood, organic matter, nutrients, chemical contaminants, and organisms, originate in upstream tributaries, wetlands, or other connected components of the river system. Water movement through the river system is the primary, but certainly not the only, mechanism providing physical connectivity within river networks. Movement of biota and reproductive materials link aquatic habitats and populations in different locations through processes important for the survival of individuals, populations, and species, and are critical to their persistence at local and regional scales. Similarly, aquatic food webs connect terrestrial ecosystems, streams, wetlands, and downstream waters. Climate, watershed topography, soil and aquifer permeability, the number and types of contributing waters, their spatial distribution in the watershed, interactions among aquatic organisms, and human alteration of watershed features can act individually or in concert to influence stream and wetland connectivity to, and effects on, downstream waters. In some cases, materials traveling shorter distances enter downstream waters with less transformation or dilution, thus increasing their effect; in other cases, sequential transformations such as nutrient spiraling connect distant water bodies in ways that increase their effects on downstream waters. The timing of connectivity also is important, as demonstrated by infrequent, intense events that temporarily connect nearby or distant streams or wetlands to rivers with large, long-lasting effects on downstream structure and function.

The mechanisms by which material and biological linkages affect downstream waters, classified here into five functional categories (source, sink, refuge, transformation, and lag) modify the timing of transport and the quantity and quality of resources available to downstream communities, producing a range of effects over multiple temporal and spatial scales. Thus, *connectivity* (or *isolation*) of streams, wetlands, and open-waters enables (or prevents) the movement of materials and organisms downstream; and *functions* within streams, wetlands, and open-waters determine the effects of transported materials and dispersing organisms on downstream waters. Important downstream effects thus produced are summarized in individual section or case study conclusions and in the Executive Summary (see Chapter 1).

Stream channels and wetlands or open-waters that together form river networks are clearly connected to downstream waters in ways that profoundly influence their condition and function. The connectivity and effects of wetlands and open-waters that are not structurally linked to other waters by stream channels and their lateral extensions are more difficult to address in such a review. Leibowitz (2003) states that the difficulty of answering the question, “are ‘isolated’ wetlands isolated?” arises from the fact that wetlands in unidirectional landscape settings occur within a continuum between completely isolated and fully connected, and that isolation in such wetland systems is a matter of degree (Leibowitz, 2003). Our review, which includes numerous case studies of unidirectional wetland systems, supports this statement and underlines the need to avoid generalizations about either connectivity or isolation based on insufficient information, especially wetland type or class (e.g., prairie pothole) or geographical isolation. Additionally, our review supports the need for a landscape perspective of connectivity in which the effects of small water bodies in a watershed are evaluated in aggregate. The overall strength of a connection, and the magnitude of its downstream effect, are the result of the cumulative effect of multiple, individual water bodies whose hydrology and ecology are tightly coupled with the local and regional geological and biological processes that formed them.

Connectivity has long been a central tenet for the study of water. The River Continuum Concept (Vannote et al., 1980) viewed the entire length of rivers, from source to mouth, as a complex hydrologic gradient with predictable longitudinal patterns of ecological structure and function, in which downstream communities are structured, in part, by upstream communities and processes (Vannote et al., 1980; Battin et al., 2009). The Serial Discontinuity Concept (Ward and Stanford, 1983) built upon the River Continuum Concept to better understand how dams and impoundments disrupt the longitudinal patterns of flowing waters with predictable effects downstream. The Spiraling Concept (Webster and Patten, 1979; Newbold et al., 1981; Elwood et al., 1983) described how the connectivity in river networks can be evaluated and quantified as materials cycle from dissolved forms to transiently stored forms taken up by living organisms and then released back to the water (see Figure 3-14). While these previous frameworks focused on the longitudinal connections of river ecosystems, the subsequent Flood Pulse Concept (Junk et al., 1989) examined the importance of lateral connectivity to adjacent floodplains, including wetlands and open-waters, through seasonal expansion and contraction of flood waters. Ward (1989) summarized the importance of connectivity to lotic ecosystems along longitudinal, lateral, vertical (surface-subsurface), and temporal dimensions, and concluded that running water ecosystems are open systems that greatly interact both with contiguous habitats and other ecosystems in the surrounding landscape.

While scientists long focused on the hydrologic connectivity represented by the physical structure of river networks, more recently they have incorporated the network structure explicitly in conceptual frameworks to describe ecological patterns in river ecosystems, and the processes linking them to other watershed components, including wetlands and open-waters (Power and Dietrich, 2002; Benda et al., 2004; Nadeau and Rains, 2007a; Rodriguez-Iturbe et al., 2009). Application of metapopulation theory and population genetic theory to natural populations has greatly improved our understanding of the role of dispersal and migration in the demographic persistence, community assembly, and evolution of aquatic species (Hastings and Harrison, 1994; Moilanen and Hanski, 1998; Hanski, 1999; Pannell and Charlesworth, 2000; Fagan, 2002; Bohonak and Jenkins, 2003; Waples, 2010; Fronhofer et al., 2012). Network Dynamic Hypothesis (Benda et al., 2004) reexamines the earlier, linearly driven concepts within context of the patchy and stochastic nature of lotic ecosystems described by others (e.g., Resh et al., 1988; Townsend, 1989; Rice et al., 2001). The Network Dynamic Hypothesis was a physically based framework for predicting heterogeneity patterns seen along a river attributed to confluence effects of tributaries, reflecting a more realistic river network perspective (Benda et al., 2004). Bunn and Arthington (2002) identified natural variability of flows and associated lateral and longitudinal connectivity of stream channels and floodplains as two of the four principle mechanisms linking hydrology to aquatic biodiversity of riverine species (see also Leigh et al., 2010). In a novel study of an ecosystem complex of interlinked estuarine, tidal wetland, and freshwater habitats, Sheaves (2009) focused on the ecology of the key connections among the different habitat types, rather the ecology of each habitat type by itself. This case study emphasized the importance of ecological connectivity—which includes process-based connections that maintain habitat function (e.g., nutrient dynamics, trophic function) as well as movements of individuals—in the persistence of aquatic organisms, populations, communities, and species, over the full range of conceptual time scales.

