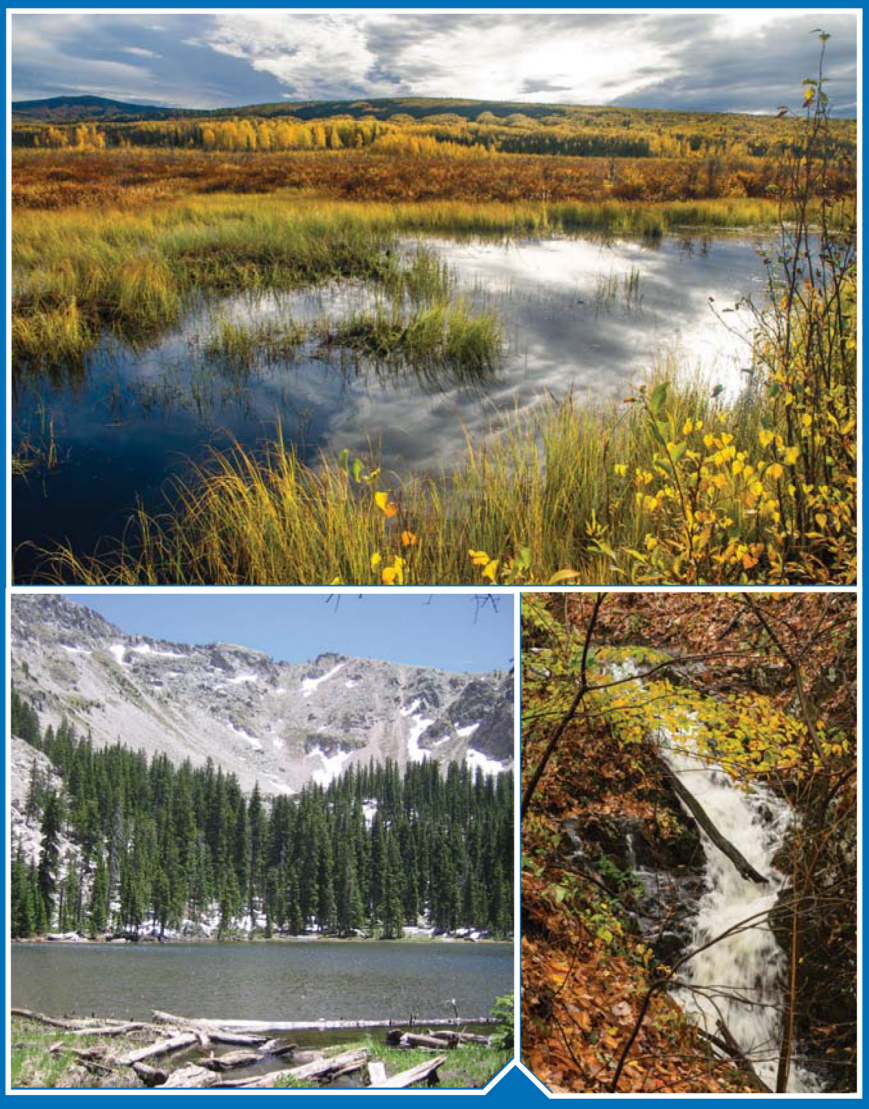
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United States
Environmental Protection
Agency

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



Office of Research and Development
NCEA (Washington DC, Cincinnati OH), NERL (Cincinnati OH, Las Vegas NV) and NHEERL (Corvallis OR)

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CONNECTIVITY OF STREAMS AND WETLANDS TO DOWNSTREAM WATERS: A REVIEW AND SYNTHESIS OF THE SCIENTIFIC EVIDENCE

Office of Research and Development
U.S. Environmental Protection Agency
Washington, DC

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LIST OF ABBREVIATIONS AND ACRONYMS

CWA	Clean Water Act
DEM	digital elevation model
DOC	dissolved organic carbon
FPOM	fine particulate organic matter
GW	groundwater flowpath
HUC	Hydrologic Unit Code
NHD	National Hydrography Dataset
PPR	prairie pothole region
USDA-ARS	United States Department of Agriculture, Agricultural Research Services
U.S. ACE	United States Army Corps of Engineers
U.S. EPA	United States Environmental Protection Agency
USGS	United States Geological Survey

LIST OF UNITS AND VARIABLES

A	drainage area
C	Celsius
c	scaling power constant
cm	centimeter
d	day
g	gram
ha	hectare
hr	hour
kg	kilogram
km	kilometer
L	liter
m	meter
mg	milligram
Mg	megagram
mm	millimeter
µM	micromolar
N	metric normal temperature and pressure
ng	nanogram
Pg	petagram
Q	discharge
s	second
t	metric ton
τ_o	shear stress
V	velocity
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's (U.S. EPA's) Office of Research and Development. It reviews and evaluates evidence from peer-reviewed sources that were published or in press by December 2014. Throughout this document, terms are used with their generally recognized scientific meaning. We have provided definitions of technical terms in the Glossary (Appendix A). Two previous drafts prepared on 1 February 2011 and 12 July 2011 were reviewed by U.S. EPA and U.S. 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. An external review draft released in September 2013 (600/R-11/098B) was reviewed by U.S. EPA staff and a panel of the U.S. EPA's Science Advisory Board (SAB) that convened 16–18 December 2013 (SAB report number EPA-SAB-15-001, available online at www.epa.gov/sab). The 27 topic experts comprising the SAB panel are listed in the **Reviewers** section. In addition, comments from the public were received through the docket or at the SAB panel meeting. Comments from these sources were considered and used to improve the clarity and scientific rigor of the document.

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EXECUTIVE SUMMARY

BACKGROUND

The objective of the Clean Water Act is to restore and maintain the chemical, physical, and biological integrity of the nation's waters. The U.S. Environmental Protection Agency's (U.S. EPA's) Office of Research and Development developed this report to inform rulemaking by the U.S. EPA and U.S. Army Corps of Engineers (U.S. ACE) on the definition of "waters of the United States" under the Clean Water Act (CWA). Its purpose is to summarize current scientific understanding about the connectivity and mechanisms by which streams and wetlands, singly or in aggregate, affect the physical, chemical, and biological integrity of downstream waters. The focus of the review is on surface and shallow subsurface connections of small or temporary streams, nontidal wetlands, and certain open waters. Because this report is a technical review of peer-reviewed scientific literature, it neither considers nor sets forth legal standards for CWA jurisdiction, nor does it establish EPA policy.

The report is organized into six chapters. Chapter 1 outlines the purpose, scientific context, and approach of the report. Chapter 2 describes the components of a river system and watershed; the types of physical, chemical, and biological connections that link those components; the factors that influence connectivity at various temporal and spatial scales; and methods for quantifying connectivity. Chapter 3 reviews literature on connectivity in stream networks in terms of physical, chemical, and biological connections and their resulting effects on downstream waters. Chapter 4 reviews literature on the connectivity and effects of nontidal wetlands and certain open waters on downstream waters. Chapter 5 applies concepts and evidence from previous chapters to six case studies from published literature on Carolina and Delmarva bays, oxbow lakes, prairie potholes, prairie streams, southwestern streams, and vernal pools. Chapter 6 summarizes key findings and conclusions, identifies data gaps, and briefly discusses research approaches that could fill those gaps. A glossary of scientific terms used in the report

and detailed case studies of selected systems (summarized in Chapter 5) are included in Appendix A and Appendix B, respectively.

SUMMARY OF MAJOR CONCLUSIONS

Based on the review and synthesis of more than 1,200 publications from the peer reviewed scientific literature, the evidence supports five major conclusions. Citations have been omitted from the text to improve readability; please refer to individual chapters for supporting publications and additional information.

Conclusion 1: Streams

The scientific literature unequivocally demonstrates that streams, individually or cumulatively, exert a strong influence on the integrity 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. Streams are the dominant source of water in most rivers, and the majority of tributaries are perennial, intermittent, or ephemeral headwater streams. Headwater streams also convey water into local storage compartments such as ponds, shallow aquifers, or stream banks, and into regional and alluvial aquifers; these local storage compartments are important sources of water for maintaining baseflow in rivers. In addition to water, streams transport sediment, wood, organic matter, nutrients, chemical contaminants, and many of the organisms found in rivers. The literature provides robust evidence that 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 upstream and downstream habitats during one or more stages of their life cycles, or provide food resources to downstream communities. In addition to material transport and biological connectivity, ephemeral, intermittent, and perennial flows influence fundamental biogeochemical processes by connecting channels and shallow ground water with other landscape elements. Physical, chemical, and biological connections between streams and downstream waters interact via integrative processes such as nutrient spiraling, in which stream communities assimilate and chemically transform large quantities of nitrogen and other nutrients that otherwise would be transported directly downstream, increasing nutrient loads and associated impairments due to excess nutrients in downstream waters.

Conclusion 2: Riparian/Floodplain Wetlands and Open Waters

The literature clearly shows that wetlands and open waters in riparian areas and floodplains are physically, chemically, and biologically integrated with rivers via functions that improve downstream water quality, including the temporary storage and deposition of channel-forming sediment and woody debris, temporary storage of local ground water that supports baseflow in

rivers, and transformation and transport of stored organic matter. Riparian/floodplain wetlands and open waters improve water quality through the assimilation, transformation, or sequestration of pollutants, including excess nutrients and chemical contaminants such as pesticides and metals, that can degrade downstream water integrity. In addition to providing effective buffers to protect downstream waters from point source and nonpoint source pollution, these systems form integral components of river food webs, providing nursery habitat for breeding fish and amphibians, colonization opportunities for stream invertebrates, and maturation habitat for stream insects. Lateral expansion and contraction of the river in its floodplain result in an exchange of organic matter and organisms, including fish populations that are adapted to use floodplain habitats for feeding and spawning during high water, that are critical to river ecosystem function. Riparian/floodplain wetlands and open waters also affect the integrity of downstream waters by subsequently releasing (desynchronizing) floodwaters and retaining large volumes of stormwater, sediment, and contaminants in runoff that could otherwise negatively affect the condition or function of downstream waters.

Conclusion 3: Non-floodplain Wetlands and Open Waters

Wetlands and open waters in non-floodplain landscape settings (hereafter called "non-floodplain wetlands") provide numerous functions that benefit downstream water integrity. These functions include storage of floodwater; recharge of ground water that sustains river baseflow; retention and transformation of nutrients, metals, and pesticides; export of organisms or reproductive propagules to downstream waters; and habitats needed for stream species. This diverse group of wetlands (e.g., many prairie potholes, vernal pools, playa lakes) can be connected to downstream waters through surface-water, shallow subsurface-water, and ground-water flows and through biological and chemical connections.

In general, connectivity of non-floodplain wetlands occurs along a gradient (Conclusion 4), and can be described in terms of the frequency, duration, magnitude, timing, and rate of change of water, material, and biotic fluxes to downstream waters. These descriptors are influenced by climate, geology, and terrain, which interact with factors such as the magnitudes of the various functions within wetlands (e.g., amount of water storage or carbon export) and their proximity to downstream waters to determine where wetlands occur along the connectivity gradient. At one end of this gradient, the functions of non-floodplain wetlands clearly affect the condition of downstream waters if a visible (e.g., channelized) surface-water or a regular shallow subsurface-water connection to the river network is present. For non-floodplain wetlands lacking a channelized surface or regular shallow subsurface connection (i.e., those at intermediate points along the gradient of connectivity), generalizations about their specific effects on downstream waters from the available literature are difficult because information on both function and connectivity is needed. Although there is ample evidence that non-floodplain wetlands provide hydrologic, chemical, and biological functions that affect material fluxes, to date, few scientific studies explicitly addressing connections between non-floodplain wetlands and river networks have been published in the peer-reviewed literature. Even fewer publications specifically focus

on the frequency, duration, magnitude, timing, or rate of change of these connections. In addition, although areas that are closer to rivers and streams have a higher probability of being connected than areas farther away when conditions governing the type and quantity of flows—including soil infiltration rate, wetland storage capacity, hydraulic gradient, etc.—are similar, information to determine if this similarity holds is generally not provided in the studies we reviewed. Thus, current science does not support evaluations of the degree of connectivity for specific groups or classes of wetlands (e.g., prairie potholes or vernal pools). Evaluations of individual wetlands or groups of wetlands, however, could be possible through case-by-case analysis.

Some effects of non-floodplain wetlands on downstream waters are due to their isolation, rather than their connectivity. Wetland "sink" functions that trap materials and prevent their export to downstream waters (e.g., sediment and entrained pollutant removal, water storage) result because of the wetland's ability to isolate material fluxes. To establish that such functions influence downstream waters, we also need to know that the wetland intercepts materials that otherwise would reach the downstream water. The literature we reviewed does provide limited examples of direct effects of wetland isolation on downstream waters, but not for classes of wetlands (e.g., vernal pools). Nevertheless, the literature we reviewed enables us to conclude that sink functions of non-floodplain wetlands, which result in part from their relative isolation, will affect a downstream water when these wetlands are situated between the downstream water and known point or nonpoint sources of pollution, and thus intersect flowpaths between the pollutant source and downstream waters.

Conclusion 4: Degrees and Determinants of Connectivity

Watersheds are integrated at multiple spatial and temporal scales by flows of surface water and ground water, transport and transformation of physical and chemical materials, and movements of organisms. Although all parts of a watershed are connected to some degree—by the hydrologic cycle or dispersal of organisms, for example—the degree and downstream effects of those connections vary spatially and temporally, and are determined by characteristics of the physical, chemical, and biological environments and by human activities.

Stream and wetland connections have particularly important consequences for downstream water integrity. Most of the materials—broadly defined as any physical, chemical, or biological entity—in rivers, for example, originate from aquatic ecosystems located upstream or elsewhere in the watershed. Longitudinal flows through ephemeral, intermittent, and perennial stream channels are much more efficient for transport of water, materials, and organisms than diffuse overland flows, and areas that concentrate water provide mechanisms for the storage and transformation, as well as transport, of materials.

Connectivity of streams and wetlands to downstream waters occurs along a continuum that can be described in terms of the frequency, duration, magnitude, timing, and rate of change of water, material, and biotic fluxes to downstream waters. These terms, which we refer to collectively as

connectivity descriptors, characterize the range over which streams and wetlands vary and shift along the connectivity gradient in response to changes in natural and anthropogenic factors and, when considered in a watershed context, can be used to predict probable effects of different degrees of connectivity over time. The evidence unequivocally demonstrates that the stream channels and riparian/floodplain wetlands or open waters that together form river networks are clearly connected to downstream waters in ways that profoundly influence downstream water integrity. The connectivity and effects of non-floodplain wetlands and open waters are more variable and thus more difficult to address solely from evidence available in peer-reviewed studies.

Variations in the degree of connectivity influence the range of functions provided by streams and wetlands, and are critical to the integrity and sustainability of downstream waters. Connections with low values of one or more descriptors (e.g., low-frequency, low-duration streamflows caused by flash floods) can have important downstream effects when considered in the context of other descriptors (e.g., large magnitude of water transfer). At the other end of the frequency range, high-frequency, low-magnitude vertical (surface-subsurface) and lateral flows contribute to aquatic biogeochemical processes, including nutrient and contaminant transformation and organic matter accumulation. The timing of an event can alter both connectivity and the magnitude of its downstream effect. For example, when soils become saturated by previous rainfall events, even low or moderate rainfall can cause streams or wetlands to overflow, transporting water and materials to downstream waters. Fish that use nonperennial or perennial headwater stream habitats to spawn or rear young, and invertebrates that move into seasonally inundated floodplain wetlands prior to emergence, have life cycles that are synchronized with the timing of flows, temperature thresholds, and food resource availability in those habitats.

Conclusion 5: Cumulative Effects

The incremental effects of individual streams and wetlands are cumulative across entire watersheds and therefore must be evaluated in context with other streams and wetlands. Downstream waters are the time-integrated result of all waters contributing to them. For example, the amount of water or biomass contributed by a specific ephemeral stream in a given year might be small, but the aggregate contribution of that stream over multiple years, or by all ephemeral streams draining that watershed in a given year or over multiple years, can have substantial consequences on the integrity of the downstream waters. Similarly, the downstream effect of a single event, such as pollutant discharge into a single stream or wetland, might be negligible but the cumulative effect of multiple discharges could degrade the integrity of downstream waters.

In addition, when considering the effect of an individual stream or wetland, all contributions and functions of that stream or wetland should be evaluated cumulatively. For example, the same stream transports water, removes excess nutrients, mitigates flooding, and provides refuge for

fish when conditions downstream are unfavorable; if any of these functions is ignored, the overall effect of that stream would be underestimated.

SUPPORT FOR MAJOR CONCLUSIONS

This report synthesizes a large body of scientific literature on the connectivity and mechanisms by which streams, wetlands, and open waters, singly or in aggregate, affect the physical, chemical, and biological integrity of downstream waters. The major conclusions reflect the strength of evidence currently available in the peer-reviewed scientific literature for assessing the connectivity and downstream effects of water bodies identified in Chapter 1 of this report.

The conclusions of this report were corroborated by two independent peer reviews by scientists identified in the front matter of this report.

The term connectivity is defined in this report as the degree to which components of a watershed are joined and interact by transport mechanisms that function across multiple spatial and temporal scales. Connectivity is determined by the characteristics of both the physical landscape and the biota of the specific system. Our review found strong evidence supporting the central roles of the physical, chemical, and biological connectivity of streams, wetlands, and open waters—encompassing varying degrees of both connection and isolation—in maintaining the structure and function of downstream waters, including rivers, lakes, estuaries, and oceans. Our review also found strong evidence demonstrating the various mechanisms by which material and biological linkages from streams, wetlands, and open waters affect downstream waters, classified here into five functional categories (source, sink, refuge, lag, and transformation; discussed below), and modify the timing of transport and the quantity and quality of resources available to downstream ecosystems and communities. Thus, the currently available literature provided a large body of evidence for assessing the types of connections and functions by which streams and wetlands produce the range of observed effects on the integrity of downstream waters.

We identified five categories of functions by which streams, wetlands, and open waters influence the timing, quantity, and quality of resources available to 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 stormwater.

These functions are not mutually exclusive; for example, the same stream or wetland can be both a source of organic matter and a sink for nitrogen. The presence or absence of these functions, which

depend on the biota, hydrology, and environmental conditions in a watershed, can change over time; for example, the same wetland can attenuate runoff during storm events and provide ground-water recharge following storms. Further, some functions work in conjunction with others; a lag function can include transformation of materials prior to their delayed release. Finally, effects on downstream waters should consider both actual function and potential function. A potential function represents the capacity of an ecosystem to perform that function under suitable conditions. For example, a wetland with high capacity for denitrification is a potential sink for nitrogen, a nutrient that becomes a contaminant when present in excessive concentrations. In the absence of nitrogen, this capacity represents the wetland's potential function. If nitrogen enters the wetland (e.g., from fertilizer in runoff), it is removed from the water; this removal represents the wetland's actual function. Both potential and actual functions play critical roles in protecting and restoring downstream waters as environmental conditions change.

The evidence unequivocally demonstrates that the stream channels and riparian/floodplain wetlands or open waters that together form river networks are clearly connected to downstream waters in ways that profoundly influence downstream water integrity. The body of literature documenting connectivity and downstream effects was most abundant for perennial and intermittent streams, and for riparian/floodplain wetlands. Although less abundant, the evidence for connectivity and downstream effects of ephemeral streams was strong and compelling, particularly in context with the large body of evidence supporting the physical connectivity and cumulative effects of channelized flows that form and maintain stream networks.

As stated in Conclusion 3, the connectivity and effects of wetlands and open waters that lack visible surface connections to other water bodies are more difficult to address solely from evidence available in the peer-reviewed literature. The limited evidence currently available shows that these systems have important hydrologic, water-quality, and habitat functions that can affect downstream waters where connections to them exist; the literature also provides limited examples of direct effects of non-floodplain wetland isolation on downstream water integrity. Currently available peer-reviewed literature, however, does not identify which types or classes of non-floodplain wetlands have or lack the types of connections needed to convey the effects on downstream waters of functions, materials, or biota provided by those wetlands.

KEY FINDINGS FOR MAJOR CONCLUSIONS

This section summarizes key findings for each of the five major conclusions, above and in Chapter 6 of the report. Citations have been omitted from the text to improve readability; please refer to individual chapters for supporting publications and additional information.

Conclusion 1, Streams: Key Findings

- Streams are hydrologically connected to downstream waters via channels that convey surface and subsurface water either year-round (i.e., perennial flow), weekly to seasonally (i.e., intermittent flow), or only in direct response to precipitation (i.e., ephemeral flow). Streams are

the dominant source of water in most rivers, and the majority of tributaries are perennial, intermittent, or ephemeral headwater streams. For example, headwater streams, which are the smallest channels where streamflows begin, are the cumulative source of approximately 60% of the total mean annual flow to all northeastern U.S. streams and rivers.

- In addition to downstream transport, headwaters convey water into local storage compartments such as ponds, shallow aquifers, or stream banks, and into regional and alluvial aquifers. These local storage compartments are important sources of water for maintaining baseflow in rivers. Streamflow typically depends on the delayed (i.e., lagged) release of shallow ground water from local storage, especially during dry periods and in areas with shallow ground-water tables and pervious subsurfaces. For example, in the southwestern United States, short-term shallow ground-water storage in alluvial floodplain aquifers, with gradual release into stream channels, is a major source of annual flow in rivers.
- 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 help structure stream and river channels by slowing the flow of water through channels and providing substrate and habitat for aquatic organisms.
- There is strong evidence that headwater streams function as nitrogen sources (via export) and sinks (via uptake and transformation) for river networks. For example, one study estimated that rapid nutrient cycling in small streams with no 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 lead to eutrophication and hypoxia, in which over-enrichment causes dissolved oxygen concentrations to fall below the level necessary to sustain most aquatic animal life in the stream and streambed. Thus, the influence of streams on nutrient loads can have significant repercussions for hypoxia in downstream waters.
- Headwaters provide habitat that is critical for completion of one or more life-cycle stages of many aquatic and semiaquatic species capable of moving throughout river networks. Evidence is strong that headwaters provide habitat for complex life-cycle completion; refuge from predators, competitors, parasites, or adverse physical conditions in rivers (e.g., temperature or flow extremes, low dissolved oxygen, high sediment); and reservoirs of genetic- and species-level diversity. Use of headwater streams as habitat is especially critical 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). The presence of these species within river networks provides robust evidence of biological connections between headwaters and larger rivers; because these organisms also transport nutrients and other materials as they migrate, their presence also provides evidence of biologically mediated chemical connections. In prairie streams, many fishes swim upstream into tributaries to release eggs, which develop as they are transported downstream.

- Human alterations affect the frequency, duration, magnitude, timing, and rate of change of connections between headwater streams, including ephemeral and intermittent streams, and downstream waters. Human activities and built structures (e.g., channelization, dams, ground-water withdrawals) can either enhance or fragment longitudinal connections between headwater streams and downstream waters, while also constraining lateral and vertical exchanges and tightly controlling the temporal dimension of connectivity. In many cases, research on human alterations has enhanced our understanding of the headwater stream-downstream water connections and their consequences. Recognition of these connections and effects has encouraged the development of more sustainable practices and infrastructure to reestablish and manage connections, and ultimately to protect and restore the integrity of downstream waters.