The processes and effects of interest here are those relevant to concepts of “chemical, physical, and biological integrity,” the objective of Clean Water Act programs and basis for the assessment endpoints and metrics used in local, state, and national biomonitoring programs. Figure 6-1 is a simplified conceptual diagram relating hydrologic, chemical, and biological connectivity of freshwater systems to metrics and indicators used in EPA's national assessments of streams, rivers, lakes, wetlands, and coastal waters. Monitoring programs emphasize integrative, biological measures of water resource structure and function to detect impairments, identify probable causes, and take corrective action. Biological communities are essential components of sustainable, highly functioning aquatic ecosystems. Additionally, biological organisms and communities integrate the effects of transitory and chronic stressors present in the environment and have been used for decades to successfully track changes in the condition of water resources at local, regional, and national scales (Karr, 1991; Barbour et al., 1995; Stoddard et al., 2006; Paulsen et al., 2008). Altered connectivity produces a suite of stressors by modifying the natural biological processes, material fluxes, and energy fluxes that link watershed components (see Figure 6-1) with measurable effects on downstream ecosystems. Relating observed effects to probable causes requires not only reliable measures of candidate stressors and observed effects, but also a clear understanding of the intermediate processes that link them mechanistically (US EPA, 2010). Multiple indicators and measures have been proposed for detecting and quantifying altered connectivity (With et al., 1997; Tischendorf and Fahring, 2000; Moilanen and Nieminen, 2002; Calabrese and Fagan, 2004; Martin and Soranno, 2006; Fullerton et al., 2010; Hermoso et al., 2012). In some cases, the impairment results from structural alteration of landscape attributes (e.g., dam construction, channel incision, loss of overland dispersal corridors). These impairments are relatively easier to detect and quantify than impairment of functional processes (e.g., altered nutrient dynamics, reduced gene flow), but both have important consequences for the short- and long-term integrity of freshwater ecosystems. Palmer and Febria (2012) propose that a combination of structural and functional metrics will perform better than either type individually to monitor condition and identify causes of impairment for restoration. This approach is appropriate for detecting and assessing altered connectivity, which has both structural and functional definitions and is an integral component of both aspects of aquatic ecosystem integrity. To this end, systematic approaches that are rooted in landscape analysis and which incorporate hydroecological dynamics present in streams and in wetland complexes are more likely to be successful in providing information useful for inferring when and where altered connectivity is a cause of impairment to national water resources.