Conclusion 2, Riparian/Floodplain Wetlands and Open Waters: Key Findings

- Riparian areas and floodplains connect upland and aquatic environments through both surface and subsurface hydrologic flowpaths. These areas are therefore uniquely situated in watersheds to receive and process waters that pass over densely vegetated areas and through subsurface zones before the waters reach streams and rivers. When pollutants reach a riparian or floodplain wetland, they can be sequestered in sediments, assimilated into wetland plants and animals, transformed into less harmful or mobile forms or compounds, or lost to the atmosphere. Wetland potential for biogeochemical transformations (e.g., denitrification) that can improve downstream water quality is influenced by local factors, including anoxic conditions and slow organic matter decomposition, shallow water tables, wetland plant communities, permeable soils, and complex topography.
- Riparian/floodplain wetlands can reduce flood peaks by storing and desynchronizing floodwaters. They can also maintain river baseflows by recharging alluvial aquifers. Many studies have documented the ability of riparian/floodplain wetlands 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.
- Riparian areas and floodplains store large amounts of sediment and organic matter from upstream and from upland areas. For example, riparian areas have been shown to remove 80–90% of sediments leaving agricultural fields in North Carolina.
- Ecosystem function within a river system is driven in part by biological connectivity that links diverse biological communities with the river system. Movements of organisms that connect aquatic habitats and their populations, even across different watersheds, are 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 result in an exchange of matter and organisms, including fish populations that are adapted to use floodplain habitats

for feeding and spawning during high water. Wetland and 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 commonly use both streams and riparian/floodplain wetlands to hunt, forage, overwinter, rest, or hide from predators. Birds can spatially integrate the watershed landscape through biological connectivity.

Conclusion 3, Non-floodplain Wetlands and Open Waters: Key Findings

- 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 could be widespread across eastern portions of the prairie pothole region. This work also indicates that reducing water storage capacity of wetlands by connecting formerly isolated potholes through ditching or drainage to the Devils Lake and Red River basins could increase stormflow and contribute to downstream flooding. In many agricultural areas already crisscrossed by extensive drainage systems, total streamflow and baseflow are increased 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 example, 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.
- Non-floodplain wetlands act as sinks and transformers for various pollutants, especially nutrients, which at excess levels can adversely impact human and ecosystem health and pose a serious pollution problem in the United States. In one study, sewage wastewaters were applied to forested wetlands in Florida for 4.5 years; more than 95% of the phosphorus, nitrate, ammonium, and total nitrogen were removed by the wetlands during the study period, and 66–86% of the nitrate removed was attributed to the process of denitrification. In another study, sizeable phosphorus retention (0.3 to 8.0 mg soluble reactive P m^{-2} d^{-1}) occurred in marshes that comprised only 7% of the lower Lake Okeechobee basin area in Florida. A non-floodplain 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 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 onsite nutrient removal by non-floodplain wetlands is substantial and geographically widespread. The effects of this removal on rivers are generally not reported in the literature.

- Non-floodplain wetlands provide unique and important habitats for many species, both common and rare. Some of these species require multiple types of waters to complete their full life cycles, including downstream waters. Abundant or highly mobile species play important roles in transferring energy and materials between non-floodplain wetlands and downstream waters.
- Biological connections are likely to occur between most non-floodplain wetlands and downstream waters through either direct or stepping stone movement of amphibians, invertebrates, reptiles, mammals, and seeds of aquatic plants, 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 wetlands and river networks. Migratory birds can be an important vector of long-distance dispersal of plants and invertebrates between non-floodplain wetlands and the river network, although their influence has not been quantified. Whether those connections are of sufficient magnitude to impact downstream waters will either require estimation of the magnitude of material fluxes or evidence that these movements of organisms are required for the survival and persistence of biota that contribute to the integrity of downstream waters.
- Spatial proximity is one important determinant of the magnitude, frequency and duration of connections between wetlands and streams that will ultimately influence the fluxes of water, materials and biota between wetlands and downstream waters. However, proximity alone is not sufficient to determine connectivity, due to local variation in factors such as slope and permeability.
- The cumulative influence of many individual wetlands within watersheds can strongly affect the spatial scale, magnitude, frequency, and duration of hydrologic, biological and chemical fluxes or transfers of water and materials to downstream waters. Because of their aggregated influence, any evaluation of changes to individual wetlands should be considered in the context of past and predicted changes (e.g., from climate change) to other wetlands within the same watershed.
- Non-floodplain wetlands can be hydrologically connected directly to river networks through natural or constructed channels, nonchannelized surface flows, or subsurface flows, the latter of which can travel long distances to affect downstream waters. 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 hydrologic, chemical, and biological connections to downstream waters.

- Non-floodplain 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 ground-water aquifers; geographically isolated wetlands that have local ground-water or occasional surface-water connections to downstream waters; and geographically isolated wetlands that have minimal hydrologic connection to other water bodies (but which could include surface and subsurface connections to other wetlands). This gradient can exist among wetlands of the same type or in the same geographic region.
- Caution should be used in interpreting connectivity for wetlands that have been designated as "geographically isolated" because (1) the term can be applied broadly to a heterogeneous group of wetlands, which can include wetlands that are not actually 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, 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. For example, a recent study examined hydrologic connectivity in a complex of wetlands on the Texas Coastal Plain. The wetlands in this complex have been considered to be a type of geographically isolated wetland; however, collectively they are connected both geographically and hydrologically 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 out through an intermittent stream into downstream waters. Thus, wetland complexes could have connections to downstream waters through stream channels even when the individual wetland components are geographically isolated.

Conclusion 4, Degrees and Determinants of Connectivity: Key Findings

- The surface-water and ground-water flowpaths (hereafter, hydrologic flowpaths), along which water and materials are transported and transformed, determine variations in the degree of physical and chemical connectivity. These flowpaths are controlled primarily by variations in climate, geology, and terrain within and among watersheds and over time. Climate, geology, and terrain are reflected locally in factors such as rainfall and snowfall intensity, soil infiltration rates, and the direction of ground-water flows. These local factors interact with the landscape positions of streams and wetlands relative to downstream waters, and with functions (such as the removal or transformation of pollutants) performed by those streams and wetlands to determine connectivity gradients.
- Gradients of biological connectivity (i.e., the active or passive movements of organisms through water or air and over land that connect populations) are determined primarily by species

assemblages, and by features of the landscape (e.g., climate, geology, terrain) that facilitate or impede the movement of organisms. The temporal and spatial scales at which biological pathways connect aquatic habitats depend on characteristics of both the landscape and species, and overland transport or movement can occur across watershed boundaries. Dispersal is essential for population persistence, maintenance of genetic diversity, and evolution of aquatic species. Consequently, dispersal strategies reflect aquatic species' responses and adaptations to biotic and abiotic environments, including spatial and temporal variation in resource availability and quality. Species' traits and behaviors encompass species-environment relationships over time, and provide an ecological and evolutionary context for evaluating biological connectivity in a particular watershed or group of watersheds.

- Pathways for chemical transport and transformation largely follow hydrologic flowpaths, but sometimes follow biological pathways (e.g., nutrient transport from wetlands to coastal waters by migrating waterfowl, upstream transport of marine-derived nutrients by spawning of anadromous fish, uptake and removal of nutrients by emerging stream insects).
- Human activities alter naturally occurring gradients of physical, chemical, and biological connectivity by modifying the frequency, duration, magnitude, timing, and rate of change of fluxes, exchanges, and transformations. For example, connectivity can be reduced by dams, levees, culverts, water withdrawals, and habitat destruction, and can be increased by effluent discharges, channelization, drainage ditches and tiles, and impervious surfaces.

Conclusion 5, Cumulative Effects: Key Findings

- Structurally and functionally, stream-channel networks and the watersheds they drain are fundamentally cumulative in how they are formed and maintained. Excess water from precipitation that is not evaporated, taken up by organisms, or stored in soils and geologic layers moves downgradient by gravity as overland flow or through channels carrying sediment, chemical constituents, and organisms. These channels concentrate surface-water flows and are more efficient than overland (i.e., diffuse) flows in transporting water and materials, and are reinforced over time by recurrent flows.
- Connectivity between streams and rivers provides opportunities for materials, including nutrients and chemical contaminants, to be transformed chemically as they are transported downstream. Although highly efficient at the transport of water and other physical materials, streams are dynamic ecosystems with permeable beds and banks that interact with other ecosystems above and below the surface. The exchange of materials between surface and subsurface areas involves 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 opportunity for transformation of material (e.g., biological uptake, assimilation, or beneficial transformation) in intervening stream reaches increases with distance to the river.

Nutrient spiraling, the process by which nutrients entering headwater streams are transformed by various aquatic organisms and chemical reactions as they are transported downstream, is one example of an instream alteration that exhibits significant beneficial effects on downstream waters. Nutrients (in their inorganic form) that enter a 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 into the stream via excretion and decomposition (i.e., in their organic form), 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.

- Cumulative effects across a watershed must be considered when quantifying the frequency, duration, and magnitude of connectivity, to evaluate the downstream effects of streams and wetlands. For example, although the probability of a large-magnitude transfer of organisms from any given headwater stream in a given year might be low (i.e., a low-frequency connection when each stream is considered individually), headwater streams are the most abundant type of stream in most watersheds. Thus, the overall probability of a large-magnitude transfer of organisms is higher when considered for all headwater streams in a watershed—that is, a high-frequency connection is present when headwaters are considered cumulatively at the watershed scale, compared with probabilities of transport for streams individually. Similarly, a single pollutant discharge might be negligible but the cumulative effect of multiple discharges could degrade the integrity of downstream waters. Riparian open waters (e.g., oxbow lakes), wetlands, and vegetated areas cumulatively can retain up to 90% of eroded clays, silts, and sands that otherwise would enter stream channels. The larger amounts of snowmelt and precipitation cumulatively held by many wetlands can reduce the potential for flooding at downstream locations. For example, wetlands in the prairie pothole region cumulatively stored about 11–20% of the precipitation in one watershed.
- The combination of diverse habitat types and abundant food resources cumulatively makes floodplains important foraging, hunting, and breeding sites for fish, aquatic life stages of amphibians, and aquatic invertebrates. The scale of these cumulative effects can be extensive; for example, coastal ibises travel up to 40 km to obtain food from freshwater floodplain wetlands for nesting chicks, which cannot tolerate salt levels in local food resources until they fledge.

CLOSING COMMENTS

The structure and function of downstream waters highly depend on materials—broadly defined as any physical, chemical, or biological entity—that originate outside of the downstream waters. Most of the constituent materials in rivers, for example, originate from aquatic ecosystems located upstream in the drainage network or elsewhere in the drainage basin, and are transported to the river through flowpaths illustrated in the introduction to this report. Thus, the effects of streams, wetlands, and open waters on rivers are determined by the presence of (1) physical, chemical, or biological pathways that enable (or inhibit) the transport of materials and organisms to downstream waters; and (2) functions within the streams, wetlands, and open waters that alter the quantity and quality of materials and organisms transported along those pathways to downstream waters.

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 evidence reviewed in this report, it is clear that streams and rivers are much more than a system of physical channels for efficiently conveying water and other materials downstream. The presence of physical channels, however, is a compelling 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 can 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 downgradient from such disruptions is evidence of the surface connection with the channel that is upgradient of the perceived disruption.

Although currently available peer-reviewed literature does not identify which types of non-floodplain wetlands have or lack the types of connections needed to convey functional effects to downstream waters, additional information (e.g., field assessments, analysis of existing or new data, reports from local resource agencies) could be used in case-by-case analysis of non-floodplain wetlands. Importantly, information from emerging research into the connectivity of non-floodplain wetlands, including studies of the types identified in Section 4.5.2 of this report, could close some of the current data gaps in the near future. Recent scientific advances in the fields of mapping, assessment, modeling, and landscape classification 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 and improve the accuracy of connectivity assessments. Emerging research that expands 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 identify waters of national importance and maintain the long-term sustainability and resiliency of valued water resources.





CHAPTER 1. INTRODUCTION

1.1 Purpose

The objective of the Clean Water Act is to restore and maintain the chemical, physical, and biological integrity of the nation's waters. The U.S. Environmental Protection Agency's (U.S. EPA's) Office of Research and Development developed this report to inform rulemaking by the U.S. EPA and U.S. ACE on the definition of "waters of the United States" under the Clean Water Act (CWA). Its purpose is to summarize current scientific understanding about the connectivity and mechanisms by which streams and wetlands, singly or in aggregate, affect the physical, chemical, and biological integrity of downstream waters. Because this report is a technical review of peer-reviewed scientific literature, it does not consider or set forth legal standards for CWA jurisdiction. Rather, the report evaluates, summarizes, and synthesizes the available peer-reviewed scientific literature to address three questions:

1. What are the physical, chemical, and biological connections to and effects of ephemeral, intermittent, and perennial streams on downstream waters (e.g., rivers, lakes, reservoirs, estuaries)?
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 open waters in non-floodplain settings (e.g., most prairie potholes, vernal pools) on downstream waters?

These questions were developed in collaboration with the U.S. EPA's Office of Water to translate regulatory questions and terminology into more scientifically relevant questions and terms (Table 1-1).

This report focuses on the physical, chemical, and biological connections (or lack thereof) by which small or temporary streams, nontidal wetlands, and certain open waters can affect the integrity of downstream waters.

In addition to a broad survey of literature responding to the three questions above, the U.S. EPA's Office of Water asked the Office of Research and Development to create six case studies with more detailed reviews of published literature on Carolina and Delmarva bays, oxbow lakes, prairie potholes, prairie streams, southwestern streams, and vernal pools.

Table 1-1. Translating connectivity-related questions between policy and science. This table presents a crosswalk of regulatory and scientific questions this report addresses. Policy questions use regulatory terms (shown in quotation marks) that lack scientific definitions or are defined differently in scientific usage. All terms used in this report reflect scientific definitions and usage.

Policy question	Science question
What tributaries have a "significant* nexus" to "traditional navigable waters"?	What are the connections to and effects of ephemeral, intermittent, and perennial streams on downstream waters?
What "adjacent" waters have a "significant* nexus" to "traditional navigable waters"?	What are the connections to and effects of riparian or floodplain wetlands and open waters on downstream waters?
What categories of "other waters" have a "significant* nexus" to "traditional navigable waters"?	What are the connections to and effects of wetlands and open waters in non-floodplain settings on downstream waters?
* "Significant," as used here, is a policy determination informed by science; it does not refer to statistical significance.	

1.2 Scientific Context

1.2.1 Concepts of Connectivity in Hydrology and Ecology

Streams, wetlands, and other surface waters interact with ground water and terrestrial environments throughout the landscape, from the mountains to the oceans. Thus, an integrated perspective of the landscape, described in this section, provides the appropriate scientific context for evaluating and interpreting evidence about the physical, chemical, and biological connectivity of streams, wetlands, and open waters to downstream waters.

Connectivity has long been a central tenet for the study of aquatic ecosystems. 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. The key pattern is that downstream communities are organized, in large part, by upstream communities and processes (Vannote et al., 1980; Battin et al., 2009). The Serial Discontinuity Concept (Ward and Stanford, 1983) built on the River Continuum Concept to improve our understanding of how dams and impoundments disrupt the longitudinal patterns of flowing waters with predictable downstream effects.

The Spiraling Concept (Webster and Patten, 1979; Newbold et al., 1981; Elwood et al., 1983) described how river network connectivity can be evaluated and quantified as materials cycle from dissolved forms to transiently stored forms taken up by living organisms, then back to dissolved forms, as they are transported downstream (Section 3.4.1). These three conceptual frameworks focused on the longitudinal connections of river ecosystems, whereas the subsequent flood pulse concept (Junk et al., 1989) examined the importance of lateral connectivity of river channels to floodplains, including wetlands and open waters, through seasonal expansion and contraction of river networks. Ward (1989) summarized the importance of connectivity to lotic ecosystems along four dimensions: longitudinal, lateral, vertical (surface-subsurface), and temporal connections; he concluded that running water ecosystems are open systems that are highly interactive with both contiguous habitats and other ecosystems in the surrounding landscape. As these conceptual frameworks illustrate, scientists have long recognized the hydrologic connectivity that the physical structure of river networks represents.

More recently, scientists have incorporated this connected network structure into conceptual frameworks describing 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, 2007; Rodriguez-Iturbe et al., 2009). The Network Dynamic Hypothesis (Benda et al., 2004) is a physically based framework for predicting patterns of habitat heterogeneity observed along a river, based on dynamics that generate potential biological "hotspots" at tributary confluences. It essentially reexamines earlier, linearly driven frameworks given the patchy and stochastic nature of lotic ecosystems (e.g., Resh et al., 1988; Townsend, 1989; Rice et al., 2001), and thus reflects a more realistic river network perspective. Bunn and Arthington (2002) identified natural flow variability and associated lateral and longitudinal connectivity of stream channels and floodplains as two principal mechanisms linking hydrology to aquatic biodiversity of riverine species (also Leigh et al., 2010). In addition, 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). Sheaves (2009) emphasized the key ecological connections—which include process-based connections that maintain habitat function (e.g., nutrient dynamics, trophic function) and movements of individual organisms—throughout a complex of interlinked freshwater, tidal wetland, and estuarine habitats as critical for the persistence of aquatic species, populations, and communities over the full range of time scales.

1.2.2 Connectivity Gradients and Descriptors

The landscape and flowpath perspectives illustrated in Figure 1-1 draw heavily from the connectivity frameworks described in Section 1.2.1. These perspectives are essential to understanding connections from streams, wetlands, and open waters that affect the integrity of downstream waters. **Connectivity** is defined here as the degree to which components of a watershed are joined and interact by **transport mechanisms** that function across multiple spatial and temporal scales (Section 2.3.2.1). The primary transport mechanisms considered in this report are surface-water and shallow ground-water flows,

Table 1-2. Dimensions of watershed connectivity.	
Dimension	Examples and flowpaths in Figure 1-1 or Figure 1-2
Longitudinal	Streamflow and downstream transport of materials, organisms (1-1A); hyporheic flow (1-1A); ground-water flow through local and larger scale aquifers (1-1A), aquatic or overland movement of organisms in or along stream channels (1-1B); biogeochemical transport and transformation (1-1B) (Alexander et al., 2007; Freeman et al., 2007)
Lateral	Overbank flow and transport from channels into banks, floodplains, and riparian areas (1-1A); spillage and transport from wetlands and open waters into streams (1-1A); overland flow and interflow (1-1A); ground-water recharge from streams and wetlands (1-1A); bank storage (1-1A); transport or movement of organisms between streams and wetlands or open waters (1-1B) (Ward, 1989; Stanford and Ward, 1993)
Vertical	Surface-subsurface exchange of water, materials, organisms (1-1A and 1-1B); ground-water recharge from streams and wetlands (1-1A); atmospheric losses (1-1A) (Amoros and Bornette, 2002; Banks et al., 2011)
Temporal	Variable source area (1-2); seasonal cycles of wetland inundation and outflow to streams (1-1A); migration or diapause of aquatic organisms (1-1B) (Hewlett and Hibbert, 1967; Bohonak and Jenkins, 2003; Zedler, 2003)

transport and transformation of physical and chemical materials, and movements of aquatic and semiaquatic organisms, all of which connect watersheds in four dimensions (Table 1-2). Figure 1-1 illustrates the continuous hydrologic flowpaths (Figure 1-1A) and biological pathways (Figure 1-1B) that connect watershed components spatially; Figure 1-2 illustrates the temporal dynamics of hydrologic flowpaths (Sections 2.2.3 and 2.3.2.2).

Although all parts of a watershed are connected to some degree—by the hydrologic cycle or dispersal of organisms, for example—the degree of connectivity among aquatic components varies along a continuum from highly connected to highly isolated. This continuum can be described in terms of the **frequency, duration, magnitude, timing,** and **rate of change** (Poff et al., 2007) of physical and chemical fluxes to and biological exchanges with downstream waters. These terms, which we refer to collectively as **connectivity descriptors**, characterize the range over which streams and wetlands vary and shift along the connectivity gradient in response to changes in natural and anthropogenic factors and, when considered in a watershed context, can be used to predict probable effects of different degrees of connectivity over time. These and similar descriptors are used in hydrology and disturbance ecology to characterize the variability and alteration of natural flow regimes (Resh et al., 1988; Poff, 1992; Poff et al., 1997; Lake, 2000; Leibowitz et al., 2008). For example, in hydrology, magnitude is the amount of water moving past a fixed location per unit time, frequency is how often a particular flow magnitude occurs, duration is a measure of how long a particular flow magnitude persists, and rate of change is how quickly one type of flow changes to another. Because the presence of water determines hydrologic connectivity, these descriptors also can be used to describe the timing and magnitude of hydrologic connections. Further, they can describe other types of connections. The number of individuals immigrating or emigrating during a dispersal event, for example, could be used to determine

Figure 1-1A. Hydrologic flowpaths. Arrows are representative of surface-water and ground-water flows occurring throughout the watershed. Subsurface flows are shown within the cross section, and by faded arrows outside the cross section.

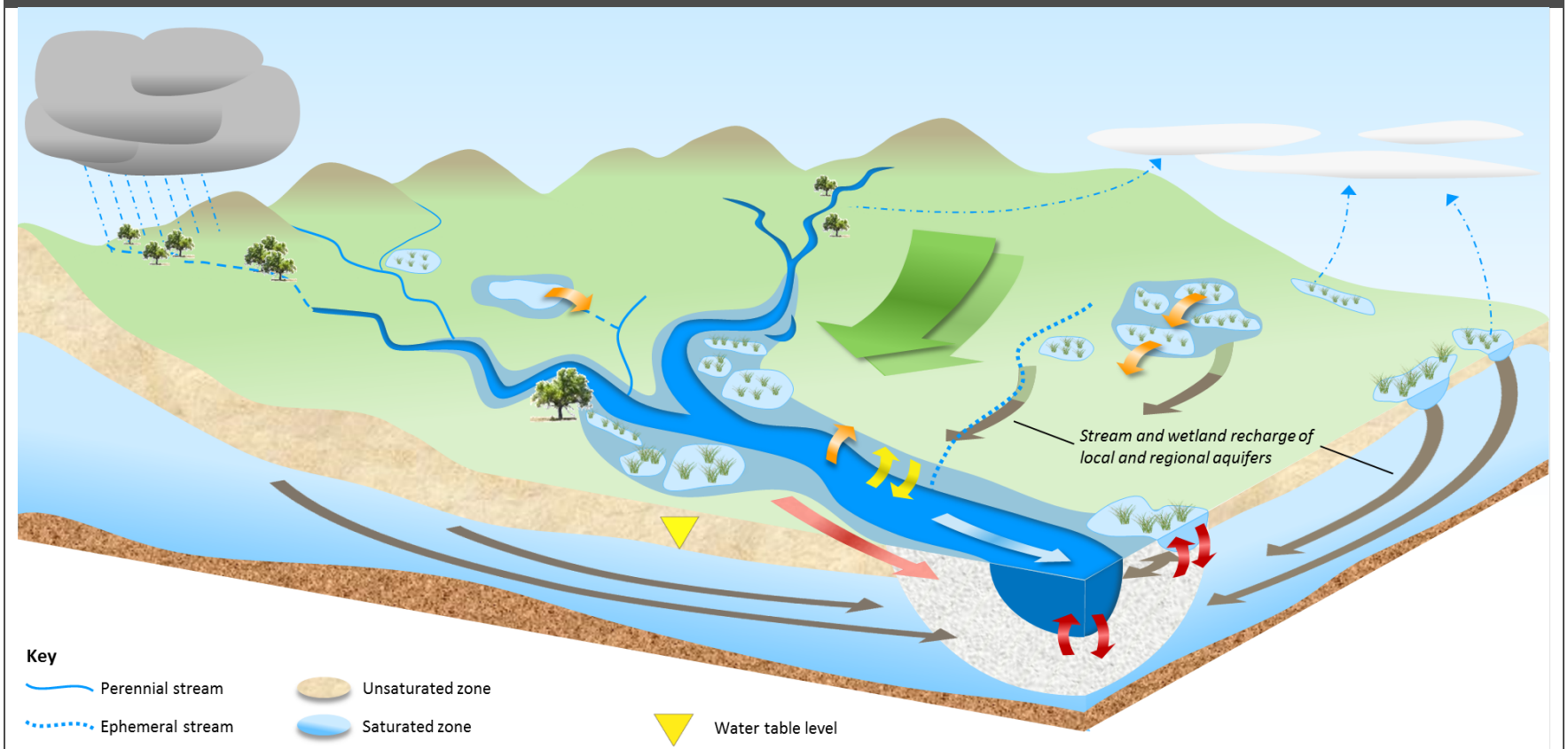


Figure 1-1B. Biological flowpaths. Arrows are representative of biological pathways occurring throughout the watershed. This figure also includes representative biogeochemical pathways occurring in streams and floodplains.

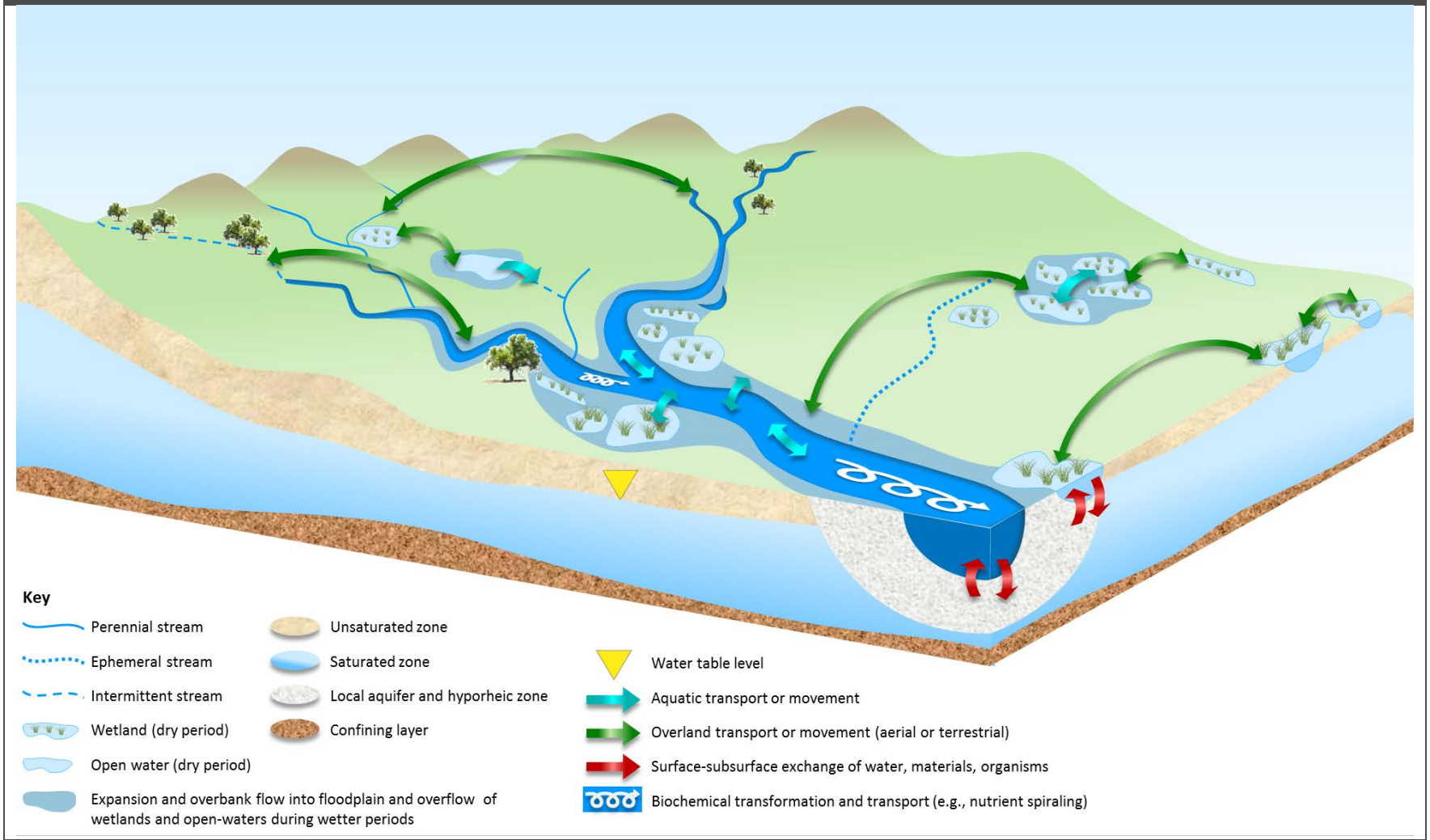
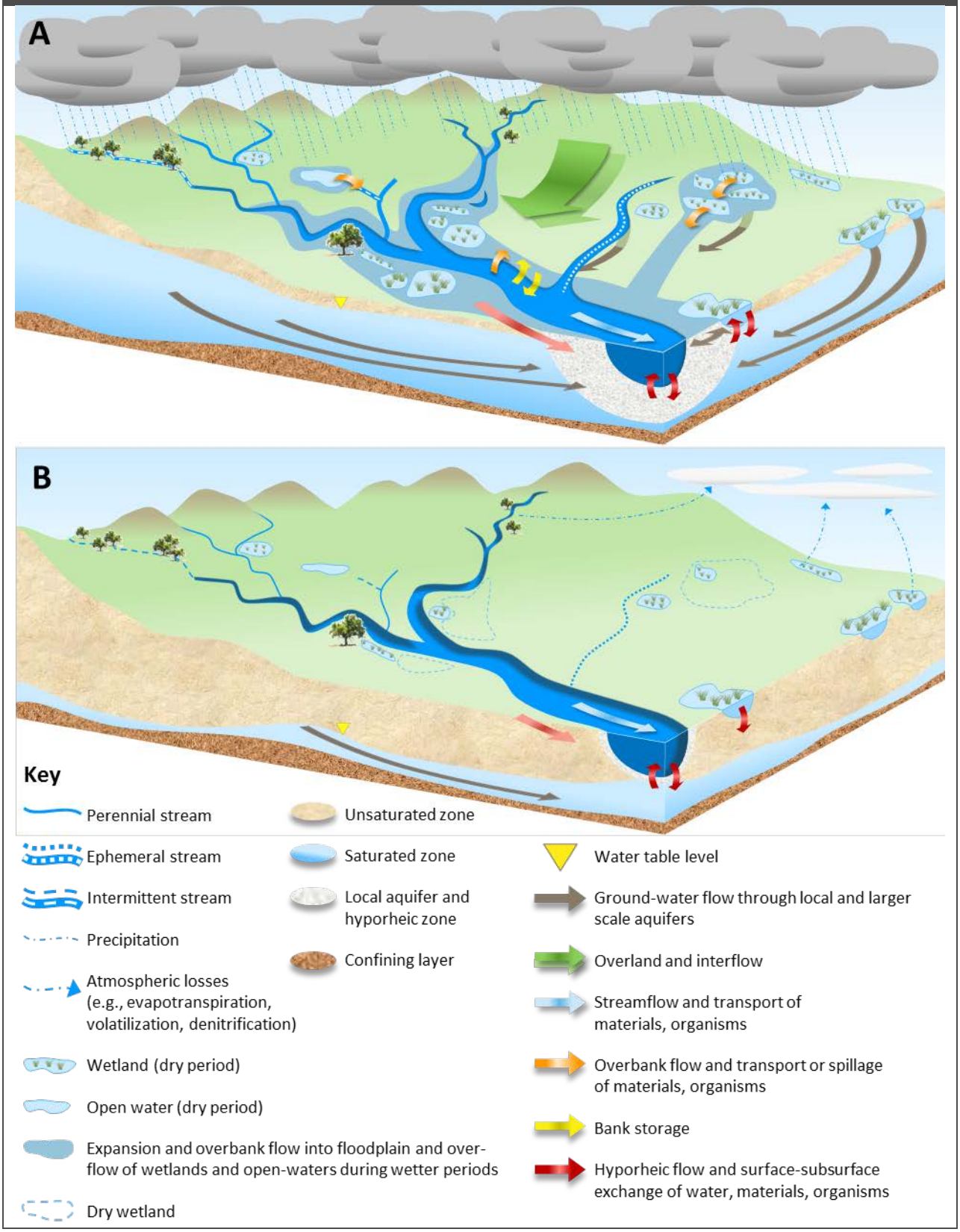


Figure 1-2. Temporal dynamics of hydrologic flowpaths. (A) A riverscape at peak hydrologic expression. (B) The same riverscape in a dry period. Intermittent and ephemeral streams, and some wetlands, are dry.



the magnitude of the event; the probability, length, and predictability of similar events could be expressed in terms of their frequency, duration, and timing; and fluctuations in dispersal could be described as the rate of change through time (e.g., across seasons or years).

Stream and wetland connections have particularly important consequences for downstream water integrity. Longitudinal flows through ephemeral, intermittent, and perennial stream channels (Figure 1-1A, blue lines and arrows) are much more efficient for transport of water, materials, and organisms than diffuse overland flows and interflows (Figure 1-1A, green arrows). Over time, stream transport pathways are reinforced by recurrent flows that maintain channel form. Areas that concentrate water also provide mechanisms for storage, transformation, and transport of materials. Differences in flow frequency, duration, magnitude, timing, and rate of change (e.g., rapid flow in mountain streams, slow flow through glacial ice or bedrock, intermittent flow in seasonal streams, ephemeral flow in arid rivers) create conditions needed for a range of ecosystem functions that affect downstream waters. Such functions include short- and long-term storage of water and sediment, transformation or sequestration of contaminants, recycling of excess nutrients, provision of habitat for aquatic and semiaquatic species, recharge of river baseflow, and provision of drinking water for humans and wildlife. For example, areas that are prone to wetting and drying cycles in response to seasonal conditions (e.g., stream and wetland perimeters shown in Figure 1-1A) are "hotspots" for chemical transformations (Vidon et al., 2010).

Ultimately, differences in the frequency, duration, magnitude, timing, and rate of change of physical, chemical, and biological connections describe different positions along the connectivity gradient and produce different types of downstream effects. For example, highly connected stream channels convey water and channel-forming sediment to rivers, whereas highly isolated wetlands can reduce flooding and store excess sediment. Connections with low values of one or more descriptors (e.g., low-frequency, short-duration flooding) can have important downstream effects when values for other descriptors are high (e.g., large-magnitude downstream transfer of floodwaters, sediment, large woody debris, and organisms). At the other end of the frequency gradient, high-frequency, low-magnitude vertical and lateral flows (Table 1-2) contribute to aquatic biogeochemical processes, including nutrient and contaminant transformation and organic matter accumulation (e.g., Brunke and Gonser, 1997; Karwan and Saiers, 2012; Lawrence et al., 2013).

In addition, timing is a key connectivity descriptor that can influence downstream waters. For example, when soils are saturated by previous rainfall events, even low or moderate rainfall can cause streams or wetlands to overflow, transporting water and materials to downstream waters. The same wetland or wetland type can attenuate floods or generate floods, depending on hydrologic conditions (Acreman and Holden, 2013). Predictable events also can profoundly influence the effects of connections. Wetlands and river networks expand and contract in response to seasonal and decadal cycles and longer term changes in environmental conditions. In wet conditions (Figure 1-2A), streams and rivers expand longitudinally into headwaters and laterally into floodplains or riparian areas, wetlands inundate and connect via surface water and ground water to other wetlands and the stream network, the water table rises, and local aquifers are recharged. In dry conditions (Figure 1-2B), the river network is limited to perennial

streams, wetlands dry down, and the water table level lowers. Seasonal flooding and drying events over an annual cycle are formative processes of physical, chemical, and biological attributes of streams in the western United States (Gasith and Resh, 1999). Large seasonal waterfowl migrations can move nutrients, plants (seeds), and invertebrates between wetlands and downgradient waters (Figuerola and Green, 2002; Green and Figuerola, 2005; Frisch et al., 2007). Fish that use nonperennial or perennial headwater stream habitats to spawn or rear young, and invertebrates that move into seasonally inundated floodplain wetlands prior to emergence, have life cycles that are synchronized with the timing of flows and flood pulses, temperature thresholds, and food resource availability in those habitats (Junk et al., 1989; Falke et al., 2010).

The surface-water and ground-water flowpaths along which water and materials are transported and transformed (Sections 2.2.2, 3.3, 3.4, 4.3.2, 4.3.3, 4.4.2, and 4.4.3; Figure 1-1A) determine variations in the degrees of physical and chemical connectivity. These flowpaths are controlled primarily by variation in climate, geology, and terrain within and among watersheds and over time. These factors have been used to group watersheds into hydrologic landscapes units that, although not necessarily spatially contiguous, are predicted to exhibit similar hydrologic function (Wolock et al., 2004; Wigington et al., 2013). Climate, geology, and terrain are reflected locally in factors such as rain and snowfall intensity, soil infiltration rates, and the direction of ground-water flows. These local factors interact with stream and wetland function and landscape position to influence degrees of connectivity through time and across space. When considered together with these local factors, hydrologic landscapes could provide a regional context for evaluating the physical and chemical connectivity of streams and wetlands in a particular watershed or group of watersheds (Section 2.4.1).

Gradients of biological connectivity (i.e., the active or passive movements of organisms through water and air and over land that connect populations of aquatic species; Sections 3.5, 4.3.4, and 4.4.4; Figure 1-1B) are determined primarily by species assemblages and by landscape features, including the factors discussed above, that facilitate or impede the movement of organisms. Organisms move across the landscape to colonize new habitats, avoid inbreeding, escape predation or competition, locate mates, and acquire resources needed to survive and reproduce. The temporal and spatial scales at which biological pathways connect aquatic habitats depend on characteristics of both the landscape and species, and overland transport or movement can occur across watershed boundaries. Dispersal is essential at higher levels of biological organization for population persistence, maintenance of genetic diversity, and evolution of aquatic species (Labbe and Fausch, 2000; Fagan, 2002; Malmqvist, 2002; Bohonak and Jenkins, 2003; Armsworth and Roughgarden, 2005). Consequently, dispersal strategies reflect aquatic species' responses and adaptations to biotic and abiotic environments, including spatial and temporal variation in resource availability and quality (e.g., Clobert et al., 2009). Dispersal-related traits and behaviors (e.g., habitat specialization, dispersal mode, behavioral response to environmental cues) therefore encompass species-environment relationships over time and provide an ecological and evolutionary context for evaluating biological connectivity in a particular watershed or group of watersheds.

Pathways for chemical transport and transformation largely follow hydrologic flowpaths (Figure 1-1A), but sometimes follow biological pathways (e.g., nutrient transport from wetlands to coastal waters by migrating waterfowl, upstream transport of marine-derived nutrients by anadromous fish, uptake and removal of nutrients by emerging stream insects; Figure 1-1B). The transport and transformation of nutrients (e.g., sequential transformations, Section 2.3.2.1; and nutrient spiraling in streams, Section 3.4.1) and other chemicals associated with water integrate physical, chemical, and biological connectivity of streams and wetlands to downstream waters (Figure 1-1B).

1.2.3 Cumulative Effects of Streams and Wetlands on Downstream Waters

Stream and wetland connectivity to downstream waters, and the resulting effects on downstream water integrity, must be considered cumulatively. First, when considering the effect of an individual stream or wetland, including the cumulative effect of all the contributions and functions that a stream or wetland provides is essential. For example, the same stream transports water, removes excess nutrients, mitigates flooding, and provides refuge for fish when conditions downstream are unfavorable; ignoring any of these functions would underestimate the overall effect of that stream.

Secondly, stream channel networks and the watersheds they drain are fundamentally cumulative in how they are formed and maintained. Excess precipitation that is not evaporated, taken up by organisms, or stored in soils and geologic layers moves downgradient as overland flow or through channels, which concentrate flows and carry sediment, chemical constituents, and organisms (Sections 3.3, 3.4, and 3.5). As flows from numerous headwater channels combine in larger channels, the volume and effects of those flows accumulate as they move through the river network. As a result, the incremental contributions of individual streams and wetlands accumulate in the downstream waters. Important cumulative effects are exemplified by ephemeral flows in arid landscapes, which are key sources of baseflow for downgradient waters (Sections 5.6 and B.5; Schlesinger and Jones, 1984; Baillie et al., 2007; Izbicki, 2007), and by the high rates of denitrification in headwater streams (Section 3.4.1). The amount of nutrients removed by any one stream over multiple years or by all headwater streams in a watershed in a given year can have substantial consequences for downstream waters (Alexander et al., 2007; Alexander et al., 2009; Böhlke et al., 2009; Helton et al., 2011). Similar cumulative effects on downstream waters have been documented for other material contributions from headwater streams (Chapter 3). For example, although the probability of a large-magnitude transfer of organisms from any given headwater stream in a given year might be low (i.e., a low-frequency connection when each stream is considered individually), headwater streams are the most abundant type of stream in most watersheds (Section 3.2). Thus, the overall probability of a large-magnitude transfer of organisms is higher when considered for all headwater streams in a watershed—that is, there is a high-frequency connection when considered cumulatively at the watershed scale, compared with probabilities of transport for streams individually. Similarly, a single pollutant discharge might be negligible but the cumulative effect of multiple discharges could degrade the integrity of downstream waters.

Evaluating cumulative contributions over time is critical in streams and wetlands with variable degrees of connectivity. For example, denitrification in a single headwater stream in any given year might not affect downstream waters; over multiple years, however, this effect could accumulate. Western vernal pools provide another example of cumulative effects over time. These pools typically occur as complexes in which the hydrology and ecology are tightly coupled with the local and regional geological processes that formed them (Section B.6). When seasonal precipitation exceeds wetland storage capacity and wetlands overflow into the river network and generate stream discharge, the vernal pool basins, swales, and seasonal streams function as a single surface-water and shallow ground-water system connected to the river network.

1.2.4 Effects of Human Activities on Connectivity

Human activities alter naturally occurring gradients of physical, chemical, and biological connectivity by modifying the frequency, duration, magnitude, timing, and rate of change of fluxes, exchanges, and transformations. For example, all dimensions of connectivity (Table 1-2) can be reduced by dams and levees (Ward and Stanford, 1983; Ligon et al., 1995; Collier et al., 1996; Wohl, 2005; Franklin et al., 2009), water withdrawals (Haag and Pfeiffer, 2012), and habitat destruction. Alternatively, connectivity can be increased by point source discharges (Brooks et al., 2006); channelization, drainage ditches, and tiles (Randall et al., 1997; Min et al., 2010); and storm drains and impervious surfaces (Booth, 1990; Paul and Meyer, 2001; Elmore and Kaushal, 2008; Walsh et al., 2012). The effects of human activities on connectivity are often complex. For example, a levee will decrease connectivity between a river channel and its floodplain at the levee site, but might increase connectivity of the channel and floodplain farther downstream, due to increased flow. Similarly, drainage ditches that increase hydrologic connectivity between isolated aquatic systems also can decrease biological connectivity through habitat loss and fragmentation.

Human activities modify the natural biological processes, material fluxes, and energy fluxes that link watershed components, resulting in a suite of stressors with measurable effects on downstream ecosystems. Some of these activities are illustrated in a hypothetical watershed (Figure 1-3). In Figure 1-3 (A), buried and ditched streams have eliminated aquatic habitat, increased downstream export of runoff and contaminants, and eliminated stream functions that could benefit downstream water quality. Figure 1-3 (B) shows a dam and reservoir that have constrained natural river expansion and contraction cycles by increasing water storage, trapping sediment, and regulating the volume and timing of river discharge. Dams and reservoirs also block upstream movement of migrating fish and other organisms, alter riparian areas, and impair riparian and floodplain wetland functions. In Figure 1-3 (C), levees and channelization have disconnected the river from its floodplain; decreased exchange of water, materials, and biota between the channel bed and hyporheic zone; and eliminated stream and wetland habitats. In addition, levees decrease the volume of river discharge at the levee site, but increase discharge downstream of the levee site. In Figure 1-3 (D), urban stormwater drainage has increased export of runoff and contaminants from impervious surface areas, altered stream temperature, and impaired instream habitats. In Figure 1-3 (E), drained and ditched wetlands have impaired wetland habitat and functions; increased downstream export of excess nutrients and

Figure 1-3. Effects of human alterations on watershed connectivity. See Section 1.2.4 for description of alterations illustrated in A-G.