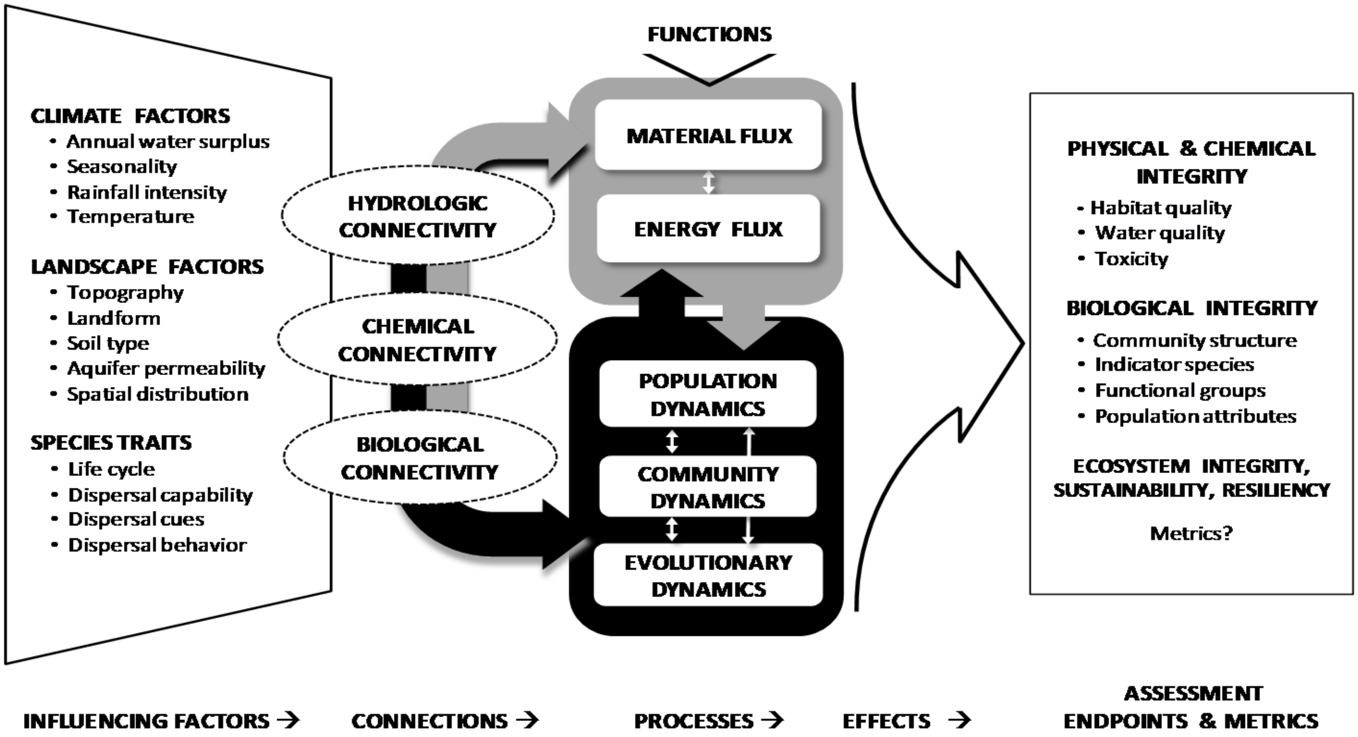


Figure 6-1. The role of connectivity in maintaining the physical, chemical and biological integrity of water. Climate, landscape, and species' traits (Influencing Factors) interact to form hydrologic, chemical, and biological connections that alter the material and energy fluxes, and biological dynamics (Processes) linking watershed components. The mechanisms by which these linkages affect downstream waters (Functions) modify the timing of transport and the quantity and quality of resources available to downstream communities. The effects of interest here are those associated with the concept of "integrity" in downstream waters. Biomonitoring programs have developed structural metrics for assessing physical habitat, water quality, and biological assemblages as indicators of the physical, chemical, and biological "integrity" of downstream waters (Assessment Endpoints and Metrics). New metrics are needed to monitor the range of downstream effects produced by altered connectivity—the multiple critical linkages between climate, landscape, biodiversity, and ecosystem function—and to assess the long-term sustainability and resiliency of aquatic ecosystems.

Currently, case-by-case analysis in unidirectional landscape settings is technically challenging. Accurate assessment of the connectivity and effects of these systems typically requires time- and resource-intensive field studies that have limited geographic scope relative to the landscape areas in which such wetlands and open-waters occur. However, recent scientific advances in the fields of mapping (e.g., Heine et al., 2004; Tiner, 2011; Lang et al., 2012), assessment (e.g., McGlynn and McDonnell, 2003; Gergel, 2005; McGuire et al., 2005; Ver Hoef et al., 2006; Leibowitz et al., 2008; Moreno-Mateos et al., 2008; Lane and D'Amico, 2010; Ver Hoef and Peterson, 2010; Shook and Pomeroy, 2011; Powers et al., 2012), and landscape classification (e.g., Wigington et al., 2012) indicate that increasing availability of high-resolution data sets, promising new technologies for watershed-scale analyses, and methods for classifying landscape units by hydrologic behavior can facilitate such assessments by broadening their scope and improving their accuracy. Tools that expand our ability to detect and monitor ecologically-relevant connections at appropriate scales, metrics to accurately measure effects on downstream integrity, and management practices that apply what we already know about ecosystem function, will contribute to our ability to maintain the long-term sustainability and resiliency of valued freshwater and coastal water resources.

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APPENDIX A. GLOSSARY

Absorption—A reversible process that occurs when molecules in one state or phase penetrate those of another phase.

Adsorption—Adhesion of molecules to a surface, either physically or chemically. Physical adsorption occurs when the surface tension of a solid causes molecules to be held at its surface; this can be reversible, depending on environmental conditions. Chemical adsorption occurs when chemicals bond at the surface of a solid, and is not readily reversible.

Allochthonous—Describing organic material that originates from outside of streams, rivers, wetlands, or lakes (e.g., terrestrial plant litter, soil).

Alluvial Aquifer—An aquifer with geologic materials deposited by a stream or river (alluvium) that retains a hydraulic connection with the depositing stream.

Alluvial Deposits—*See* Alluvium.

Alluvial Groundwater—Groundwater occurring in an alluvial aquifer.

Alluvium—Deposits of clay, silt, sand, gravel, or other particulate materials that have been deposited by a stream or other body of running water in a streambed, on a flood plain, on a delta, or at the base of a mountain.

Anastomosing Channel—A multithreaded stream or river channel where the channels (distributaries) branch and rejoin farther downstream; distributary channels are separated by stable islands (usually vegetated) that are large relative to the size of the channels.

Anoxic Conditions—Without detectable dissolved oxygen; anaerobic.

Aquatic Ecosystem—Any aquatic environment, including all of the environment's living and nonliving constituents and the interactions among them.

Aquifer—A geologic formation (e.g., soil, rock, alluvium) with permeable materials partially or fully saturated with groundwater which yields groundwater to a well, spring, or stream.

Artificial Drainage—Use of artificial channels or subsurface structures to drain an area by increasing the rate of flow of water from the area.

Assimilatory Processes—The incorporation or transformation of simple compounds into more complex compounds.

Autochthonous—Describing organic matter that originates from production within streams, rivers, wetlands, or lakes (e.g., periphyton, macrophytes, phytoplankton).