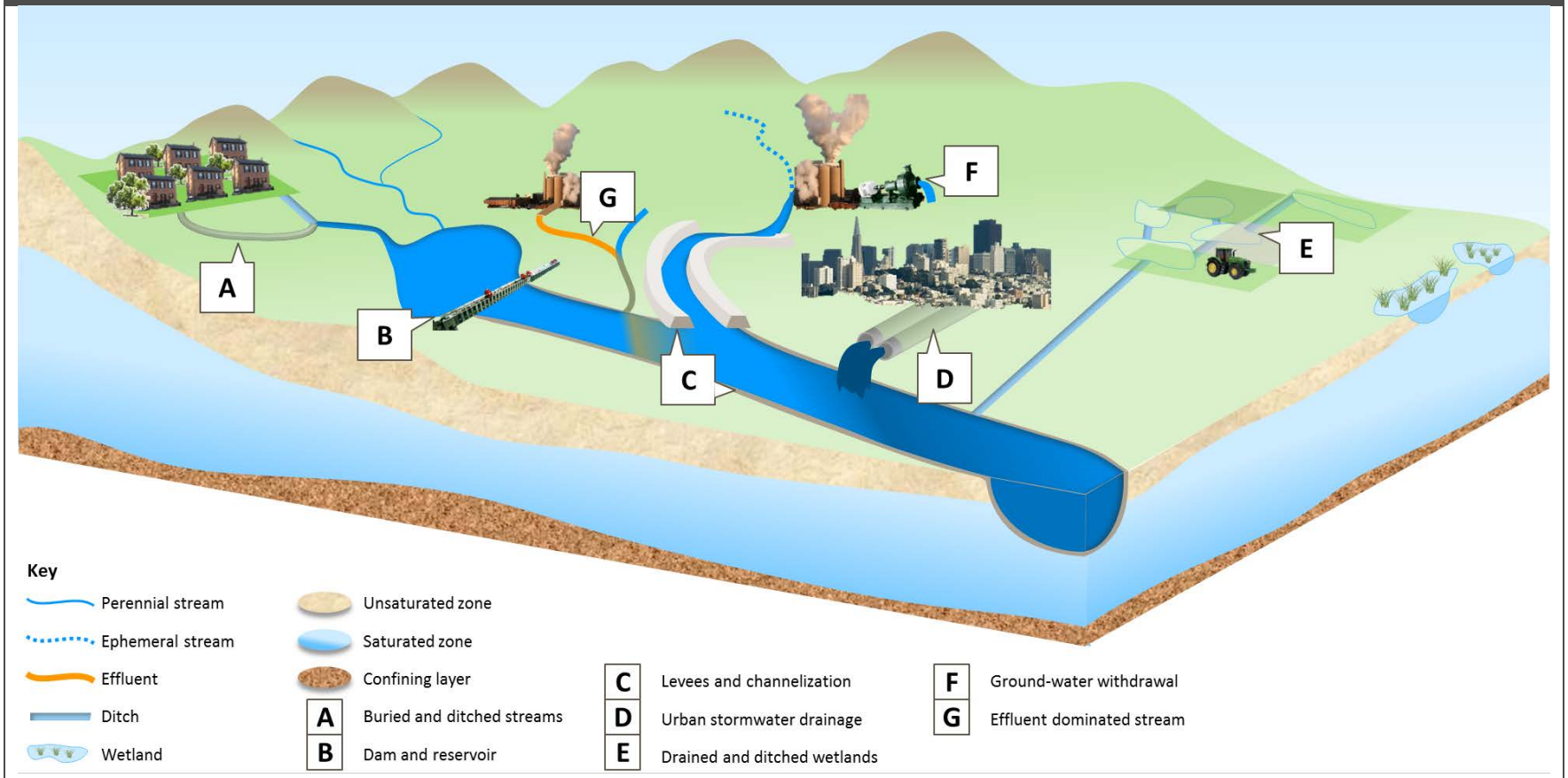
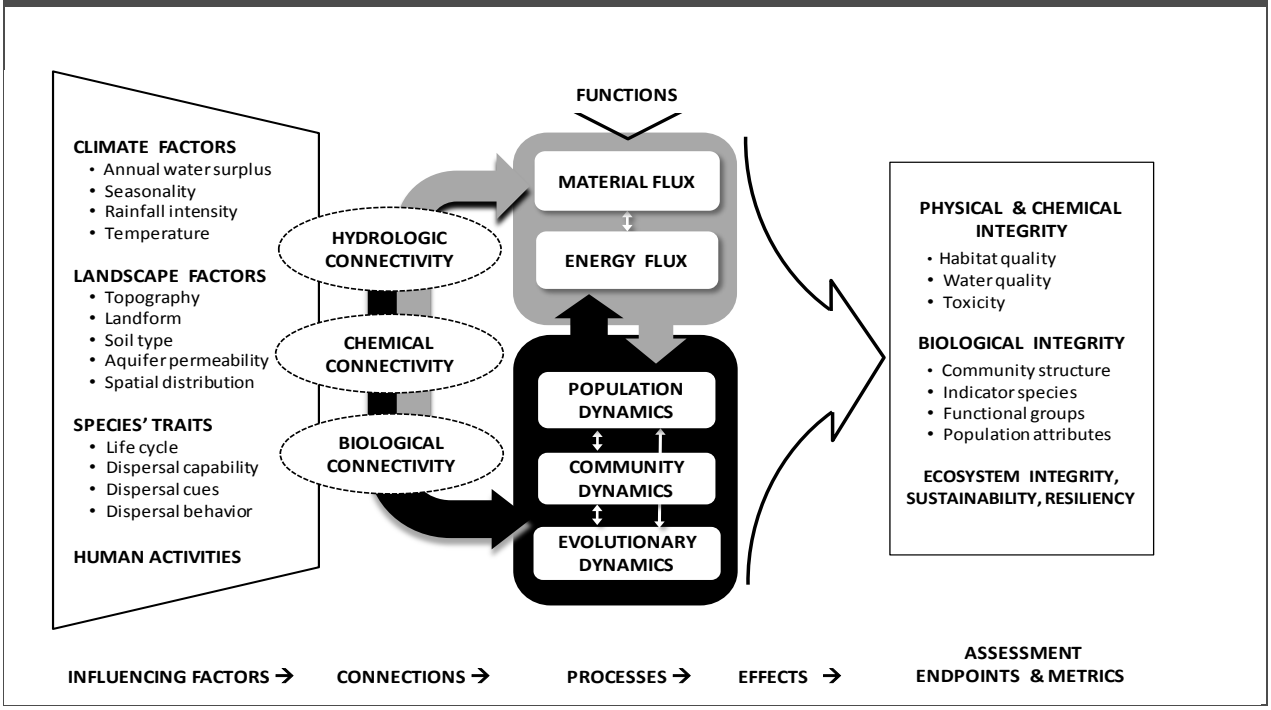


Figure 1-4. The role of connectivity in maintaining the physical, chemical, and biological integrity of water. Climate, landscape, and species' traits (Influencing Factors) interact to form Connections (hydrologic, chemical, and biological) that control the frequency, duration, magnitude, timing, and rate of change of material and energy fluxes, and biological dynamics (Processes) linking watershed components. The Functions by which these connections affect downstream waters modify the timing of transport and the quantity and quality of resources available to downstream communities. 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).



other contaminants; and decreased recharge of local and regional aquifers. In Figure 1-3 (F), ground-water withdrawal has lowered the water table, disconnecting surface water and ground water, thereby causing local streams and wetlands to dry. Finally, in Figure 1-3 (G), pollutant discharges into effluent-dominated streams have altered the volume and timing of streamflow, and increased the export of contaminants into streams. Because watersheds typically experience multiple covarying stressors, determining the cause of a specific downstream effect can be difficult. 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 (U.S. EPA, 2010; Farrar et al., 2014).

Multiple indicators and measures have been proposed for detecting and quantifying changes in connectivity associated with human activities (With et al., 1997; Tischendorf and Fahrig, 2000; Moilanen and Nieminen, 2002; Calabrese and Fagan, 2004; Martin and Soranno, 2006; Fullerton et al., 2010; Hermoso et al., 2012). Impairments that result from structural alteration of landscape attributes (e.g., dam construction, channel incision, loss of overland dispersal corridors) are relatively easier to detect and quantify than impairments 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) proposed that ecosystem impairment can be better identified and diagnosed by a combination of structural and functional metrics than by either type alone. Because connectivity can be defined in both structural and functional terms and is an integral component of aquatic ecosystem integrity, this approach is more appropriate for detecting and assessing effects of altered connectivity. To this end, systematic approaches that are rooted in landscape analysis and which incorporate hydroecological dynamics present in streams and wetland complexes (Section 2.4.6) are likely to provide useful information for inferring when and where altered connectivity is a cause of impairment to water resources.

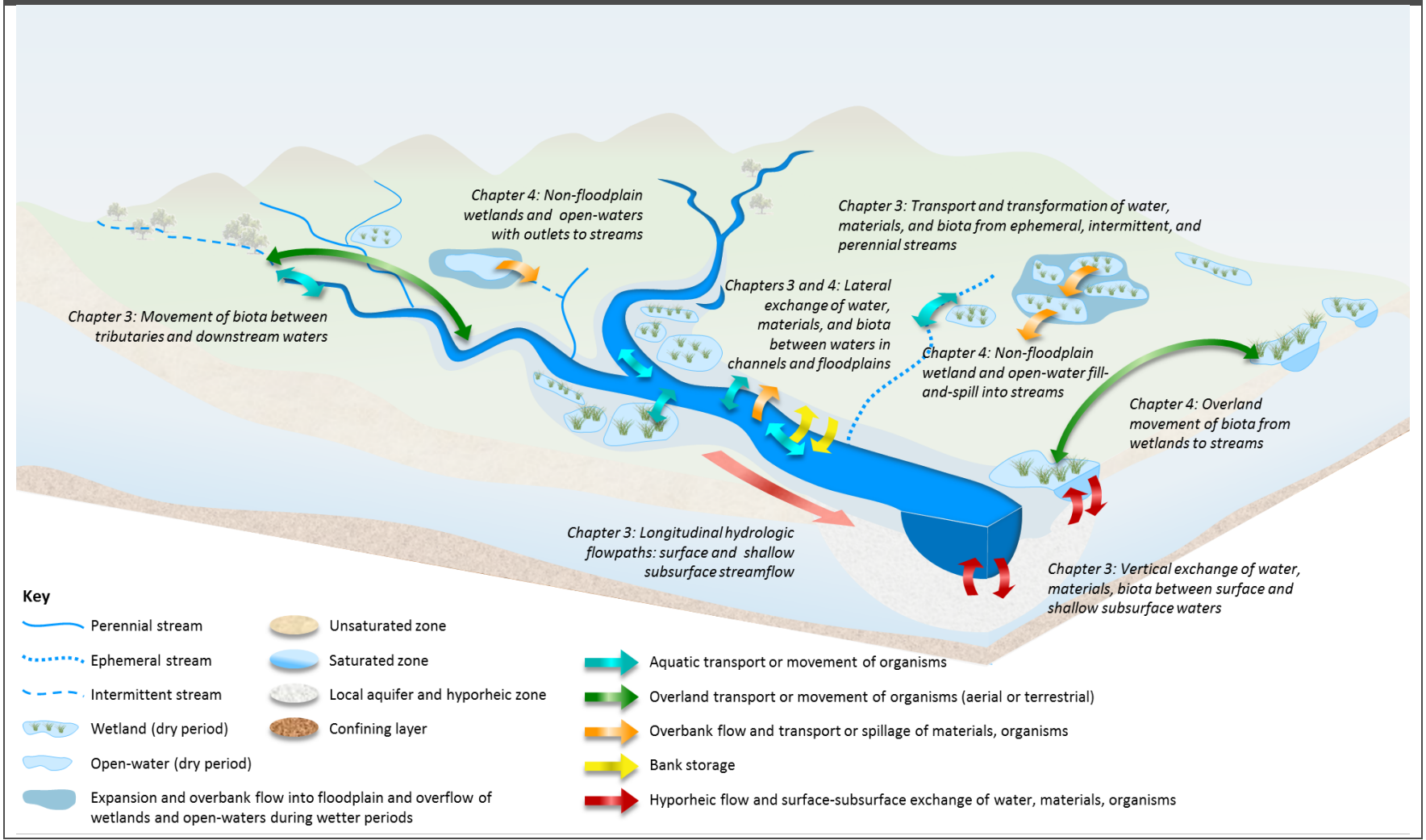
1.3 Report Approach

In this report, we focus entirely on peer-reviewed, publicly accessible sources of information about surface-water and ground-water (particularly shallow ground-water) connections and interactions from streams, wetlands, and open waters that influence the function and condition of downstream surface waters (Figure 1-5). Information about connections among water bodies of the same type (e.g., wetland-to-wetland or headwater stream-to-headwater stream connections) and connections from terrestrial systems to downstream waters are considered out of scope (Figure 1-5).

The topical scope of this report was chosen to consider waters that often fall under the purview of the CWA. As a scientific review, however, this report does not consider or make judgments regarding legal standards for CWA jurisdiction. Our review of subsurface flows emphasizes shallow (local) ground water, because flows in this category have the greatest interchange with surface waters (Winter et al., 1998) although 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). As with any literature review, readers should refer to the cited publications for quantitative information, such as flow distance, depth, duration, timing, and magnitude, about specific surface-water and ground-water connections, and for other details about the systems and studies discussed in this report.

To identify connections and effects of streams, wetlands, and other water bodies on downstream waters, we used two types of evidence from peer-reviewed, published literature: (1) direct evidence that demonstrated a connection or effect (e.g., observed transport of materials or movement of organisms from streams or wetlands to downstream waters) and (2) indirect evidence that suggested 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 headwater streams are connected to downstream segments, another body of evidence shows those downstream segments are linked to other

Figure 1-5. Waters and connections considered to be within scope for this report.



segments farther downstream, and so on. This approach, which borrows from weight-of-evidence approaches in causal analysis (Suter et al., 2002; Suter and Cormier, 2011), is an effective way to synthesize the diversity of evidence needed to address questions at larger spatial and longer temporal scales than are often considered in individual scientific studies.

1.3.1 Selection and Screening of Scientific Materials

We searched the scientific literature for information on the types of waters, connections, and downstream effects identified in the report objectives and scope (Section 1.1; Figure 1-5). We conducted keyword searches using terms inclusive of the types of waters, connections, and downstream effects of interest (e.g., [wetland* AND [river* OR stream*] AND [connect* OR isolat*]]). Because simple keyword searches would have omitted relevant publications, we also searched for literature on related topics. Topics included conceptual frameworks of watershed and landscape connectivity; hydrologic flowpaths among watershed components; biogeochemical transformation and cycling in streams and wetlands; natural or artificial tracers of difficult-to-observe flows (e.g., ground-water flow, gene flow); chemical and biological processes associated with aquatic habitat fragmentation and spatial isolation; and climate or landscape factors that influence connectivity or isolation. We also reviewed citations provided by peer-review panels and in public comments on drafts of the report. We then screened those results and selected the most relevant publications for review and synthesis in this report, based on the criteria in Figure 1-6.

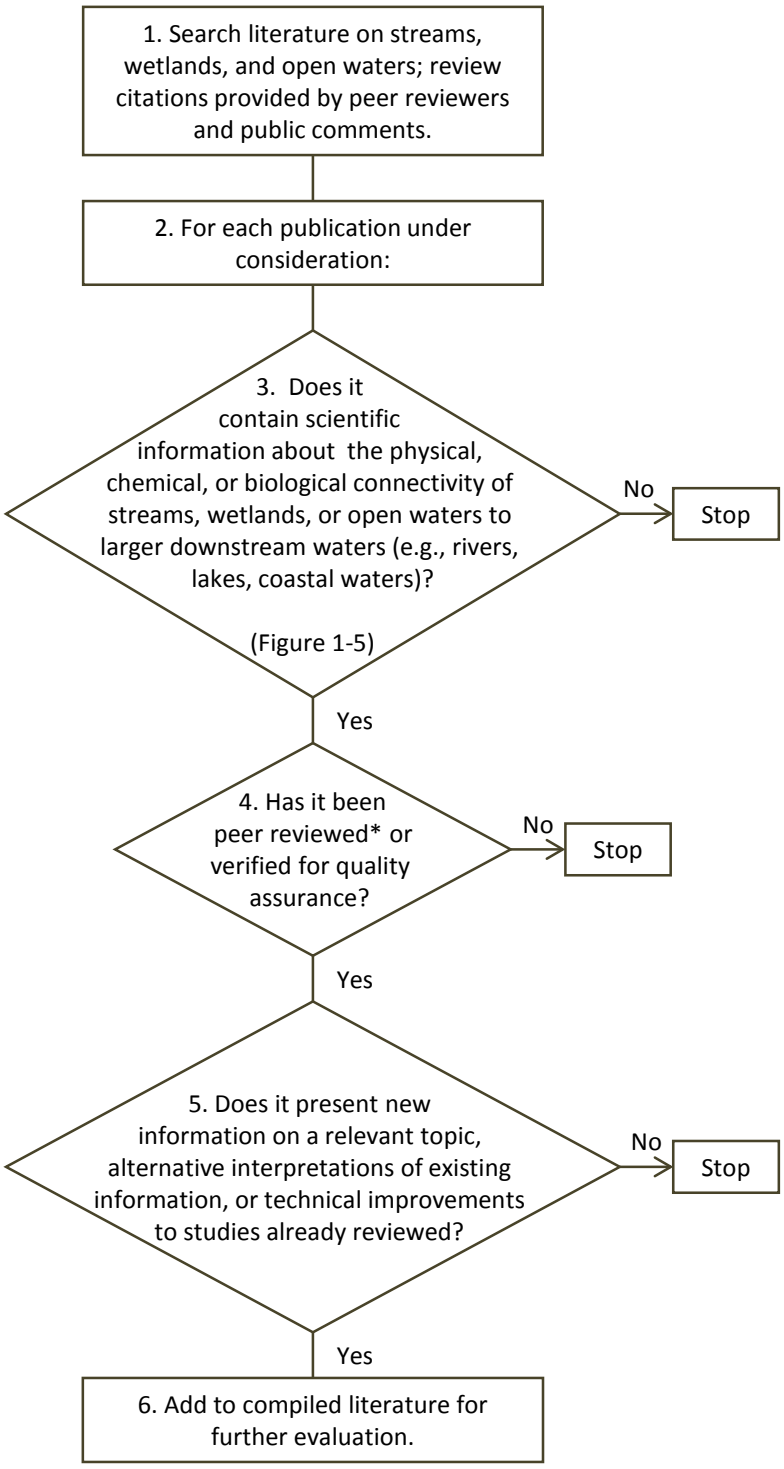
We used science citation databases and search engines available through Web of Science™ and Google Scholar™ to search primary (original research) and secondary (review) literature. These searches included examination of references citing or cited in relevant publications obtained through specific searches.

Because the breadth and depth of topics covered in this report made an exhaustive literature review impractical, we emphasized highly influential papers on relevant topics, review papers that summarized multiple studies in narrative form, meta-analyses that used statistical methods to combine results from multiple independent studies into a single evaluation of evidence, and superseding editions or versions of published research. Publications that did not provide new information, an alternative perspective or interpretation of evidence, or a technical improvement (e.g., improved accuracy or better study design) were not summarized in the report to avoid redundancy and excessive length and detail.

We summarized the relevant literature in narrative form and organized each chapter into lines of evidence pertaining to different types of connections (physical, chemical, biological) for different types of systems (streams, riparian/floodplain wetlands, non-floodplain wetlands). Lines of evidence were evaluated for strength, consistency, mechanistic plausibility, and relevance to the endpoints identified in the report objectives. Finally, conclusions for each of the report's three questions were derived from the key findings, and placed in context with concepts and evidence provided in each chapter.

Cited in this report are 1,353 references. Most were published in refereed scientific journals (86%), as scientific reports by federal agencies that follow peer-review guidelines of the Office of Management and

Figure 1-6. Flow chart for screening and compiling literature.



* Peer review is the formal evaluation of scientific information by independent experts who were not involved in the work but have equivalent scientific and technical expertise. Its purpose is to ensure that materials accepted for publication have been critically reviewed and revised as needed to meet the documented standards of scientific integrity and quality for specific journals or organizations. All reports published by the U.S. EPA Office of Research and Development meet or exceed peer-review requirements established by the Office of Management and Budget (OMB, 2004).

Budget (4%), or scientific books (~9%). The remaining citations refer to photographs, maps, non-federal reports, or websites (<1%) that provide supplemental information.

1.3.2 Report Structure

The report is organized into six chapters. Chapter 1 outlines the purpose, scientific context, and approach of the report. Chapter 2 describes the components of a river system and watershed; the types of physical, chemical, and biological connections that link those components; the factors that influence connectivity at various temporal and spatial scales; and methods for quantifying connectivity. Chapter 3 reviews literature on connectivity in stream networks in terms of physical, chemical, and biological connections and their resulting effects on downstream waters. Chapter 4 reviews literature on the connectivity and effects of nontidal wetlands and certain open waters on downstream waters. Chapter 5 applies concepts and evidence from previous chapters to the case studies detailed in Appendix B. Chapter 6 presents the five major conclusions of this report, with a summary of key findings from the literature synthesized to develop these conclusions. It also discusses the relative abundance of literature on topics reviewed in this report, and briefly discusses emerging research that can close some current data gaps identified in the report. A glossary of scientific terms used in the report and detailed case studies of selected systems (summarized in Chapter 5) are included in Appendix A and Appendix B, respectively.

1.4 Summary

This report evaluates, summarizes, and synthesizes available peer-reviewed scientific literature on the connectivity and mechanisms by which streams, wetlands, and open waters, singly or in aggregate, affect the physical, chemical, and biological integrity of downstream waters.

Connectivity has long been a central tenet for the study of aquatic ecosystems. Watersheds are integrated at multiple spatial and temporal scales by flows of surface water and ground water, transport and transformation of physical and chemical materials, and movements of organisms. Although all parts of a watershed are connected, the degrees and downstream effects of those connections vary; the effects also are influenced by characteristics of the physical environment, the biological environment, and by human activities in the watershed.

Variation in the degree of connectivity is critical to the integrity and sustainability of downstream waters, and can be described in terms of the frequency, duration, magnitude, timing, and rate of change of fluxes to and biological exchanges with downstream waters. These descriptors characterize the range over which streams and wetlands vary and shift along connectivity gradients and the probable effects of different types (hydrologic, chemical, biological) and degrees of connectivity over time. Gradients of physical, chemical, and biological connectivity are controlled primarily by variation in climate, geology, terrain, aquatic organisms, and human activities within and among watersheds, and over time.

Ultimately, differences in the frequency, duration, magnitude, timing, and rate of change of physical, chemical, and biological connections describe different positions along the connectivity gradient and

produce different types of downstream effects. Connections with low values of one or more descriptors (e.g., low-frequency, short-duration floods) can have important downstream effects when values for other descriptors are high (e.g., large-magnitude transfers of floodwaters, sediment, large woody debris, and organisms downstream). At the other end of the frequency gradient, the effects of high-frequency, low-magnitude vertical and lateral flows strongly contribute to biogeochemical functions, including nutrient and contaminant transformation and organic matter accumulation.

Stream channel networks and the watersheds they drain are fundamentally cumulative in how they are formed and maintained. The downstream consequences (e.g., the amount and quality of materials that eventually reach a river) are determined by the aggregate effect of contributions and sequential alterations that begin at the source waters and function along continuous flowpaths to the watershed outlet. Cumulative effects across a watershed must therefore be considered when quantifying the frequency, duration, and magnitude of connectivity, to evaluate the downstream effects of streams, wetlands, and open waters.





CHAPTER 2. AN INTEGRATED SYSTEMS PERSPECTIVE ON INTERACTIONS OF WATERSHEDS, STREAMS, WETLANDS, AND DOWNSTREAM WATERS

2.1 Introduction

A river is the time-integrated result of all waters contributing to it, and connectivity is the property that spatially integrates the individual components of the watershed. In discussions 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, 2007; Rodriguez-Iturbe et al., 2009). Such interpretation requires that freshwater resources be viewed within a landscape—or systems—context (Baron et al., 2002). Addressing the questions asked in this report (Section 1.1), 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 describes this integrated systems perspective. Section 2.2 outlines the basic hydrologic foundation of river systems. Section 2.3 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 2.4 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, similar exchanges of water, influenced by many of the same factors, also occur between rivers, lakes, estuaries, and marine waters.

2.2 An Introduction to River Systems

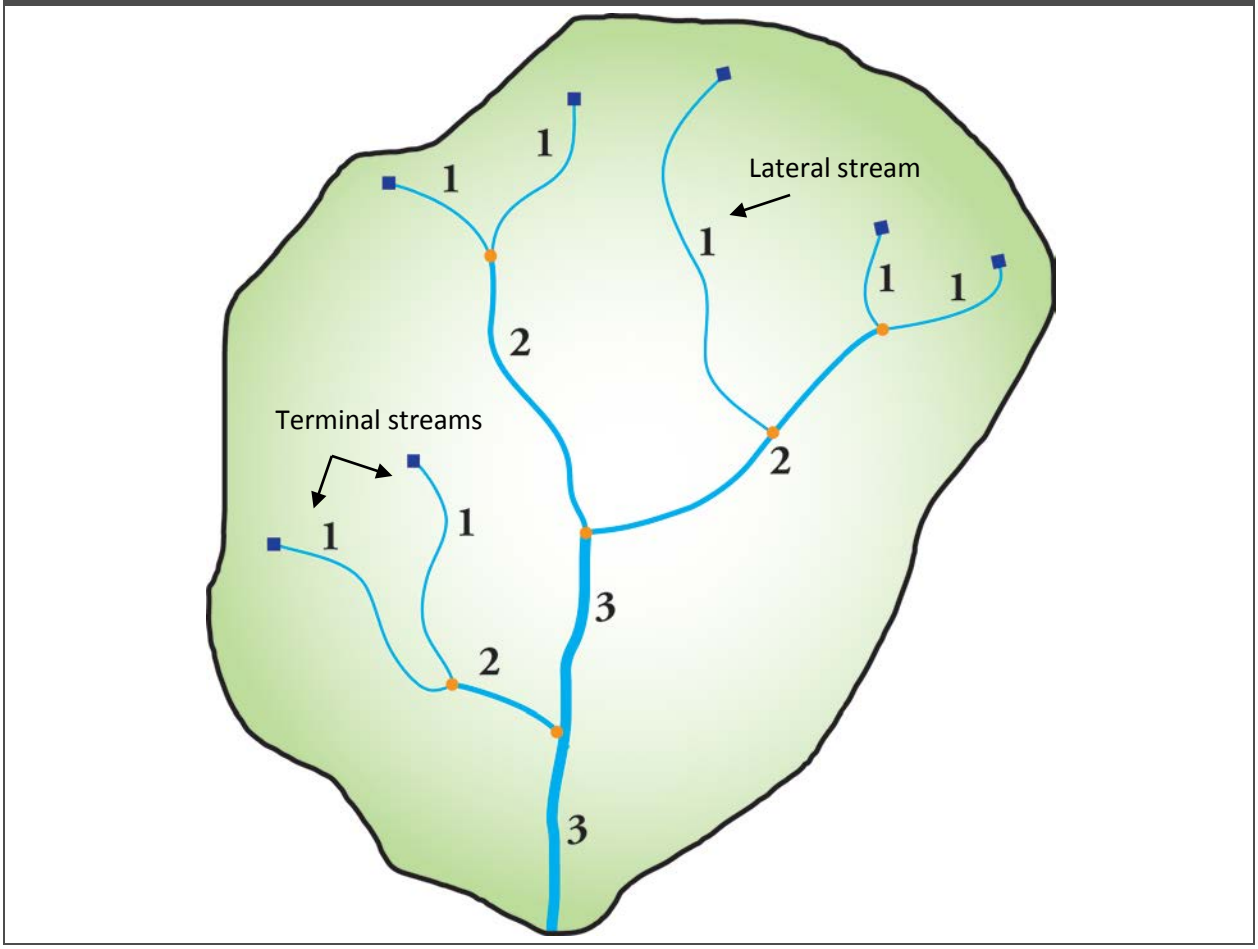
2.2.1 River System Components

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 (but permeable) bottom and lateral boundaries. Although bed and bank structures might in places appear to be disrupted (e.g., bedrock outcrops, braided channels, flow-through wetlands), the continuation of the bed and bank downgradient from such disruptions is evidence of the surface connection with the channel that is upgradient of the perceived disruption. Such disruptions are associated with changes in the gradient and in the material over and through which the water flows. If a disruption in the bed and bank structure prevented connection, the area downgradient would lack a bed and bank, be colonized with terrestrial vegetation, and be indiscernible from the nearby 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 (Sections 2.2.2 and 2.2.3) from a watershed to a river and includes the river itself. Watershed boundaries traditionally are defined topographically, such as by ridges, but ground-water sources and losses can 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 streamflows 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., 2006b; Nadeau and Rains, 2007), where stream order is a classification system based on the position of the stream in the river network (Figure 2-1; Strahler, 1957). The point at which stream or river channels intersect within a river network is called a **confluence** (Figure 2-1). 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.

One weakness of classification based on stream order is that it disregards the contributions of lower order streams where they join a higher order stream. Link magnitude, an alternative method for classifying streams, 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

Figure 2-1. A generalized example of a river network within its watershed. Blue lines illustrate the river network, within the light green area of its watershed. Numbers represent Strahler stream order, with streams increasing in order when two streams of equal order join. Blue squares indicate channel heads, and orange dots depict confluences.



magnitude of a segment accounts for all contributing lower order streams regardless of their position in river networks. For some properties, link magnitude might better reflect the aggregate upstream contributions to downstream waters.

Mock (1971) presented a classification of the streams comprising stream or river networks. He designated first-order streams that intersect other first-order streams 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** (Figure 2-1)**.**

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 (Figure 2-1). 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 also can 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).

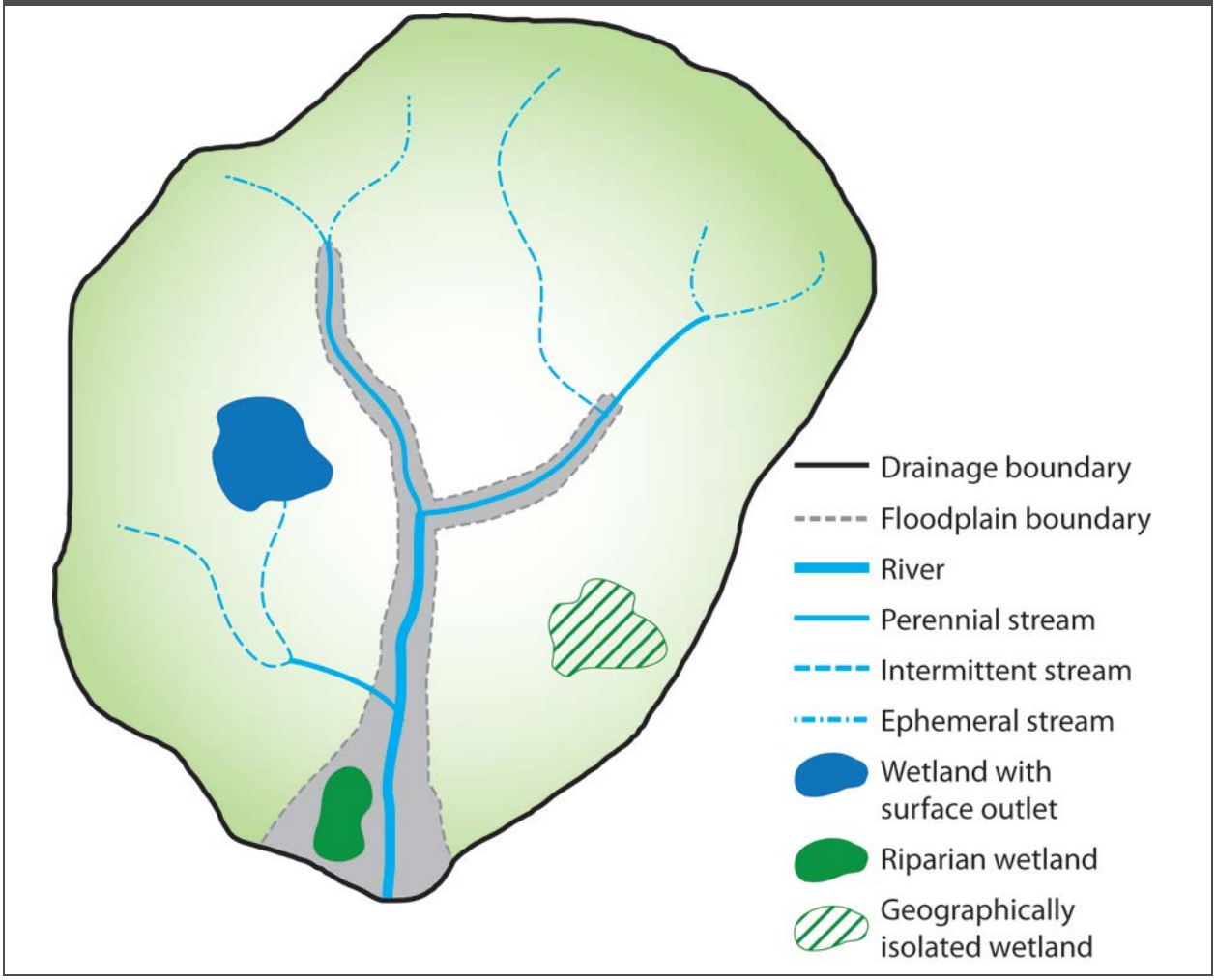
Surface-water hydrologic connectivity within river network channels occurs, in part, through the unidirectional movement of water from channels at higher elevations to ones at lower elevations—that is, hydrologic connectivity exists because water flows downhill. In essence, the river network represents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

A **river system** (Figure 2-2) consists of a river network and its entire watershed. It includes all connected or isolated surface-water bodies (e.g., lakes and wetlands), any ground-water 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).

Streamflow and the quantity and character of sediment—interacting with watershed geology, terrain, soils and vegetation—shape morphological changes in the stream channel that occur from river network headwaters to lower rivers (Montgomery, 1999; Church, 2002). Headwater streams are typically erosion zones in which sediment from the base of adjoining hillslopes moves directly into stream channels and is transported downstream. As stream channels increase in size and decrease in slope, a mixture of erosion and deposition processes usually is at work. At some point in the lower portions of river networks, sediment deposition becomes the dominant process and floodplains form. **Floodplains** are level areas bordering stream or river channels that are formed by sediment deposition from those channels under present climatic conditions (Figure 2-3). These natural geomorphic features are inundated during moderate to high water events (Leopold, 1994; Osterkamp, 2008). Floodplain and associated river channel forms (e.g., meandering, braided, anastomosing) are determined by interacting fluvial factors, including sediment size and supply, channel gradient, and streamflow (Church, 2002, 2006). **Terraces** are historical floodplains, formed under different climatic conditions, that are no longer connected to the river or stream channel that formed them (Figure 2-3).

Both riparian areas and floodplains are important components of river systems (Figure 2-3). **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 adjoining 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 have high biodiversity (Naiman et al., 2005). They occur near lakes and estuarine-marine shorelines and along river networks,

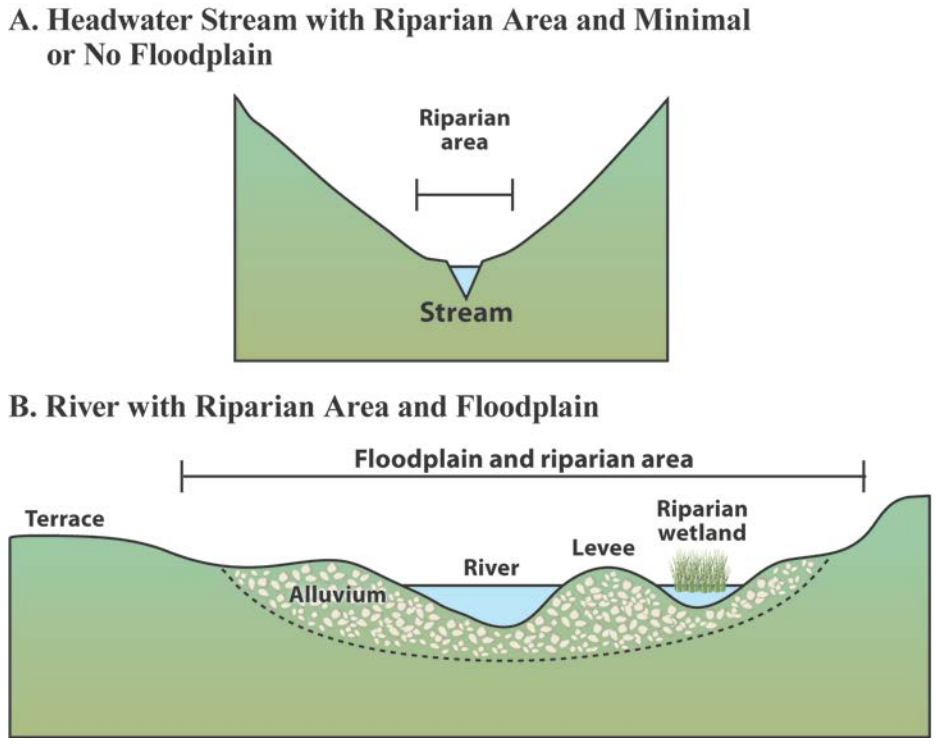
Figure 2-2. Elements of a river system. These elements include: the drainage basin (light green area), river network (rivers and streams), and other water bodies (riparian/floodplain wetlands, lakes, and wetlands in non-floodplain settings). Note that the non-floodplain wetland that lacks a stream outlet also would be considered "geographically isolated" *sensu* Tiner (2003b).



where their width can vary from narrow bands along headwater streams (Figure 2-3A) to broad zones that encompass the floodplains of large rivers (Figure 2-3B).

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 (Figures 2-2 and 2-3). 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" (https://www.fema.gov/floodplain-management/flood-zones). The 100-year floodplain can but need not coincide with the geomorphic floodplain. 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

Figure 2-3. Hypothetical cross-sections of (A) a headwater stream and (B) a large river within a river network. The headwater stream in (A) is a constrained reach with a narrow riparian area and no floodplain; the river in (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 varies depending on the criteria used for delineation.



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 Code of Federal Regulations 328.3(b); see also USACE, 1987). Thus, 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 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 this report focuses on downstream connectivity (Section 1.3), we consider two landscape settings in which wetlands occur based on directionality of hydrologic flows. Directionality of flow also is included as a component of hydrodynamic setting in the hydrogeomorphic approach (Brinson, 1993; Smith et al., 1995) and as an element of water flowpath 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 (Section 2.3.2).

A **non-floodplain wetland setting** is a landscape setting where the potential exists for unidirectional, lateral hydrologic flows from wetlands to the river network through surface water or ground water. Such a setting 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 toward a river network would be considered a non-floodplain setting, regardless of the magnitude and duration of flows and of travel times. In this document, we therefore refer to wetlands that occur in these settings as **non-floodplain wetlands**.

A **riparian or floodplain wetland setting** is a landscape setting (e.g., floodplains, most riparian areas, lake and estuarine fringes) that is subject to bidirectional, lateral hydrologic flows. Wetlands in riparian/floodplain settings can have some of the same types of hydrologic connections as those in non-floodplain settings. In addition, wetlands in these settings 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). Given our interest in addressing the effects of wetlands on downstream waters (Section 1.1), we have focused in particular on the subset of these wetlands that occur in riparian areas with and without floodplains (collectively referred to hereafter as **riparian/floodplain wetlands**); we generally do not address wetlands at lake and estuarine fringes. **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 use of landscape setting to define riparian/floodplain wetlands and non-floodplain wetlands is similar to the use of landscape position by Tiner (2011) to supplement the Cowardin et al. (1979) classification. Our use of riparian/floodplain wetland setting is generally consistent with Tiner's estuarine, lotic, and lentic landscape positions, whereas our non-floodplain setting is similar to his terrene category (Tiner, 2011). One important difference is that Tiner (2011) would consider a wetland to be 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 to be in a riparian/floodplain setting.

The terms "riparian/floodplain" and "non-floodplain" 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 settings. For example, a palustrine emergent wetland (Cowardin et al., 1979) could be located outside a floodplain, 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 riparian/floodplain if it had both an input and output channel because water from the stream flows into and affects the wetland. A depressional wetland with a surface outlet and no inlet or with no outlets and inlets, however, would be considered non-floodplain because water could flow downgradient only from the wetland to the river network, and not from a stream to the wetland. Similarly, a riverine wetland (Smith et al., 1995) that is the origin for a stream would be considered non-floodplain if it had no input channel,

even though it occurs in a riparian area. In most cases, however, riverine wetlands would be considered riparian/floodplain. 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 waterborne materials can be transported only from the wetland to the river network for a non-floodplain wetland, whereas waterborne materials can be transported from the wetland to the river network and from the river network to the wetland for a riparian/floodplain wetland. In the latter case, there is a mutual, interacting effect on the structure and function of both the wetland and river network. In contrast, a non-floodplain wetland can affect a river through the transport of waterborne material, but the opposite is not true. Note that we limit our use of riparian/floodplain and non-floodplain landscape settings to describe the direction of hydrologic flow; the terms cannot be used to describe directionality of geochemical or biological flows. For example, mobile organisms can move from a stream to a non-floodplain wetland (e.g., Subalusky et al., 2009a; Subalusky et al., 2009b). In Alaska, transport of live salmon or their carcasses from streams to riparian areas by brown bears (*Ursus arctos*) account for more than 20% of riparian nitrogen budgets (Helfield and Naiman, 2006). Although this example is in a riparian/floodplain setting, it shows how geochemical fluxes can be decoupled from hydrologic flows.

Both non-floodplain and riparian/floodplain wetlands can include **geographically isolated wetlands**, or wetlands completely surrounded by uplands (Tiner, 2003b). These wetlands have no apparent surface-water outlets, but can hydrologically connect to downstream waters through spillage or ground water. 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, riparian/floodplain wetland that is subject to periodic inundation from the river network. Although the term "geographically isolated" could be misconstrued as implying functional isolation, the term has been defined in the peer-reviewed literature to refer specifically to wetlands surrounded by uplands. Furthermore, the literature explicitly notes that geographic isolation does not imply functional isolation (Leibowitz, 2003; Tiner, 2003b). Discussion of geographically isolated wetlands is essential because hydrologic connectivity (an element of connectivity, which is the focus of this document) is generally difficult to characterize for these wetlands. The difficulty arises because hydrologic monitoring or additional information and analyses would be necessary to determine whether surface or subsurface hydrologic connections occur for such wetlands.

2.2.2 River System Hydrology

River system hydrology is controlled by hierarchical factors that result in a broad continuum of belowground and aboveground hydrologic flowpaths connecting river basins and river networks (Winter, 2001; Wolock et al., 2004; Devito et al., 2005; Poole et al., 2006; Wagener et al., 2007; Poole, 2010; Bencala et al., 2011; Jencso and McGlynn, 2011). At the broadest scale, regional climate interacts with river-basin terrain and geology to shape inherent hydrologic infrastructure that bounds the nature of basin hydrologic flowpaths. Different climate-basin combinations form identifiable hydrologic

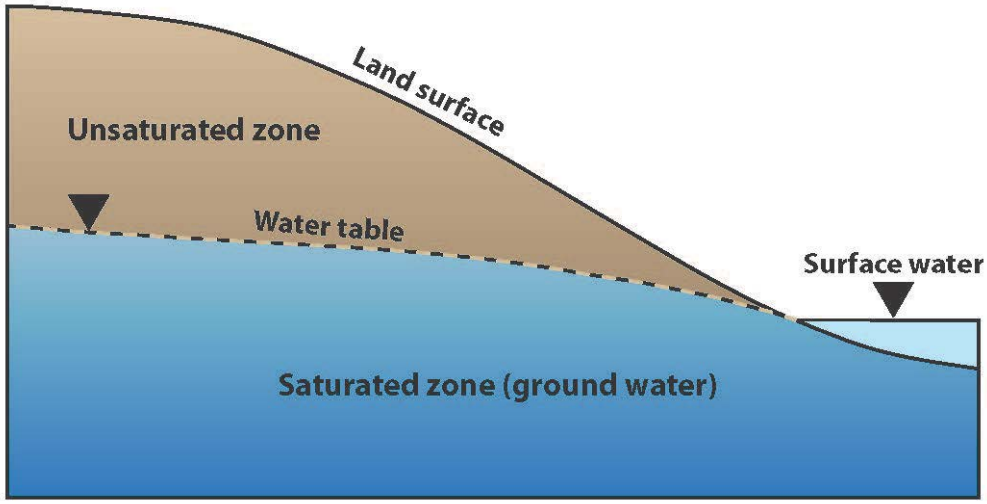
landscape units with distinct hydrologic characteristics (Winter, 2001; Wigington et al., 2013). Buttle (2006) posited three first-order controls of watershed streamflow generated under specific hydroclimatic conditions: (1) the ability of different landscape elements to generate runoff by surface or subsurface lateral flow of water; (2) the degree of hydrologic linkage among landscapes by which surface and subsurface runoff can reach river networks; and (3) the capacity of the river network itself to convey runoff downstream to the river-basin outlet. River and stream waters are influenced by not only basin-scale or larger ground-water systems, but also local-scale, vertical and lateral hydrologic exchanges between water in channels and sediments beneath and contiguous with river network channels (Ward, 1989; Woessner, 2000; Malard et al., 2002; Bencala, 2011). The magnitude and importance of river-system hydrologic flowpaths at all spatial scales can radically change over time at hourly to yearly temporal scales (Junk et al., 1989; Ward, 1989; Malard et al., 1999; Poole et al., 2006).

Because interactions between ground waters and surface waters are essential processes in rivers, knowledge of basic ground-water hydrology is necessary to understand the interactions between surface and subsurface water and their relationship to connectivity within river systems. Subsurface water occurs in two principal zones: the unsaturated zone and the saturated zone (Figure 2-4; 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. **Ground water** refers to any water that occurs and flows (**saturated ground-water flow**) in the saturated zone beneath a watershed surface (Winter et al., 1998). Rapid flow (**interflow**) of water can occur through large pore spaces in the unsaturated zone (Beven and Germann, 1982).

Traditionally, geologic formations in which ground water occurs are divided into two major categories: (1) **aquifers**, which are saturated geologic units capable of transmitting significant amounts of water under ordinary hydraulic gradients; and (2) **aquicludes**, which are saturated geologic units that are *not* capable of transmitting significant quantities of water (aquicludes 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** (Figure 2-4). 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) are present in the midst of highly permeable materials such as sand (Freeze, 1971). **Confined aquifers** are bounded by an underlying confining unit and an overlying confining unit and typically lack a direct connection with current surface and atmospheric conditions (Figure 2-5). Water in confined aquifers is often pressurized, and, consequently, water levels in wells

Figure 2-4. 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. Ground water and ground-water flow occur in the saturated zone. If a surface-water body is connected to the ground-water system, the water table intersects the water body at or near the surface of its shoreline. Modified from Winter et al. (1998).

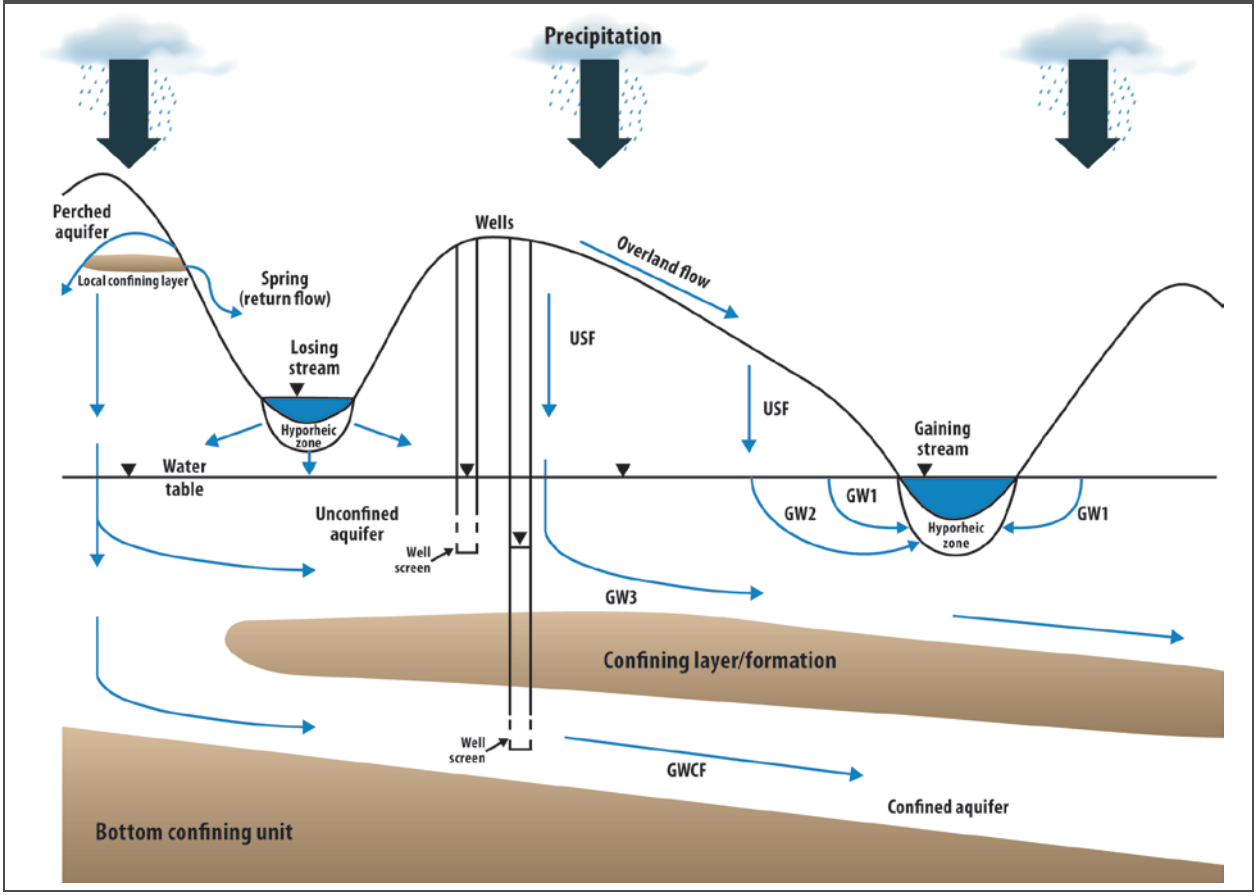


penetrating confined aquifers occur at elevations above the upper confining unit. The surface of the water levels in wells penetrating a confined aquifer is called the **potentiometric surface**. Confined aquifers typically occur deeper below the land surface than unconfined aquifers and generally have less frequent influence on surface waters than unconfined aquifers.