Bank Storage—Storage of water that flows from a stream to an alluvial aquifer during a flood or period of high streamflow. The volume of water is stored and released after the high-water event over days to weeks. The volume of water stored and the timing of release depends on the hydraulic properties of the alluvial aquifer.

Baseflow—Sustained flow of a stream (or river) in the absence of stormflow (direct runoff). Natural baseflow is sustained by groundwater discharge in the stream network. Baseflow also can be sustained by human sources (e.g., irrigation recharges to groundwater).

Basin—*See* Drainage Basin.

Bedrock—Solid rock underlying loose deposits such as soil or alluvium.

Bidirectional Wetland—A wetland that occurs in a bidirectional wetland setting. *See* Bidirectional Wetland Setting.

Bidirectional Wetland Setting—A landscape setting (e.g., floodplains and most riparian areas) that is subject to bidirectional hydrologic flows between wetlands and the river network through surface water or groundwater. *See* Unidirectional Wetland Setting.

Bifurcation—The branching of a stream or river network.

Bifurcation Ratio—For a stream or river network, the ratio of the number of stream segments of a given stream order to the number of stream segments of the next higher order. This ratio provides a measure of the degree of branching within networks.

Bog—A peat-accumulating wetland that is generally nutrient poor.

Braided Channel—A multithreaded channel where the channels (distributaries) branch and rejoin farther downstream and the channels are separated by mobile, transient bars (poorly vegetated) that are small relative to the size of the channels.

Carolina Bays—Elliptical, ponded, depressional wetlands that range along the Atlantic coastal plain from northern Florida to New Jersey. *See* Delmarva Bays.

Catchment—The area drained by a stream, river, or other water body; typically defined by the topographic divides between one water body and another. *Synonymous with* Watershed *and* Drainage Basin.

Channel—A natural or constructed passageway or depression of perceptible linear extent that conveys water and associated material downgradient.

Channelization—A type of artificial drainage in which complex channels are straightened to increase the rate of water flow from an area.

Channelized Flow—Flow that occurs in a natural or artificial channel.

Condition—General health or quality of an ecosystem, typically assessed using one or more indicators.

Confined Aquifer—An aquifer bounded above and below by confining units of distinctly lower permeability than that of the aquifer itself.

Confluence—The point at which two stream channels intersect to form a single channel.

Connectivity—The degree to which components of a river system are joined, or connected, by various transport mechanisms; connectivity is determined by the characteristics of both the physical landscape and the biota of the specific system.

Contributing Area—Location within a watershed/river network that serves as a source of streamflow or material flux.

Contaminants—Any material that might be harmful to humans or other biological organisms when released to the environment.

Deep Groundwater—Groundwater flow systems having the deepest and longest flowpaths; also referred to as regional groundwater flow systems, they can occur underneath local and intermediate groundwater flow systems. *See* Local Groundwater, Regional Groundwater.

Deep Percolation—Drainage of soil water downward by gravity below the maximum effective depth of the root zone toward storage in subsurface strata.

Delmarva Bays—Carolina bays that are geographically specific to the Delmarva Peninsula. These wetlands frequently have the same elliptical shape and orientation as Carolina bays, but can lack the shape or rim. *See* Carolina Bays.

Dendritic Stream Network—A stream network pattern of branching tributaries (see Figure 3-19B).

Depressional Wetland—A wetland occupying a topographic low point that allows the accumulation of surface water. Depressional wetlands can have any combination of inlets and outlets or lack them completely. Examples include kettles, prairie potholes, and Carolina bays. This category also includes slope wetlands (wetlands associated with surface discharge of groundwater or saturated overflow with no channel formation).

Diadromous—Migratory between fresh and salt waters.

Direct Runoff—Runoff that occurs in direct response to precipitation. *See* Stormflow.

Discharge—The volume of water (surface water or groundwater) that passes a given location over a given period of time; the rate of runoff. Often expressed as $ft^3\ s^{-1}$ or $m^3\ s^{-1}$.

Discontinuous Flow—Refers to stream or river reaches that have flow in one part of the reach but not another part of the reach. *See* Reach.

Dispersal—Movement by organisms or reproductive materials (e.g., seeds, eggs, genes) away from an existing population or parent organism.

Drainage Area—The spatial extent of a drainage basin. Typically expressed in mi^2 or km^2.

Drainage Basin—The area drained by a stream, river, or other water body; typically defined by the topographic divides between one water body and another. *Synonymous with* Catchment *and* Watershed.

Drainage Density—The total length of stream channels per unit area (e.g., per mi^2, km^2).

Endorheic Basins—A closed basin with no outflows to other water bodies.

Ephemeral Stream—A stream or river that flows briefly in direct response to precipitation; these channels are above the water table at all times.

Eutrophication—Natural or artificial enrichment of a water body by nutrients, typically phosphates and nitrates. If enrichment leads to impairment (e.g., toxic algal blooms), eutrophication is a form of pollution.

Evapotranspiration—The loss of water to the atmosphere that is the combination of evaporation and transpiration losses. Transpiration is the loss of water vapor to air by plants.

Fen—A peat-accumulating wetland characterized by mineral-rich water inputs.

Flood—The occurrence of stream or river flow of such magnitude that it overtops the natural or artificial banks in a reach of the stream or river; where a floodplain exists, a flood is any flow that spreads over or inundates the floodplain. Floods can also result from rising stages in lakes and other water bodies.

Flood (100-year)—Flood level (stage or discharge) with a 1% probability of being equaled or exceeded in a given year.

Flood Flows—Discharge or flow of sufficient magnitude (or greater) to cause a flood.

Flood Stage—The stage at which streams or rivers overtop their natural or artificial banks.

Floodwater—Water associated with a flood event.

Floodplain—A level area bordering a stream or river channel that was built by sediment deposition from the stream or river under present climatic conditions and is inundated during moderate to high flow events. Floodplains formed under historic or prehistoric climatic conditions can be abandoned by rivers and form terraces.

Floodplain Wetland—A wetland that occurs in a floodplain.

Flow—Water movement above ground or below ground.

Flow Duration Class—A classification that assigns streamflow duration to ephemeral, intermittent, or perennial classes.

Flow Regime—The timing of streamflow.

Flowpath—*See* Hydrologic Flowpath.

Flux—Flow of materials between system components per unit time.

Gaining Stream or Wetland—A wetland, stream or river reach that experiences a net gain of water from groundwater (see Figure 3-5). In this situation, the water table elevation in the vicinity of the stream or wetland is higher than the stream or wetland water surface. Conditions conducive to losing or gaining streams and wetlands can change over short distances within river networks and river basins. *See* Losing Stream or Wetland.

Geographically Isolated Wetland—A wetland that is completely surrounded by uplands; for example, hydrophytic plant communities surrounded by terrestrial plant communities or undrained hydric soils surrounded by nonhydric soils. This term is often misunderstood to mean hydrologically isolated. Geographically isolated wetlands vary in their degree of hydrologic and biotic connectivity.

Groundwater—Any water that occurs and flows in the saturated zone. *See* Saturated Zone.

Groundwater Discharge —The flow of groundwater to surface waters; discharge areas occur where the water tables intersect land surfaces. *See* Seep, Spring.

Groundwater Discharge Wetland—A wetland that receives groundwater discharge.

Groundwater Flow—Flow of water in the subsurface saturated zone.

Groundwater Flow-through Wetland—A wetland that has both groundwater inputs and outputs. Groundwater enters the wetland through the upgradient direction and exits the wetland downgradient.

Groundwater Recharge—The process by which groundwater is replenished; a recharge area occurs where precipitation water infiltrates a water surface and is transmitted downward to the saturated zone (aquifer).

Groundwater Recharge Wetland—A wetland that recharges groundwater.

Groundwater Reservoir—A saturated body of groundwater having loosely definable spatial limits.

Groundwater System—Reference to the groundwater and geologic materials comprising the saturated zone; the groundwater system as a whole is a three-dimensional flow field.

Groundwater-Surface Water Interactions—Movement of water between surface water bodies and groundwater systems. Flows can occur in either direction.

Groundwater Withdrawal—Pumping of water from aquifers for human uses.

Habitat—Environment (place and conditions) in which organisms reside.

Headwater—Areas from which water originates within a river or stream network. This term typically refers to stream channels but can also describe wetlands or open waters, such as ponds.

Headwater Stream—Headwater streams are first- to third-order streams. Headwater streams can be ephemeral, intermittent, or perennial. *See* Stream Order, Flow Duration Class.

Hillslope—A sloping segment of land surface.

Hydraulic Conductivity—A measure of the permeability of a porous media. For a given hydraulic gradient, water moves more rapidly through media with high hydraulic conductivity than low hydraulic conductivity.

Hydraulic Gradient—Slope of the water table.

Hydraulic Head—The height above a standard datum of the surface of a column of water that can be supported by the static pressure at a given point; for a well, the hydraulic head is the height of the water level in the well compared to a datum elevation.

Hydraulics—The physics of water in its liquid state.

Hydrograph—A graph of stream or river discharge over time. Stage or water table elevation also can be plotted.

Hydrograph Falling Limb—The portion of an event hydrograph in which streamflow is decreasing.

Hydrograph Rising Limb—The portion of an event hydrograph in which streamflow is increasing.

Hydrologic Event—An increase in streamflow resulting from precipitation or snowmelt.

Hydrologic Flowpath—The pathway that water follows as it moves over the watershed surface or through the subsurface environment.

Hydrology—The study of the properties, distribution, and effects of water as a liquid, solid, and gas on Earth's surface, in the soils and underlying rocks, and in the atmosphere.

Hydrologic Landscape—A landscape with a combination of geology, soils, topography, and climate that has characteristic influences on surface water and groundwater.

Hydrologic Permanence—The frequency and duration of streamflow in channels or the frequency and duration of standing water in wetlands.

Hyporheic Flow—Water from a stream or river channel that enters subsurface materials of the streambed and bank and then returns to the stream or river.

Hyporheic Exchange—Water and solutes exchanged between a surface channel and the shallow subsurface. *See* Hyporheic Flow.

Hyporheic Zone—The area adjacent to and underneath a stream or river in which hyporheic flow occurs. The dimensions of the hyporheic zone are controlled by the distribution and characteristics of alluvium and hydraulic gradients between streams and local groundwater.

Infiltration—The downward entry of water from the land surface into the subsurface.

Infiltration Capacity—The maximum rate at which infiltration can occur at a given location.

Intermediate Groundwater—Groundwater flow systems representative of the wide range of flowpath lengths and depths that occur between local and regional groundwater systems.

Intermittent—This term can also be applied to other surface water bodies and groundwater flow or level. *See* Intermittent Stream.