Traditionally, aquifers were identified based solely on their ability to support wells for water production, but in recent years hydrologists studying ground water-surface water interactions have recognized the need for a broader definition that recognizes the importance of low-flow geologic formations to aquatic ecosystems. Payne and Woessner (2010) highlighted 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 ground-water 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 ground water flows. In this report, we have adopted the Winter et al. (1998) aquifer definition. Unless otherwise noted, our discussion of ground water and aquifers is limited to unconfined systems.

Ground-water **recharge areas** occur where water from land surfaces or surface-water bodies infiltrates and moves into saturated zones. **Discharge areas** occur where water flows from saturated zones into a river network, other water bodies, or onto land surfaces. A **gaining stream (**or **wetland**; also referred to as a **discharge wetland**) within a river network receives inflow of ground water. In this situation, the water table elevation near the stream (or wetland) must be higher than the elevation of the stream water surface. In a **losing stream (**or **wetland**; i.e., **recharge wetland**), water flows from the stream (wetland) to ground water. In this situation, the water table elevation near the stream or wetland is

Figure 2-5. Cross-section showing major hydrologic flowpaths in a regional-scale stream-watershed system. USF = unsaturated flow, GW = ground-water flowpath (saturated flow); GW1, GW2, and GW3 = ground-water flowpaths of varying depth and length. GW1 represents local ground water and GW3 represents regional ground water. GWCF = ground-water flowpath in confined aquifer.



lower than the stream or wetland water surface. Conditions that determine whether streams and wetlands are gaining or losing can change over short periods of time and over short distances within river networks and river basins (Winter et al., 1998; Harrington et al., 2002; Wilson and Guan, 2004; Coes and Pool, 2005; Scanlon et al., 2006; Vivoni et al., 2006; Larned et al., 2008). Overall, however, the volume and sustainability of streamflow within river networks typically depend on contributions from ground water (Winter, 2007), especially in areas with shallow ground-water tables and pervious subsurfaces (de Vries, 1995; Kish et al., 2010).

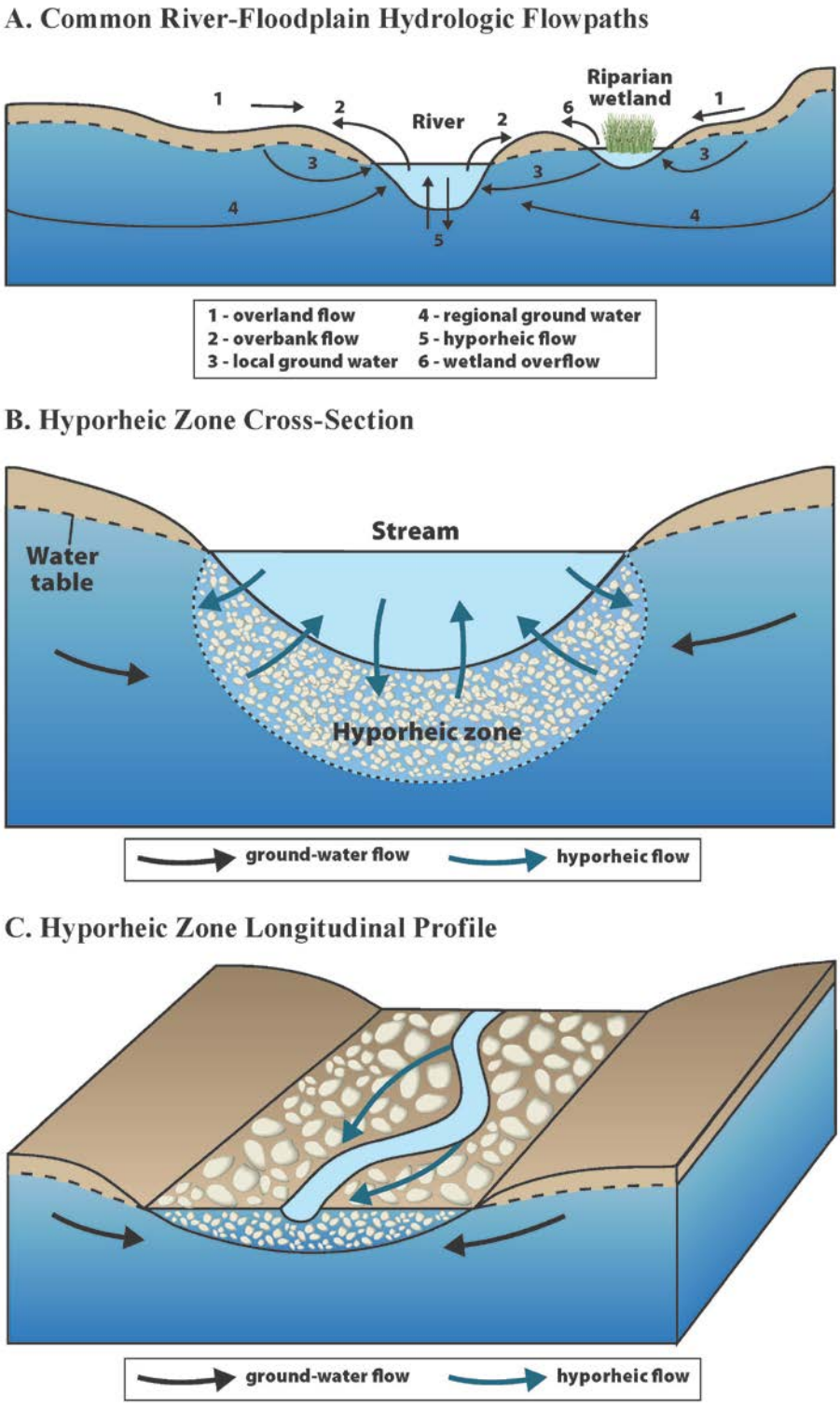
Ground-water flow systems within river basins can be complex, of varying sizes and depths, and overlie one another (Tóth, 1963; Winter et al., 1998; Haitjema and Mitchell-Bruker, 2005). Although in reality there is a continuum of flowpath lengths that occur within river basins (Bencala et al., 2011), they are commonly grouped into three categories (Figure 2-5). In **local ground-water** flow systems (also referred to as shallow ground-water flow systems), ground water flows from the highest elevations of water tables (water table highs) to nearby lowlands or surface waters (Winter and LaBaugh, 2003). Local ground-water flow is the most dynamic of ground-water flow systems, having the greatest

interchange with surface waters. If the depth-to-width ratios of aquifers are sufficiently large, regional flow systems (deepest ground-water flowpaths) also might be present. **Regional ground water** (also referred to as deep ground water) originates from precipitation in distant upland recharge areas and moves long distances, through deep regional-scale aquifers, to river networks (Figure 2-5). The contact times between ground water and subsurface materials are longer for these deep and long flow systems than for 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. An **intermediate ground-water** flow system is one in which ground water flows from a water table high to a lowland that is not immediately adjoining the water table high. Intermediate ground-water flow systems are representative of the wide range of flowpath lengths and depths that occur between local and regional ground-water systems.

Other hydrologic flowpaths are also significant in determining the characteristics of river systems. The most obvious is the downstream water movement within stream or river channels, or **open-channel flow**. River water in stream and river channels can reach riparian areas and floodplains via **overbank flow** (Figure 2-6A), which occurs when floodwaters flow over stream and river channels (Mertes, 1997). **Overland flow** is the portion of streamflow derived from net precipitation that flows over the land surface to the nearest stream channel with (Figure 2-6A; Hewlett, 1982). Overland flow can be generated by several mechanisms. **Infiltration-excess overland flow** occurs when the rainfall rates exceed the infiltration rates of land surfaces (Horton, 1945). **Saturation-excess overland flow** occurs when precipitation inputs cause water tables to rise to land surfaces so that precipitation inputs to the land surfaces cannot infiltrate and flow overland (Dunne and Black, 1970). **Return flow** occurs when water infiltrates, percolates through the unsaturated zones, enters saturated zones, and then returns to and flows over watershed surfaces, commonly at hillslope-floodplain transitions (Dunne and Black, 1970).

Alluvium (Figure 2-3B) comprises deposits of clay, silt, sand, gravel, or other particulate materials that running water has deposited in a streambed, on a floodplain, on a delta, or in a fan at the base of a mountain. These deposits occur near active river systems but also can be found in buried river valleys—the remnants of relict 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 an environment conducive to ground-water flow. **Alluvial ground water** (typically a mixture of river water and local, intermediate, and regional ground water) moves through the alluvium. Together, the alluvium and alluvial ground water comprise **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). Hyporheic exchange occurs when water moves from stream or river into alluvial deposits and then returns to the channels (Figures 2-6B and 2-6C; Bencala, 2005; Leibowitz et al., 2008). Hyporheic exchange allows for the mixing of surface water and ground water. It occurs during both high- and low-flow periods, and typically has relatively horizontal flowpaths at scales of meters to tens of meters (Bencala, 2005) and vertical flowpaths with depths ranging from centimeters to tens of meters (Stanford and Ward, 1988; Woessner, 2000 and references therein).

Figure 2-6. Hyporheic zone flows. (A) Common hydrologic flowpaths by which water flows between watersheds and river networks. (B) and (C) The three-dimensional process of hyporheic flow, or the movement of water from a river or stream to nearby alluvium and then back to the river or stream. Modified from Winter et al. (1998).



Riparian areas and floodplains can have a diverse array of hydrologic inputs and outputs, which, in turn influence riparian/floodplain wetlands. Riparian areas and floodplains receive water from precipitation; overland flow from upland areas; local, intermediate, regional ground water; and hyporheic flows (Figure 2-6A; National Research Council, 2002; Richardson et al., 2005; Vidon et al., 2010). Water flowing over the land surface in many situations can infiltrate soils in riparian areas. If low permeability subsoils or impervious clay layers are present, water contact with the plant root zone is increased and materials in the water are subject to ecological functions such as denitrification before it reaches the stream channel (Section 4.3.2; National Research Council, 2002; Naiman et al., 2005; Vidon et al., 2010).

The relative importance of the continuum of hydrologic flowpaths among river systems varies, creating streams and rivers with different flow duration (or hydrologic permanence) classes (Figures 2-2 and 2-7). **Perennial streams** or stream reaches (Figure 2-7A) typically flow year-round. They are maintained by local or regional ground-water discharge or streamflow from higher in the stream or river network. **Intermittent streams** or stream reaches (Figure 2-7B) flow continuously at certain times of the year (e.g., during certain seasons such as spring snowmelt); drying occurs when the water table falls below the channel bed elevation. **Ephemeral streams** or stream reaches (Figure 2-7C) flow briefly (typically hours to days) during and immediately following precipitation; these channels are above the 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. 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). 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 (Figure 2-8A), which might stem from multiple ground-water and surface-water sources (Dunne and Leopold, 1978). **Baseflow** is streamflow originating from ground-water discharge or seepage (locally or from higher in the river network), which sustains water flow through the channel between hydrologic events (Figure 2-8A). Perennial streams have baseflow year-round; intermittent streams have baseflow seasonally; ephemeral streams have no 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 (Figure 2-9; 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 (Figure 2-9C).

Similar to streams, the occurrence and persistence of riparian/floodplain wetland and non-floodplain wetland hydrologic connections with river networks, via surface water (both channelized and nonchannelized) or ground water, can be continuous, seasonal, or ephemeral, depending on the overall hydrologic conditions in the watershed. For example, a non-floodplain wetland might have a direct ground-water connection with a river network during wet conditions but an indirect regional ground-water connection (via ground-water recharge) under dry conditions. Geographically isolated wetlands can be hydrologically connected to the river network via nonchannelized surface flow (e.g., swales or overland flow) or ground water.

Figure 2-7. Hypothetical hydrographs illustrating maximum duration of flow ($D_{max,q}$) for (A) perennial, (B) intermittent, and (C) ephemeral streams. Source: Reprinted from Non-navigable streams and adjacent wetlands: Addressing science needs following the Supreme Court's Rapanos decision, (2008) by Leibowitz et al. with permission of Ecological Society of America.

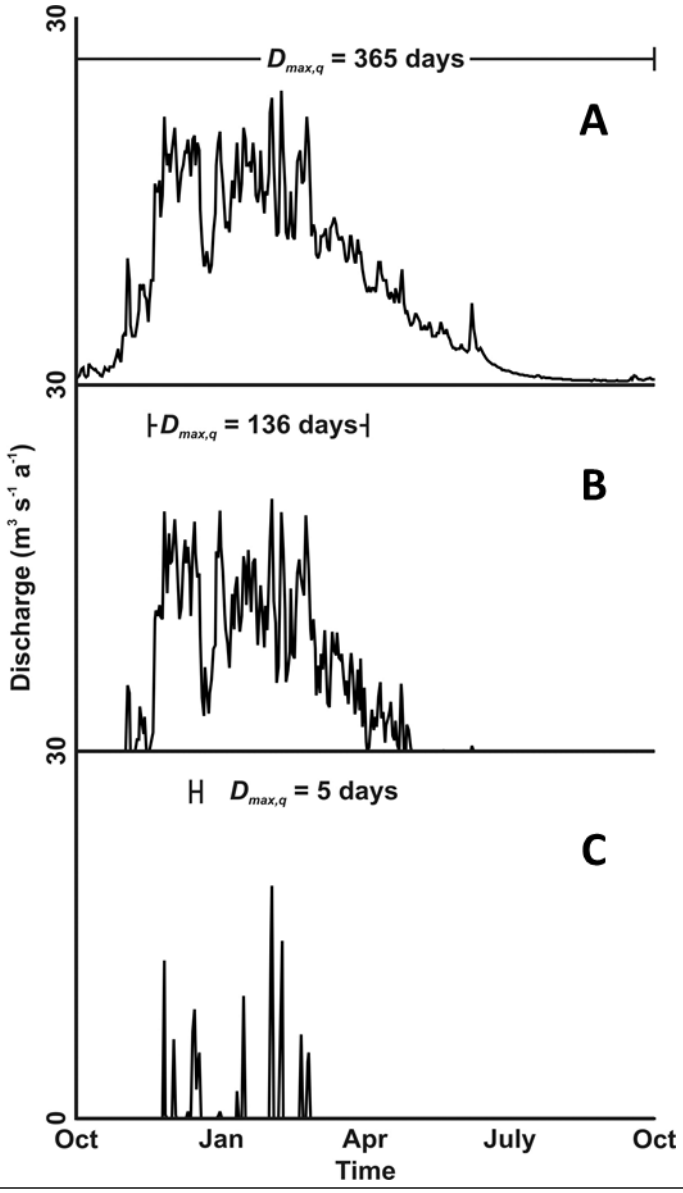


Figure 2-8. (A) Hypothetical hydrograph showing stormflow and baseflow responses to a rainfall event. (B) Expansion and contraction of flowing water in a stream network following a rainfall event. Panel B Source: Reprinted from Subsurface stormflows in the highly permeable forested watersheds of southwestern British Columbia, (1988) by Cheng et al. with permission of Elsevier.

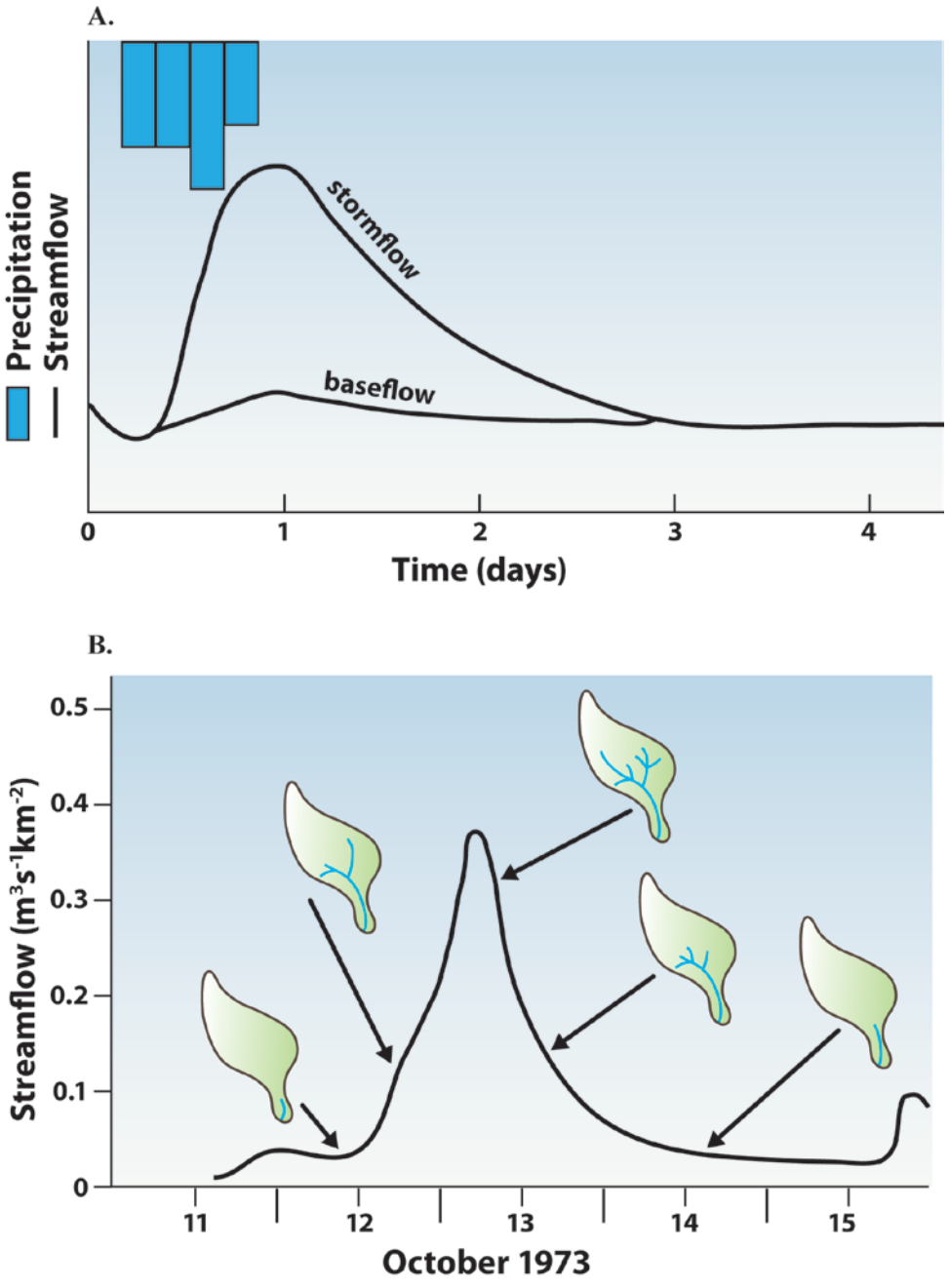
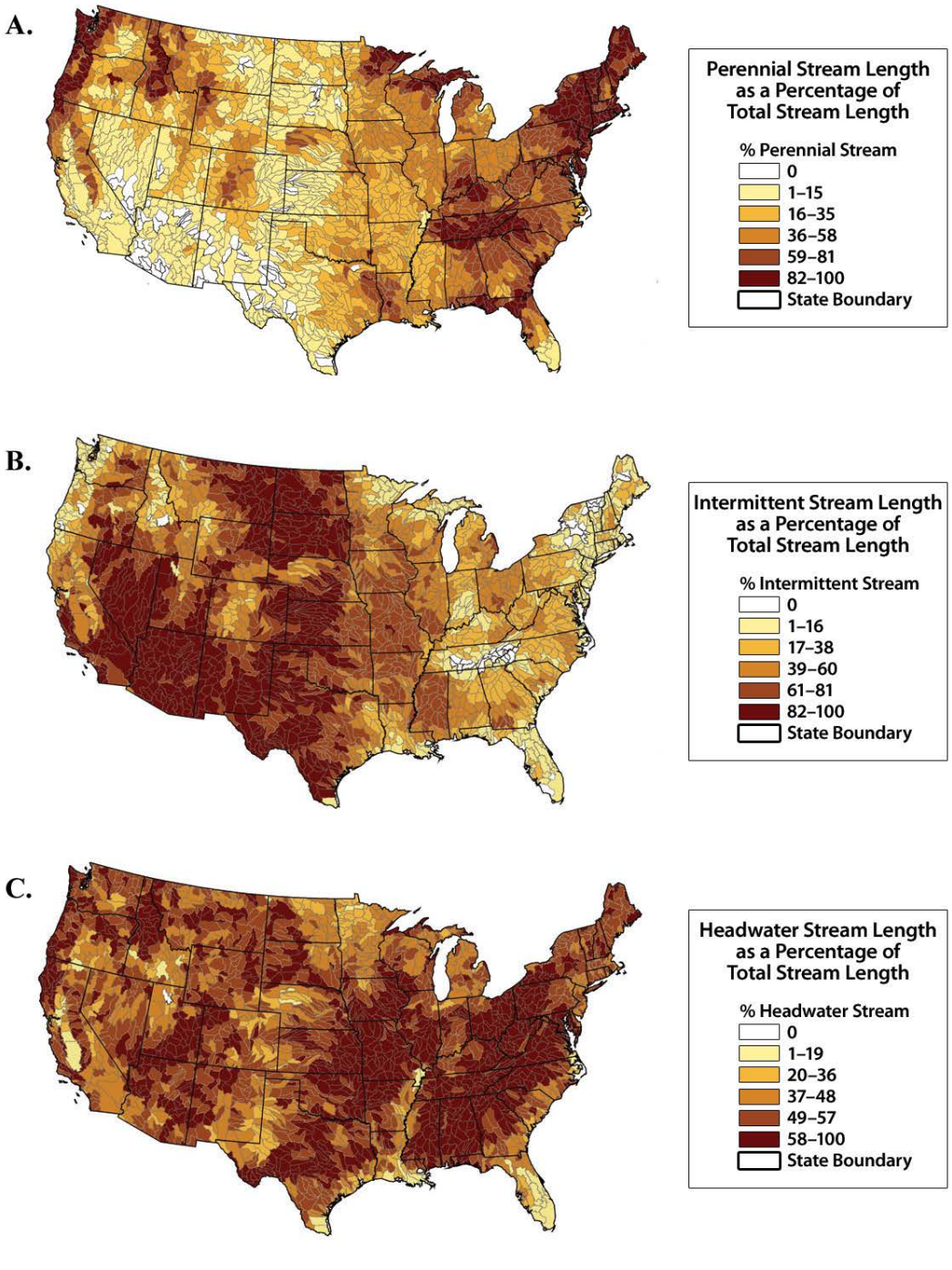


Figure 2-9. Characteristics of U.S. streams by watershed, in terms of percent of total stream length as (A) perennial, (B) intermittent, and (C) headwater streams. Data from the National Hydrography Dataset (NHD) Reach Address Database (RAD) v2.0 at 1:100,000 scale using 8-digit HUC (Hydrologic Unit Code) watersheds. Here, "intermittent" includes streams having intermittent or ephemeral flow. Note that NHD data generally do not capture streams <1.6 km (1 mile) in length, and ranges of color categories are not consistent across maps.