Intermittent Stream—A stream or portion of a stream that flows continuously only at certain times of year; for example, when it receives water from a spring, groundwater source, or from a surface source such as melting snow. At low flow, dry segments alternating with flowing segments can be present.

Inundation—To cover dry land with floodwaters.

Isolation—Condition defined by reduced or nonexistent transport mechanisms between system components.

Isotopic Tracer—*See* Stable Isotope Tracer.

Lag Function—Any function within a stream or wetland that provides temporary storage and subsequent release of materials without affecting cumulative flux (exports = imports); delivery is delayed and can be prolonged.

Lateral Source Stream—A first order stream that flows into a higher order stream.

Lentic—Of, relating to, or living in still water. *See* Lotic.

Levee (Artificial)—An engineered structure built adjacent to a stream or river from various materials to prevent flooding of surrounding areas. The levee raises the elevation of the channel height to convey greater discharge of water without flooding.

Levee (Natural)—A broad, low ridge or embankment of coarse silt and sand that is deposited by a stream on its floodplain and along either bank of its channel. Natural levees are formed by reduced velocity of flood flows as they spill onto floodplain surfaces and can no longer transport the coarse fraction of the suspended sediment load.

Local Groundwater—Groundwater with a local flow system. Water that recharges at a high point in the water table that discharges to a nearby adjacent lowland. Local groundwater flow is the most dynamic and the shallowest of groundwater flow systems. Therefore, it has the greatest interchange with surface water. Local flow systems can be underlain by intermediate and regional flow systems. Water in these deeper flow systems have longer flowpaths and longer contact time with subsurface materials. Deeper flow systems also eventually discharge to surface waters and influence their condition.

Losing Stream or Wetland—A stream, wetland, or river reach that experiences a net loss of water to a groundwater system (see Figure 3-5). In this situation, the water table elevation in the vicinity of the stream or wetland is lower than the stream or wetland water surface. Conditions conducive to losing or gaining streams and wetlands can change over short distances within river networks and river basins. *See* Gaining Stream or Wetland.

Lotic—Of, relating to, or living in moving water. *See* Lentic.

Mainstem—Term used to distinguish the larger (in terms of discharge) of two intersecting channels in a river network.

Materials—Any physical, chemical, or biological entity, including but not limited to water, heat energy, sediment, wood, organic matter, nutrients, chemical contaminants, and organisms.

Meltwater—Liquid water that results from the melting of snow, snowpacks, ice, or glaciers.

Migration—Long-distance movements undertaken by organisms on a seasonal basis.

Nutrients (In Aquatic Systems)—Elemental forms of nitrogen, phosphorus, and trace elements, including sulfur, potassium, calcium, and magnesium, that are essential for the growth of organisms but can be contaminants when present in high concentrations.

Nutrient Spiraling—Longitudinal cycles (“spirals”) of nutrient uptake and release along the river continuum. The spirals are created as aquatic organisms consume, transform, and regenerate nutrients, altering the rates of nutrient transport to downstream waters.

Open Channel Flow—Water flowing within natural or artificial channels.

Open-waters—Nontidal lentic water bodies such as lakes and oxbow lakes that are frequently small or shallow.

Overbank Flow—Streamflow that overtops a stream or river channel.

Overland Flow—The portion of streamflow derived from net precipitation that fails to infiltrate in the land surface and runs over the surface to the nearest stream channel without infiltrating at any point.

Oxbow Lakes—Water bodies that originate from the cutoff meanders of rivers and are common in floodplains of large rivers around the world.

Peatland—A wetland that accumulates partially decayed organic matter. Fens and bogs are common examples.

Perched Groundwater—Unconfined groundwater separated from an underlying body of groundwater by an unsaturated zone; perched groundwater is supported by a perching layer (bed) whose permeability is so low that water percolating downward to the underlying unsaturated zone is restricted.

Perching Layers—*See* Perched Groundwater.

Percolation—The downward movement of water through soil or rock formations.

Perennial—This term can be applied to other surface water bodies and groundwater flow or level. *See* Perennial Stream.

Perennial Stream—A stream or portion of a stream that flows year-round and is maintained by local, intermediate, or regional groundwater discharge or flow from higher in the river network.

Permanent Waters—Water bodies that contain water year-round; perennial.

Permeability—Property of a porous medium that allows it to transmit fluids under a hydraulic gradient. For a given hydraulic gradient, water will move more rapidly with high permeability materials than low permeability materials.

Phreatophyte—Plants that use water from the saturated zone.

Potentiometric Surface—The surface representing the level to which groundwater will rise in a well penetrating a confined aquifer.

Prairie Potholes—Complex of glacially formed wetlands, usually lacking natural outlets, which are found in the central United States and Canada.

Precipitation—Water that condenses in the atmosphere and falls to a land surface. Common types include rain, snow, hail, and sleet.

Precipitation Intensity—The rate at which precipitation occurs; generally refers to rainfall intensity.

Primary Production/Productivity—The fixation of inorganic carbon into organic carbon (e.g., plant and algae biomass) through the process of photosynthesis. Primary production is the first level of the stream food web, and provides most of the autochthonous carbon produced in streams. It is referred to as Gross Primary Productivity (GPP) or Net Primary Productivity (NPP), where NPP is equal to GPP minus respiration. *See* Respiration, Secondary Production/Productivity.