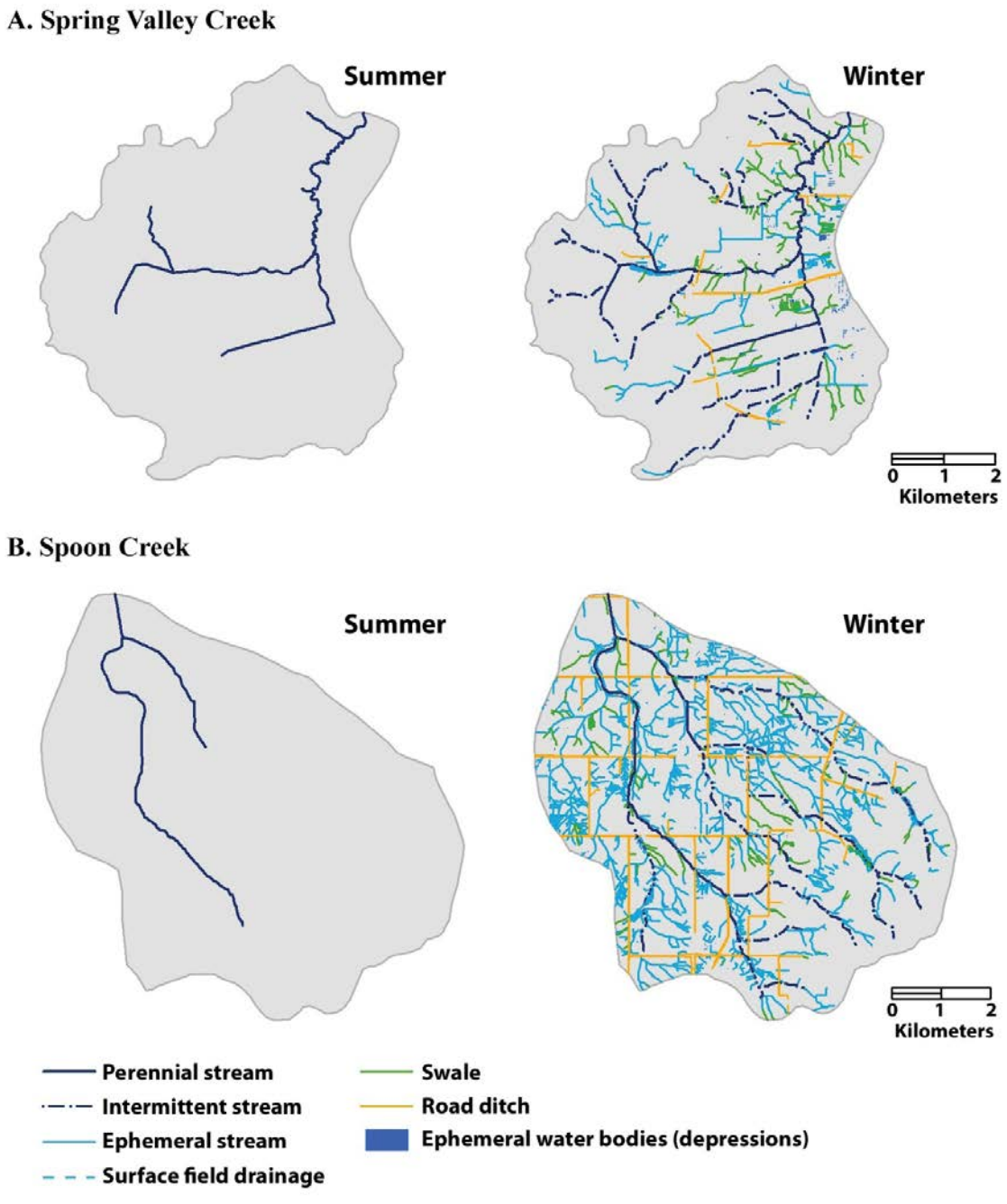
2.2.3 River Network Expansion and Contraction

The portions of river networks with flowing water 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; Dunne and Black, 1970; Day, 1978; Junk et al., 1989; Hunter et al., 2005; Wigington et al., 2005; Rains et al., 2006; Rains et al., 2008). The longitudinal expansion of channels with flowing water in response to major precipitation events represents a transient increase in the extent of headwater streams. Figure 2-10 shows the expansion of the flowing portion of two stream networks in western Oregon between dry, summer and wet, winter seasons. 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.

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 a river network to expand in two ways. First, local aquifers expand and water moves into dry channels, which increases the total length of the wet channel (Winter et al., 1998); the resulting intermittent streams will contain water during the entire wet season. Second, stormflow can cause water to enter ephemeral and intermittent streams (Figure 2-8). The larger the rainfall or snowmelt event, the greater the number of ephemeral streams and total length of flowing channels that occur within the river network. Ephemeral flows cease within days after rainfall or snowmelt ends (Figure 2-8B), causing the length of wet channels to decrease and river networks to contract. The flowing portion of river networks further shrinks as the spatial extent of aquifers with ground water 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 (Section B.5). 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 a river network, the hydrograph for a typical event broadens with a lower peak (Figure 2-11). This broadening of the hydrograph shape (Figure 2-11A) results from transient storage of water in river network channels and nearby alluvial aquifers (Fernald et al., 2001).

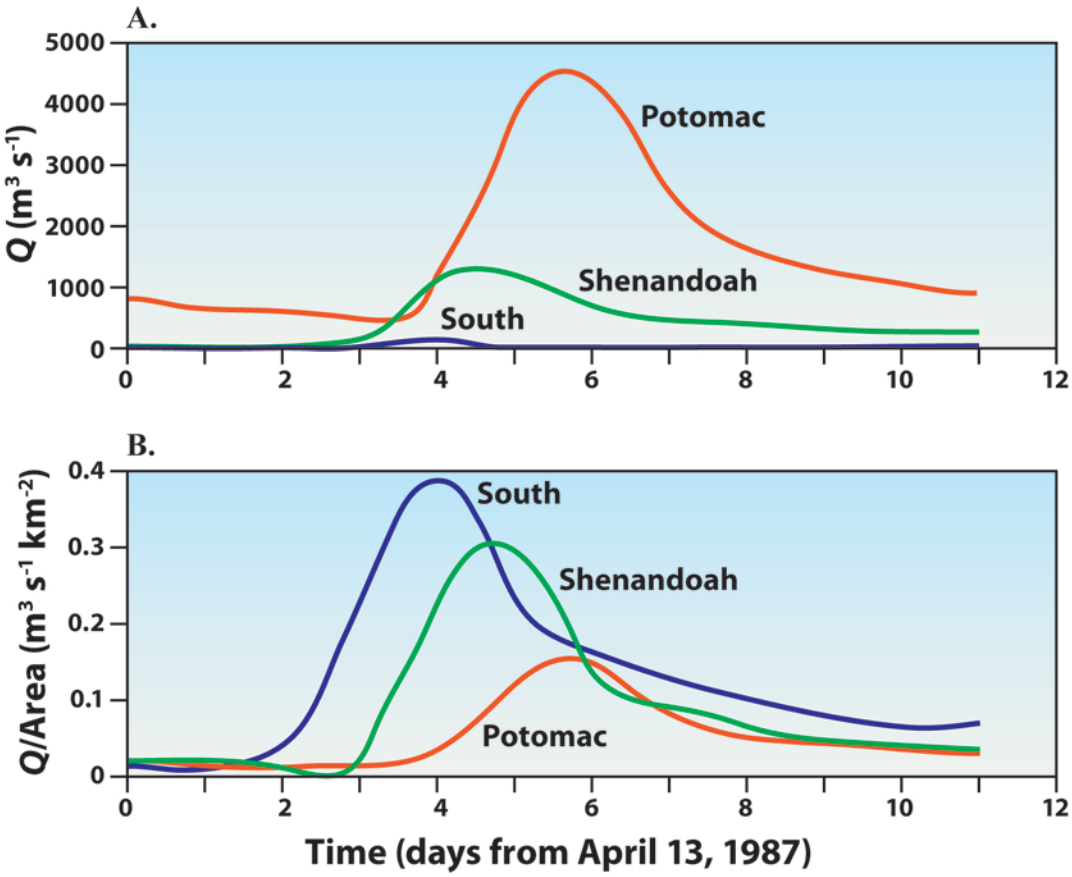
Floodplains and riparian areas can be locations with significant ground-water recharge and discharge (National Research Council, 2002; Naiman et al., 2005). During very large hydrologic events, aggregate flows from headwaters and other tributary streams can result in overbank flooding in river reaches with floodplains; this occurrence represents lateral expansion (Figure 2-12) 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

Figure 2-10. 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. Source: Reprinted from Stream network expansion: A riparian water quality factor, (2005) by Wigington et al. with permission of John Wiley & Sons.



(Wolman and Miller, 1960; Hammersmark et al., 2008). Depending on the nature of the hydraulic gradients, ground water within floodplain alluvium can move both parallel and perpendicularly to streams or rivers (National Research Council, 2002) and enter river networks at various discharge points. Bidirectional exchanges of water between ground water and river networks, including hyporheic

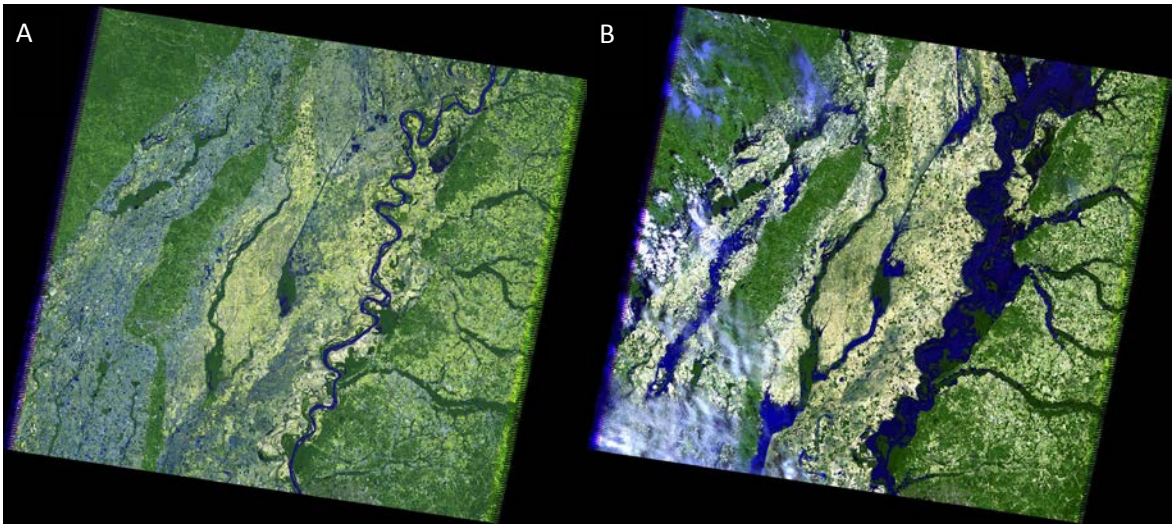
Figure 2-11. Stormflow moves downstream through the river network and interacts with lower stream reaches, floodplains, and alluvial aquifers. (A) Hydrographs for three nested rivers in the Potomac River watershed (drainage area Potomac > Shenandoah > South). (B) Hydrographs for the same three rivers with streamflow normalized by drainage area. Source: Reprinted from Elements of physical hydrology, (1998) by Hornberger et al., with permission of Johns Hopkins University Press.



flow, can occur under a wide range of streamflows, from flood flows to low flows (National Research Council, 2002; Naiman et al., 2005; Vivoni et al., 2006).

The hydrologic connections with river networks fundamentally differ for riparian/floodplain wetlands and non-floodplain 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 ground-water sources (Figure 2-6A). In contrast, hydrologic connections between non-floodplain wetlands and river networks originate via surface-water spillage or ground-water flow when water inputs exceed evapotranspiration and available storage. Although wetlands that serve as origins for streams are riparian, we group them with non-floodplain wetlands because they also have unidirectional flow through their outlet streams. In both cases, the degree of hydrologic connectivity between riparian/floodplain and non-floodplain wetlands and the river network varies with lateral expansion and subsequent contraction.

Figure 2-12. 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 U.S. Geological Survey/National Aeronautics Space Administration.



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 ground water 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 (Section 4.3.2; 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, infiltrate floodplain soils, or evapotranspire.

Many studies have documented the fact that riparian/floodplain wetlands can 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 less frequently than lower elevation areas.

The interactions 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 adjoining and under channels. In streams or river reaches constrained by topography, significant floodplain and near-channel alluvial aquifer

interactions are limited (Figure 2-3A). In reaches with floodplains, however, stormflow commonly supplies water to alluvial aquifers during high-flow periods through the process of **bank storage** (Figure 2-13; 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 (Figure 2-13C).

In summary, the extent of wetted channels is dynamic because interactions between surface water in the channel and alluvial ground water, via hyporheic exchange, determine open-channel flow. The flowing portion of river networks expands and contracts in two primary dimensions: (1) longitudinally, as intermittent and ephemeral streams wet up and dry; and (2) laterally, as floodplains and associated alluvial aquifers gain (via overbank flooding, bank storage, and hyporheic exchange) and lose (via draining of alluvial aquifers and evapotranspiration) water. Vertical ground-water exchanges between streams and rivers and underlying alluvium are also key 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).

2.3 Influence of Streams and Wetlands on Downstream Waters

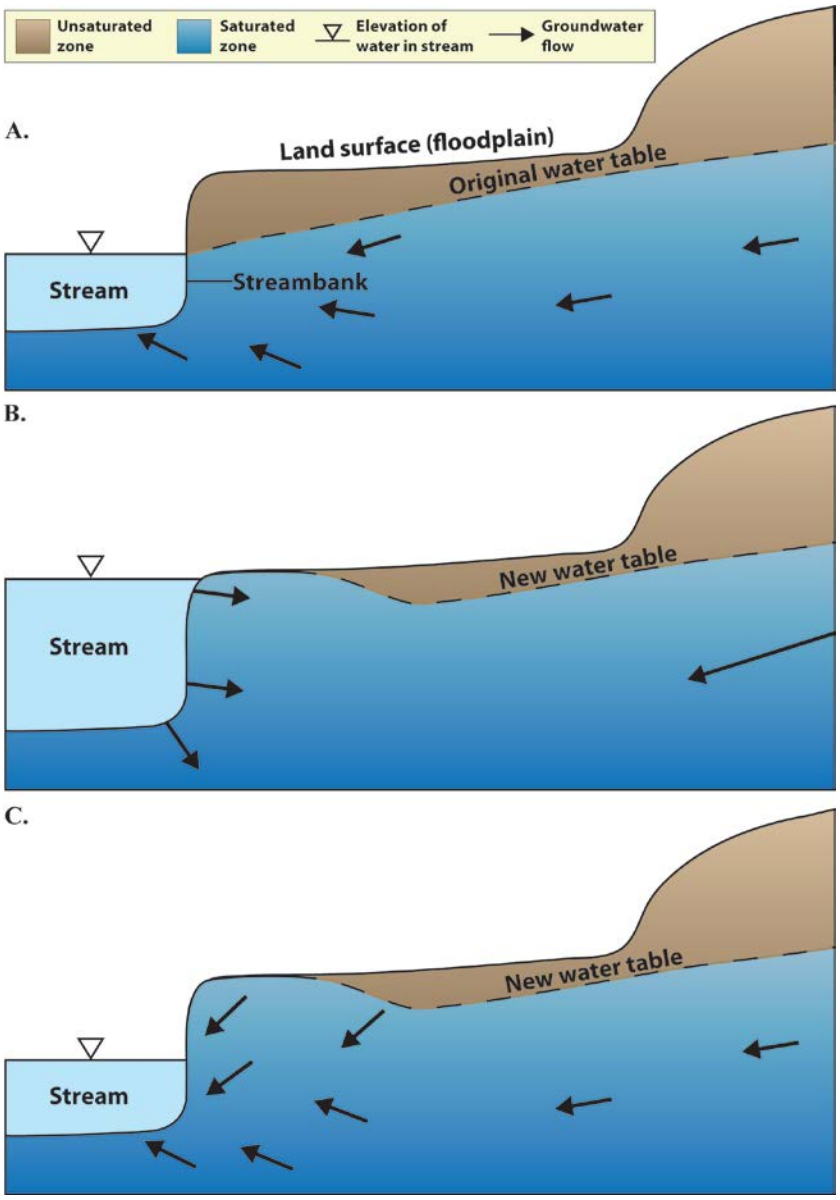
The previous section provided background on river system hydrology. In this section, we present a general overview of how streams and wetlands affect downstream waters, focusing on functions within streams and wetlands and their connectivity to rivers.

The structure and function of rivers are highly dependent on the constituent materials 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: (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.

2.3.1 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) identify three functions, or general mechanisms of action, by which streams and wetlands

Figure 2-13. The direction and magnitude of interactions between surface water and ground water can dramatically change during large hydrologic events, including floods. (A) In a hypothetical stream-floodplain cross-section, ground water flows from the alluvial aquifer to the stream before a major hydrologic event. (B) During the bank-full hydrologic event, surface water moves from the stream and becomes ground water in the alluvial aquifer. (C) After recession of the event, ground water that was stored in the alluvial aquifer during the hydrologic event flows back to the stream. This process is called bank storage, which can sustain baseflow in streams and rivers after the hydrologic event has ended. Modified from Winter et al. (1998).



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 2-1) provide a framework for understanding how physical, chemical, and biological connections between streams and wetlands and downstream waters influence river systems.

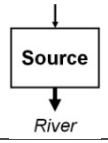
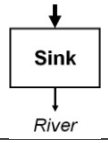
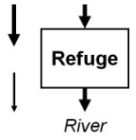
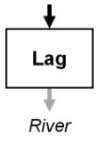
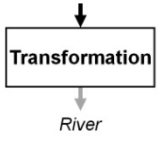
These five functions (Table 2-1) are neither static nor mutually exclusive, and often the distinctions between them are not sharp. A stream or wetland can provide different functions at the same time. These functions can vary with the material considered (e.g., acting as a source of organic matter and 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 also can have negative effects—for example, when streams and wetlands serve as sources of chemical contamination (Sections 3.4.4, 4.3.3.5, 4.3.3.6; Table 2-1). 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 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 can serve as sources of colonists for upstream tributaries).

Because many of these functions depend on import of materials and energy 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 (Sections 4.3.3.2 and 4.4.3.2): If nitrogen is imported into the wetland, the wetland can remove it by denitrification. The wetland will not serve this function, however, if nitrogen is not imported. Thus, even if a stream or wetland does not currently serve a function, it has the potential to provide that function under appropriate conditions (e.g., when material imports or environmental conditions change). Although potential functions do not actively affect downstream waters, they can be instrumental in protecting those waters from future impacts. Ignoring potential function also can lead to the paradox that degraded streams and wetlands (e.g., those receiving nonpoint-source nitrogen inputs) receive more protection than less degraded systems (Leibowitz et al., 2008).

Three factors influence the effect that material and energy fluxes from streams and wetlands have on downstream waters: (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 or wetland (e.g., a specific ephemeral stream) might be small, but the aggregate contribution by an entire class of streams or wetlands (e.g., all ephemeral streams in the river network) might be substantial. Integrating contributions over time also might be necessary, taking into account the frequency, duration, and timing of material export and delivery.

Table 2-1. Functions by which streams and wetlands affect material and energy fluxes to downstream waters. Arrows indicate material and energy imports to and exports from a stream or wetland, in terms of mass or energy; arrow widths represent relative material mass or energy and differences in arrow shades represent timing (lag) or composition (transformation) changes. Imports to 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 and energy can move downstream, upstream, or laterally into streams and wetlands. Examples of commonly exchanged materials and energy include water, heat energy, nutrients, contaminants, sediment, particulate organic matter, organisms, and reproductive propagules; note that exchange of materials and energy between streams and wetlands and downstream systems can result in positive or negative effects on downstream waters.

Function	Definition	Examples
	Net increase in a material or energy 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 or energy 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 or energy 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 or energy without affecting cumulative flux (exports = imports); delivery is delayed and can be prolonged	*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 or energy into a different form; the amount of the base material or energy is unchanged (base exports = base imports), but its composition (e.g., 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)

Considering the cumulative material fluxes that originate from a specific stream or wetland, rather than the individual materials separately, is essential in understanding the effects of material fluxes on downstream waters (Section 1.2.3).

In general, the more frequently a material is delivered to a 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. In addition, some materials are more important in defining the structure and function of a river. Using the same 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). Another example is salmon migrating to a river: They can serve as a keystone species to regulate other populations and as a source of marine-derived nutrients (Schindler et al., 2005).

2.3.2 Connectivity and Transport of Materials to and from Streams and Wetlands

2.3.2.1 Connectivity and Isolation

The functions discussed above represent general mechanisms by which streams and wetlands influence downstream waters. For these altered material and energy 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). That connectivity among river-system components, including streams and wetlands, plays a significant role in the structure and function of these systems is not a new concept. In fact, much of the theory developed to explain how these systems work focuses on connectivity and linkages between system components (e.g., Section 1.2; 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 (Section 2.2.1), water movement through the river system (Figure 2-6) 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).