Propagule—Any part of an organism that can give rise to a new individual organism. Seeds, eggs, and spores are propagules.

Reach—A length of stream channel with relatively uniform discharge, depth, area, and slope.

Recharge Area—An area in which water infiltrates the surface and reaches the zone of saturation.

Refuge Function—The protective function of a stream or wetland that allows a material to avoid mortality or loss in a nearby sink area, thereby preventing the net decrease in material flux that would otherwise have occurred (exports = imports). This term typically refers to biological materials. *See* Sink Function.

Regional Groundwater—Groundwater with a deep, regional-scale flow system; also referred to as deep groundwater. These flow systems can occur beneath local and intermediate groundwater flow systems. *See* Local Groundwater, Deep Groundwater.

Respiration—The chemical process by which organisms break down organic matter and produce energy for growth, movement, and other biological processes. Aerobic respiration uses oxygen and produces carbon dioxide.

Return Flow—Water that infiltrates into a land surface and moves to the saturated zone and then returns to the land surface (or displaces water that returns to the soil surface).

Riparian Areas—Transition areas or zones between terrestrial and aquatic ecosystems that are distinguished by gradients in biophysical conditions, ecological processes, and biota. They are areas through which surface and subsurface hydrology connect water bodies with their adjacent uplands. They include those portions of terrestrial ecosystems that significantly influence exchanges of energy and matter with aquatic ecosystems. Riparian areas are adjacent to perennial, intermittent, and ephemeral streams, lakes, and estuarine-marine shorelines. *See* Upland.

Riparian Wetland—Portions of riparian areas that meet the Cowardin et al. (1979) three-attribute definition of a wetland (i.e., having wetland hydrology, hydrophytic vegetation, or hydric soils). *See* Wetland.

River—A relatively large volume of flowing water within a visible channel, including subsurface water moving in the same direction as the surface water, and lateral flows exchanged with associated floodplain and riparian areas. *See* Stream.

River Network—A hierarchical, interconnected population of channels or swales that drain water to a river. Flow through these channels can be perennial, intermittent, or ephemeral.

River Network Expansion/Contraction—The extent of flowing water in a river network increases during wet seasons and large precipitation events and decreases during dry periods. *See* Variable Source Area.

River System—A river and its entire drainage basin (i.e., its watershed), including its river network, associated riparian areas, floodplains, alluvial aquifers, regional aquifers, connected water bodies, geographically isolated water, and terrestrial ecosystems.

Runoff—The part of precipitation, snowmelt, or other flow contributions (e.g., irrigation water) that appears in surface streams at the outlet of a drainage basin; it can originate from both above land surface (e.g., overland flow) and below land surface sources (e.g., groundwater). Units of runoff are depth of water (similar to precipitation units e.g., mm). This measurement is the depth of water if it were spread across the entire drainage basin.

Saturated Zone—Water beneath the land surface occurs in two principal zones, the unsaturated zone and the saturated zone. In the unsaturated zone, the voids in soil and geologic material contain both air and water. The upper part of the unsaturated zone is the soil-water zone. The voids in the saturated zone are completely filled with water. Water in the saturated zone is referred to as groundwater. The upper surface of the saturated zone is referred to as the water table. *See* Groundwater.

Saturation Overland Flow—Water that falls onto a saturated land surface and moves overland to the nearest stream or river.

Seasonality—Refers to the seasonal distribution of water surplus of a river system. *See* Water Surplus.

Secondary Production/Productivity—The generation of biomass of consumer organisms that feed on organic material from primary producers (algae, microbes, aquatic and terrestrial plants), and biomass of predators that feed on consumer organisms. *See* Primary Production/Productivity.

Seep—A small area where water slowly flows from the subsurface to the surface. A seep can also refer to a wetland formed by a seep; such a wetland is referred to as a groundwater slope wetland.

Seepage—Water that flows from a seep.

Shallow Groundwater—Groundwater with shallow hydrologic flowpaths. *See* Local Groundwater.

Sink Function—Any function within a stream or wetland that causes a net decrease in a material flux (imports exceed exports).

Snowpack—Accumulation of snow during the winter season; an important source of water for streams and rivers in the western United States.

Snowmelt—The complete or partial melting and release of liquid water from seasonal snowpacks.

Soil Water—*See* Saturated Zone.

Solute—A substance that is dissolved in water.

Source Area—The originating location of water or other materials that move through a river system.

Source Function—Any function within a stream or wetland that causes a net increase in a material flux (exports exceed imports).

Spillage—Overflow of water from a depressional wetland to a swale or channel.

Spring—A surface water body formed when the side of a hill, a valley bottom, or other excavation intersects a flowing body of groundwater at or below the local water table.

Stable Isotope Tracer—Certain elements such as oxygen, hydrogen, carbon, and nitrogen have multiple isotopes that occur in nature. These isotopes can be used to track the source and movement of water and other substances.

Stage—The elevation of the top of a water surface.

Stream—A relatively small volume of flowing water within a visible channel, including subsurface water moving in the same direction as the surface water, and lateral flows exchanged with associated floodplain and riparian areas. *See* River.

Stream Power—An index of the erosive capacity of flowing water in stream channels and has the mathematical form of: $\omega_a = \tau_o V$, where τ_o is the shear stress at the bed (N/m^2) and V is velocity in m/s. N is metric normal temperature and pressure.

Stream Reach—*See* Reach.

Storm—A precipitation event that produces an increase in streamflow.

Stormflow—The part of flow through a channel that occurs in direct response to precipitation; it includes surface and subsurface sources of flow. *See* Direct Runoff.

Stormflow Recession—Decrease in stormflow following a hydrologic event.

Stream Order (Strahler)—A method for stream classification based on relative position within a river network, where streams lacking upstream tributaries (i.e., headwater streams) are first-order streams and the junction of two streams of the same order results in an increase in stream order (i.e., two first-order streams join to form a second-order stream, two second-order streams join to form a third-order stream, and so on). Where streams of different order join, the larger stream’s order is retained. Stream order classifications may differ, depending upon the map scale used to determine order.

Streamflow—Flow of water through a stream or river channel. *See* Discharge.

Subsurface Stormflow—Water that infiltrates into the land surface and moves rapidly (or displaces water that moves rapidly) to streams or rivers during a hydrologic event; term does not specify a specific hydrologic flowpath.

Subsurface Water—All water that occurs below the land surface.

Surface Runoff—*See* Overland Flow.

Surface Water—Water that occurs on Earth's surface (e.g., springs, streams, rivers, lakes, wetlands, estuaries, oceans).

Surface Water Bodies—Types of water bodies that comprise surface water. *See* Surface Water.

Swale—A nonchannelized, shallow troughlike depression that carries water mainly during rainstorms or snow melt. A swale may or may not be considered a wetland depending on whether it meets the Cowardin et al. (1979) three-attribute wetland criteria. *See* Wetland.

Symmetry Ratio—The size ratio of a minor tributary ($T2$) to a major tributary ($T1$) at a confluence. Discharge ($Q2/Q1$), drainage area ($A2/A1$), or channel width ($W2/W1$) can be used to characterize the ratio of tributary size.

Terminal Source Stream—A first-order stream that intersects another first-order stream.

Terrace—A historic or prehistoric floodplain that has been abandoned by its river and is not currently in the active floodplain. *See* Floodplain.

Terrene Wetlands—"Wetlands surrounded or nearly so by uplands and lacking a channelized outlet stream; a stream may enter or exit this type of wetland but it does not flow through it as a channel; includes a variety of wetlands and natural and human-made ponds" (Tiner, 2011).

Tracer—A substance that can be used to track the source and movement of water and other substances.

Transformation Function—Any function within a stream or wetland that converts a material into a different form; the amount of the base material is unchanged (base exports equal base imports), but the mass of the different forms can vary.

Transmission Loss—The loss of runoff water by infiltration into stream and river channel beds as water moves downstream; this process is common in arid and semiarid environments.

Tributary—A stream or river that flows into a higher-order stream or river.

Tributary Junction—Where a tributary joins a higher-order stream or river.

Turnover length—The ratio of the downstream flux of organic carbon to ecosystem respiration per length of stream. It approximates the average distance that organic carbon is expected to travel before being consumed and mineralized by aquatic biota.

Unconfined Aquifer—An aquifer that has a water table; the aquifer is not bounded by lower permeability layers. *See* Confined Aquifer.

Unidirectional Wetland—A wetland that occurs in a unidirectional wetland setting. *See* Unidirectional Wetland Setting.

Unidirectional Wetland Setting—A landscape setting where there is a potential for unidirectional hydrologic flows from wetlands to the river network through surface water or groundwater. *See* Bidirectional Wetland Setting.

Unsaturated Zone—*See* Saturated Zone.

Uplands—(1) Higher elevation lands surrounding streams and their floodplains. (2) Within the wetland literature, specifically refers to any area that is not a water body and does not meet the

Cowardin et al. (1979) three-attribute wetland definition. *See* Wetland.

Valley—A depression of Earth's surface that drains water between two adjacent uplands.

Variable Source Area—Neither stormflow nor baseflow is uniformly produced from the entire surface or subsurface area of a basin. Instead, the flow of water in a stream at any given moment is under the influence of dynamic, expanding or shrinking source areas, normally representing only a few percent of the total basin areas. The source area is highly variable during stormflow. During large rainfall or snowmelt events, the flowing portions of the river network, and associated source areas, expand. As the event ends, the network and source areas contract.

Vernal Pool—Shallow seasonal wetlands that generally accumulate water during colder, wetter months and gradually dry-down during warmer, dryer months.

Water Balance—The accounting of the volume of water entering, leaving, and being stored in a hydrologic unit or area, typically a drainage basin or aquifer, during a specified period of time.

Water Body—Any sizable accumulation of water on the land surface, including but not limited to streams, rivers, lakes, and wetlands.

Water Surplus—Water that is available for streamflow or recharge of groundwater; precipitation minus evapotranspiration.

Water Table—The top of the zone of saturation of an unconfined aquifer.

Watershed—The area drained by a stream, river, or other water body; typically defined by the topographic divides between one water body and another. *Synonymous with* Catchment *and* Drainage Basin.

Wet Channel—Channel with flowing or standing water.

Wetland—An area that generally exhibits at least one of the following three attributes (Cowardin et al., 1979): (1) is inundated or saturated at a frequency sufficient to support, at least periodically, plants adapted to a wet environment; (2) contains undrained hydric soil; or (3) contains nonsoil saturated by shallow water for part of the growing season.

Wetland Storage—The capacity of a wetland to detain or retain water from various sources.