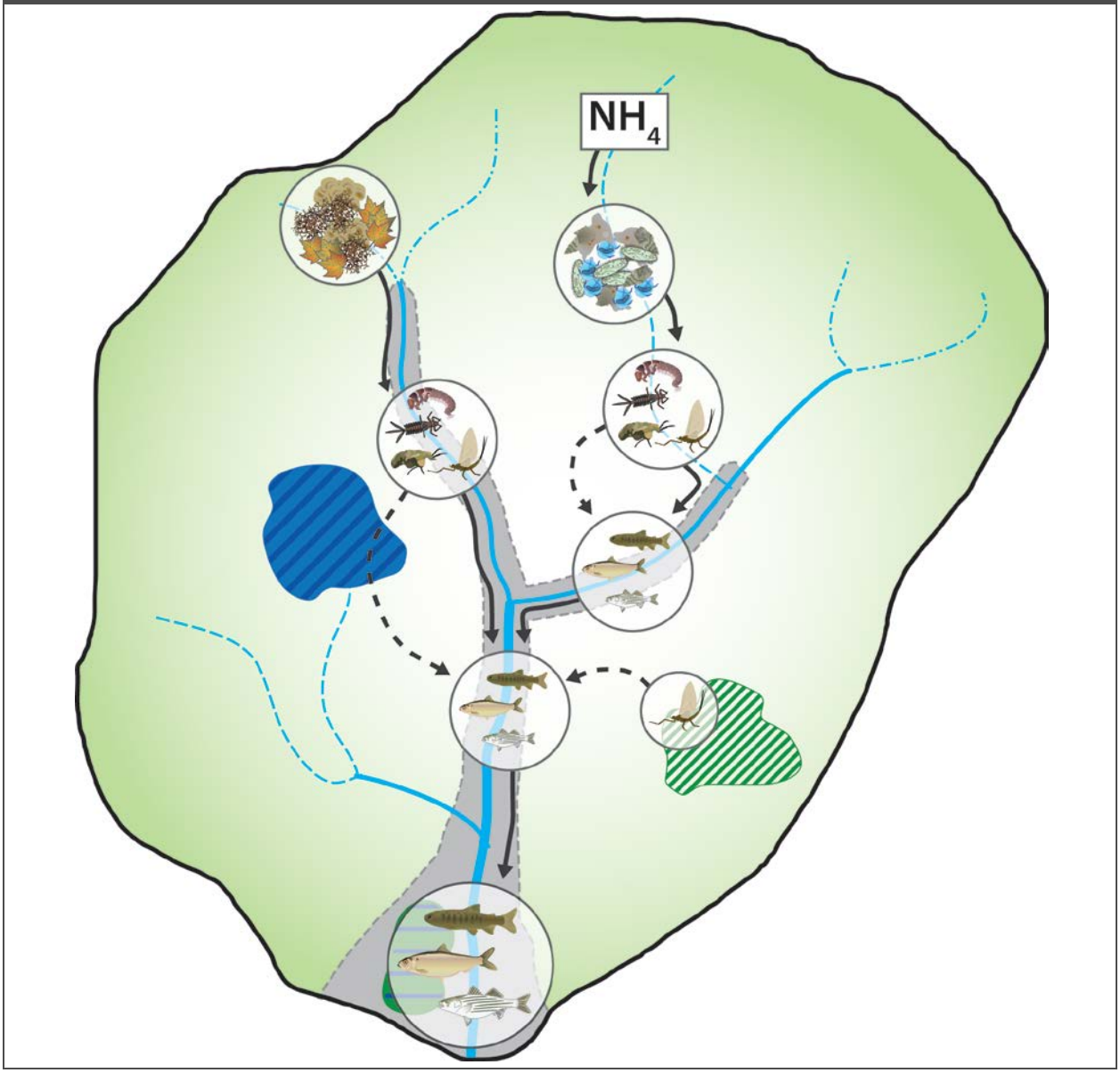
Ecosystem function within a river system is driven by interactions between the river system's physical environment and the diverse biological communities living within it (Wiens, 2002; Schroder, 2006). Thus, river system structure and function also depend on biological connectivity among the system's populations of aquatic and semiaquatic organisms. Biological connectivity refers to the movement of

organisms, including transport of reproductive materials (e.g., seeds, eggs, genes) and dormant stages, 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 (Sections 3.5, 4.3.4, and 4.4.4). Movements include dispersal, or movement away from an existing population or parent organism; migration, or long-distance movements occurring seasonally; 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); active movement with or against water flow (e.g., upstream fish migration); or active movement over land (for organisms capable of terrestrial dispersal) or through the air (for birds or insects capable of flight; Figure 1-1B). Thus, biological connectivity can occur within aquatic ecosystems or across ecosystem or watershed boundaries, and it can be multidirectional. For example, organisms can move downstream from perennial, intermittent, and ephemeral headwaters to rivers; upstream from estuaries to rivers to headwaters; and 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 our focus is on connections among components of aquatic systems (Section 1.3).

As noted in Section 2.2.3, 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 (Table 2-1). Connectivity between streams and wetlands provides opportunities for material and energy fluxes to be altered sequentially by multiple streams and wetlands as the materials are transported downstream. The aggregate effect of these sequential fluxes determines the proportion of material that ultimately reaches the river. The form of the exported material can change as it moves down the river network (Figure 2-14), 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 (Figure 2-14). Those invertebrates can drift farther downstream and be eaten by juvenile fish that eventually move into the mainstem of the river, where they continue to feed and grow.

The assessment of stream and wetland influence on rivers also is complicated by the cumulative time lag resulting from these sequential transformations and transportations. For example, removal of nutrients by streambed algal and microbial populations, subsequent feeding by fish and insects, and release by excretion or decomposition delays the export of nutrients downstream (Figure 2-14).

Figure 2-14. 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 incorporated into algal biomass (at right). Macroinvertebrates consume these basal food resources and transform them into biomass, which in turn is eaten and transformed into fish biomass in both local and downstream reaches.



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 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 nonhydrologic 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 or isolation and the five general functions (sources, sinks, refuges, lags, and transformations; Table 2-1) on downstream waters, dimensions of time and space must be considered. Water or organisms transported from distant headwater streams or wetlands generally will take longer to travel to a larger river than materials transported from streams or wetlands near the river (Section 2.4.2). This can introduce a lag between the time the function occurs and the time 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 be greater for terminal source streams, compared to higher order or lateral source streams. This is one reason why watersheds of terminal source streams often provide the greatest proportion of water for major rivers. Connectivity, however, results from many interacting factors (Section 2.4.5). For example, the relationship between stream number and order can vary with the shape of the watershed and the configuration of the network (Section 2.4.2). Thus, caution must be exercised when generalizing about these spatial and temporal relationships. Spatial and temporal variability of connectivity is discussed below, and the factors influencing them are considered in Section 2.4.

2.3.2.2 Spatial and Temporal Variability of Connectivity

Connectivity is not a fixed characteristic of a system, but varies over space and time (Ward, 1989; Leibowitz, 2003; Leibowitz and Vining, 2003). Variability in hydrologic connectivity results primarily from the longitudinal (Figures 2-8 and 2-10) and lateral (Figure 2-12) expansion and contraction of the river network and transient connection with other components of the river system (Section 2.2.3). The variability of connectivity can be described in terms of frequency, duration, magnitude, timing, and rate of change (Section 1.2.2).

The expansion and contraction of river networks affect the extent, magnitude, timing, and type of hydrologic connectivity. For example, intermittent and ephemeral streams (Figure 2-7) flow only during wetter seasons (Section 2.4) 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, 2007). 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 (Figures 2-9B

and B-5; Levick et al., 2008). Expansion and contraction also affect the magnitude of connectivity because larger flows provide greater potential for material transport (e.g., Section 3.3.2).

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, whereas intermittent streams have seasonal connectivity. The temporal characteristics of connectivity for ephemeral streams depend on the duration and timing of storm events (Figure B-10). 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, non-floodplain wetlands could have connectivity with other wetlands or streams through surface spillage (Leibowitz and Vining, 2003; Rains et al., 2008). When spillage ceases due to drier conditions, hydrologic connectivity could only occur through ground water (Rains et al., 2006; Rains et al., 2008).

When the flow of water mediates dispersal, migration, and other forms of biotic movement, 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 (Junk et al., 1989; Smock, 1994; Tockner et al., 2000; Robinson et al., 2002; Tronstad et al., 2007). Factors other than hydrologic dynamics also can 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 sizes 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 (Section 2.4.4; Semlitsch and Bodie, 2003).

Finally, just as connectivity from temporary or seasonal wetting of channels can affect downstream waters, temporary or seasonal drying also can affect river networks. Riverbeds or streambeds that temporarily dry up are used by aquatic organisms that are specially adapted to wet and dry conditions, and can serve as egg and seed banks for several organisms, including aquatic invertebrates and plants (Steward et al., 2012). These temporary dry areas also can 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).

2.4 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 four key factors—climate-watershed characteristics, spatial distribution patterns, biota, human activities and alterations. These are by no means the only factors influencing connectivity, but they illustrate how many different variables shape physical, chemical, and biological connectivity. We also examine how interactions among different factors influence connectivity, using as an example wetlands in the prairie pothole region.

2.4.1 Climate-Watershed Characteristics

The movement and storage of water in watersheds varies with climatic, geologic, physiographic, and edaphic characteristics of river systems (Winter, 2001; Wigington et al., 2013). 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 that is heavily influenced by precipitation timing and form (e.g., rain, snow), and rainfall intensity.

Annual runoff generally reflects water surplus and varies widely across the United States (Figure 2-15). Seasonality of water surplus during the year determines when and for how long runoff and ground-water 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 (Section B.5), whereas the West Coast and Pacific Northwest receive most precipitation during the winter season (Wigington et al., 2013). 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 water surplus (Section 2.2.3; Figure 2-10), when conditions for flooding are most likely. Typically, the occurrence of ephemeral and intermittent streams is greatest in watersheds with low annual runoff and high water surplus seasonality but also is 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. Infiltration-excess overland flow occurs when rainfall intensity exceeds watershed surface infiltration, and it can be an important mechanism in providing water to wetlands and river networks (Goodrich et al., 1997; 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 (Section B.5). 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 profoundly influence river network drainage patterns, distribution of wetlands, and ground-water and surface-water flowpaths. Winter (2001) described six generalized hydrologic landscape forms (Figure 2-16) common throughout the United States. Mountain

Figure 2-15. 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 are 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. The varied runoff patterns in the five rivers result from divergent climate, geology, and topography.

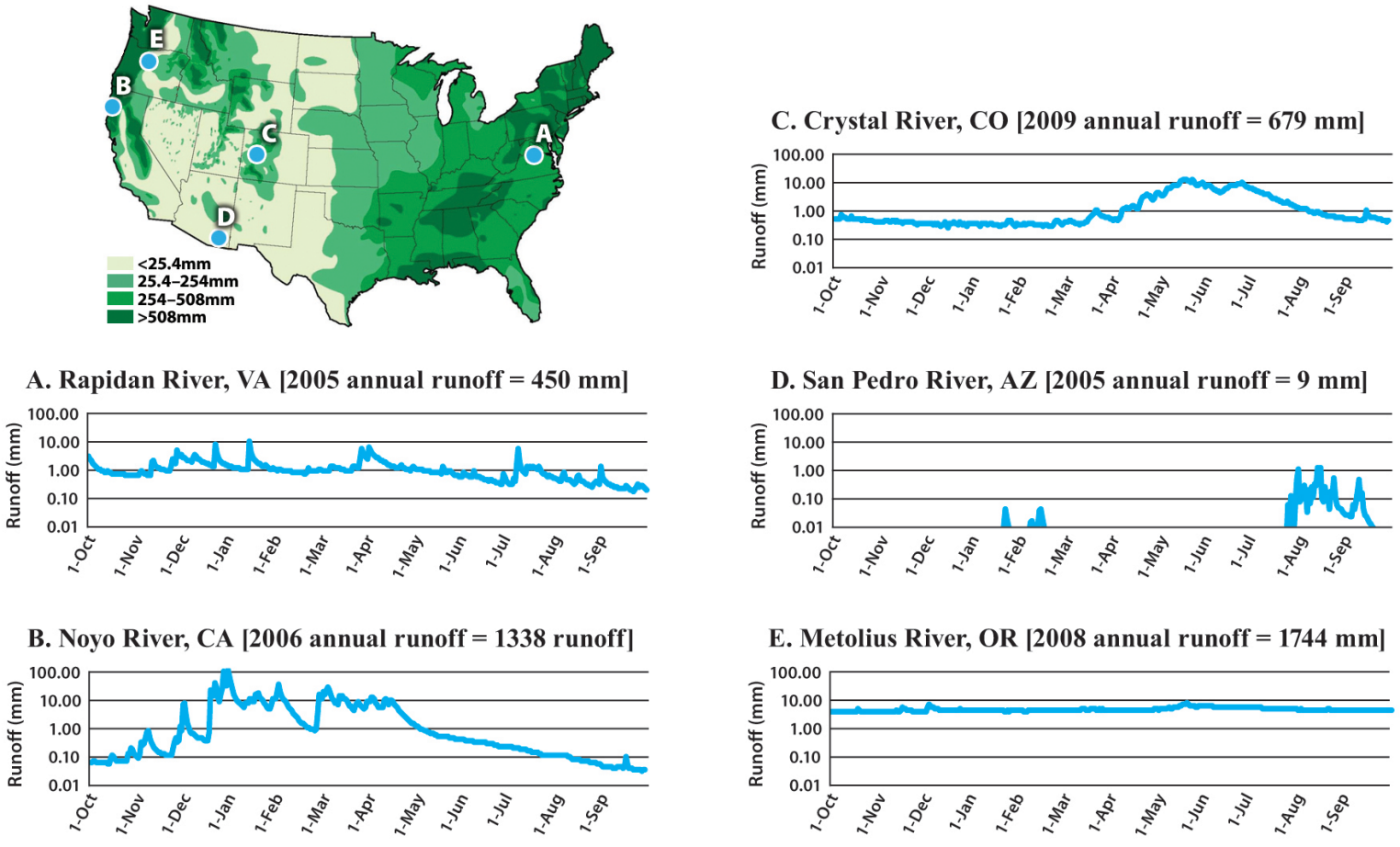
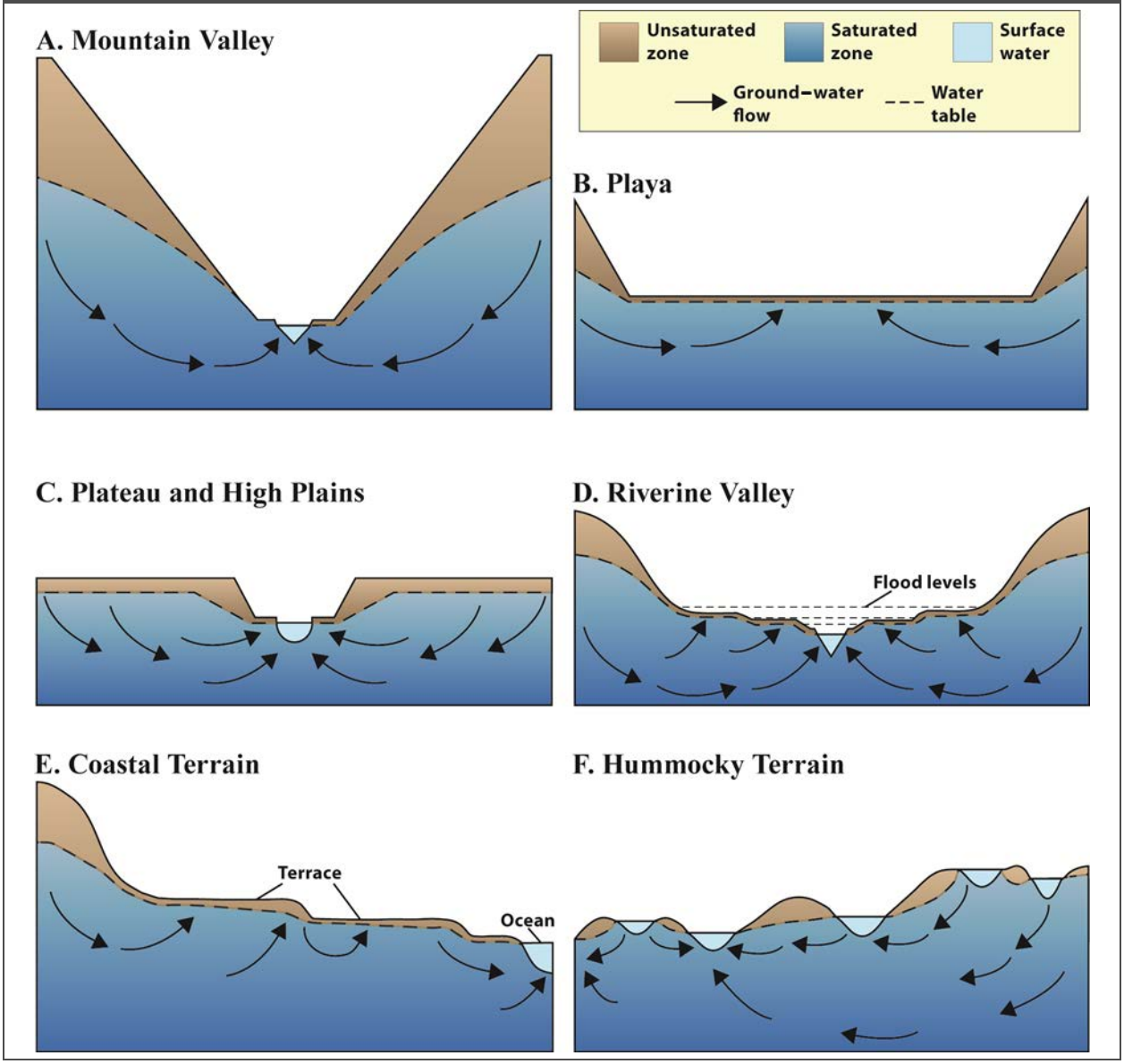


Figure 2-16. Generalized hydrologic landscape forms. (A) Mountain Valley: narrow uplands and lowlands separated by large steep valley sides; (B) Playa: large broad lowland separated from narrow uplands by steeper valley sides (playas and basins of interior drainage); (C) Plateau and High Plains: small 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).



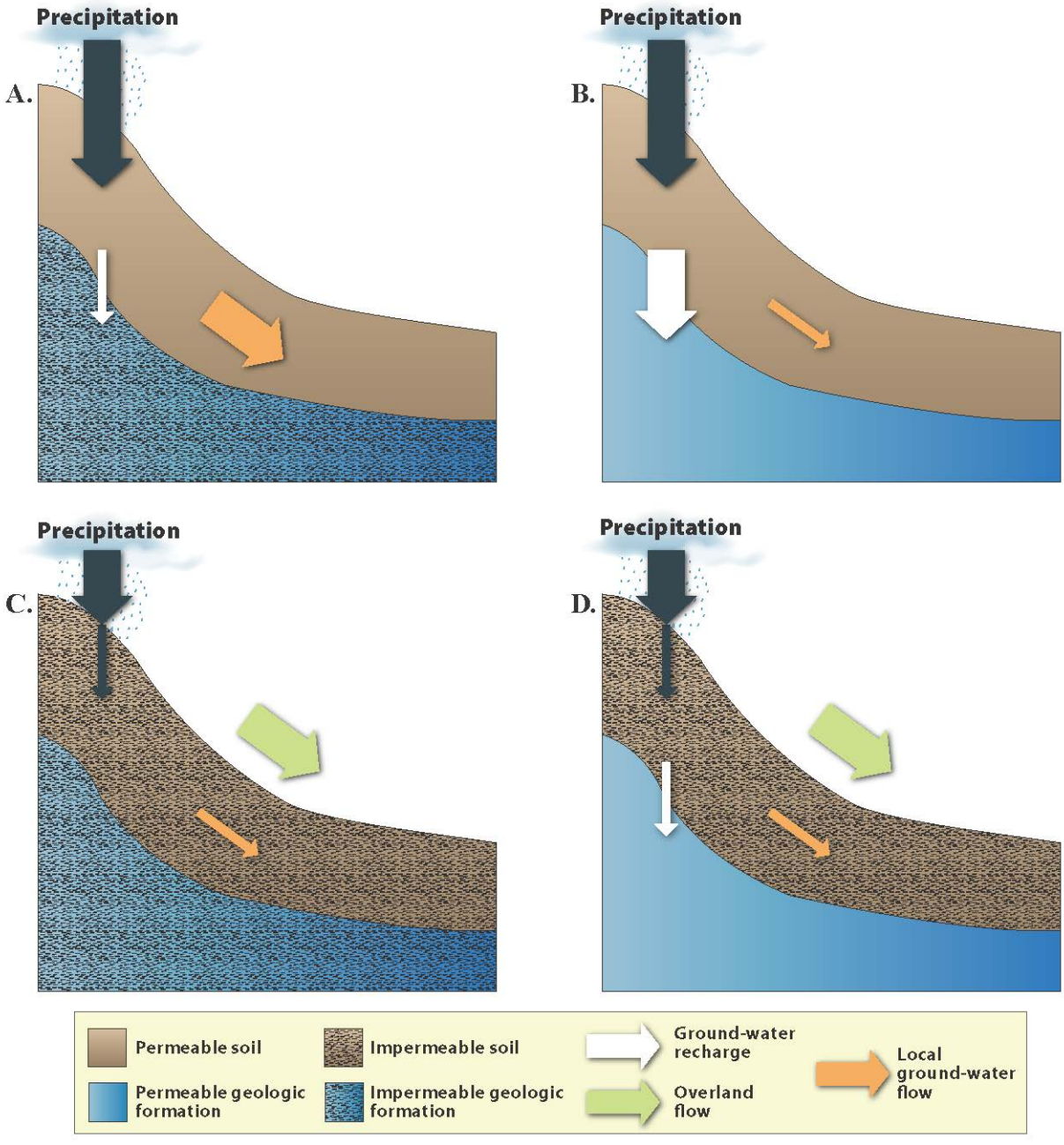
Valleys (Figure 2-16A) and Plateaus and High Plains (Figure 2-16C) have constrained valleys through which streams and rivers flow. The Mountain Valleys form has proportionally long, steep sides with narrow to nonexistent floodplains resulting in the rapid movement of water downslope. In contrast, Riverine Valleys (Figure 2-16D) have extensive floodplains that promote strong surface-water,

hyporheic water, and alluvial ground-water 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 (Figure 2-16D). Local ground-water flowpaths are especially important in Hummocky Terrain (Figure 2-16F). Constrained valleys, such as the Mountain Valley landform (Figure 2-16A), have limited opportunities for the development of floodplains and alluvial aquifers, whereas unconstrained valleys, such as the Riverine Valley landform (Figure 2-16D), provide opportunities for the establishment of floodplains. Some river basins can be contained within a single hydrologic landscape form, but larger river basins commonly comprise complexes of hydrologic landscape forms. 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-Riverine Valley complex.

Floodplain hydrologic connectivity to rivers and streams occurs primarily through overbank flooding, shallow ground-water flow, and hyporheic flow (Section 2.2). Water-table depth can influence connectivity across a range of hydrologic landscape forms, but 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 ground-water 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 a complex interaction of fluvial processes forms floodplains, 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 tends 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 important determinants of hydrologic flowpaths (Figure 2-17). Permeable soils promote infiltration that results in ground-water hydrologic flowpaths (Figures 2-17A and 2-17B), whereas the presence of impermeable soils with low infiltration capacities is conducive to overland flow (Figures 2-17C and 2-17D). In situations in which ground-water 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 (Figure 2-17A).

Figure 2-17. 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.



These local ground-water flowpaths connect portions of watersheds to nearby wetlands or streams (Figure 2-3). Alternatively, if a deep permeable geologic material (an aquifer) is present, water is likely

to move farther downward within watersheds and recharge deeper aquifers (Figure 2-17B). The permeability of soils and geologic formations both can influence the range of hydrologic connectivity between non-floodplain 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 (Figure 2-18A); a wetland can be connected to downstream waters by transient surface-water flows through swales (Figure 2-18B) or by shallow ground-water flows (Figure 2-18C); or a wetland can be hydrologically isolated from downstream waters (Figure 2-18D) because it recharges a deep ground-water 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 (Figure 2-15).

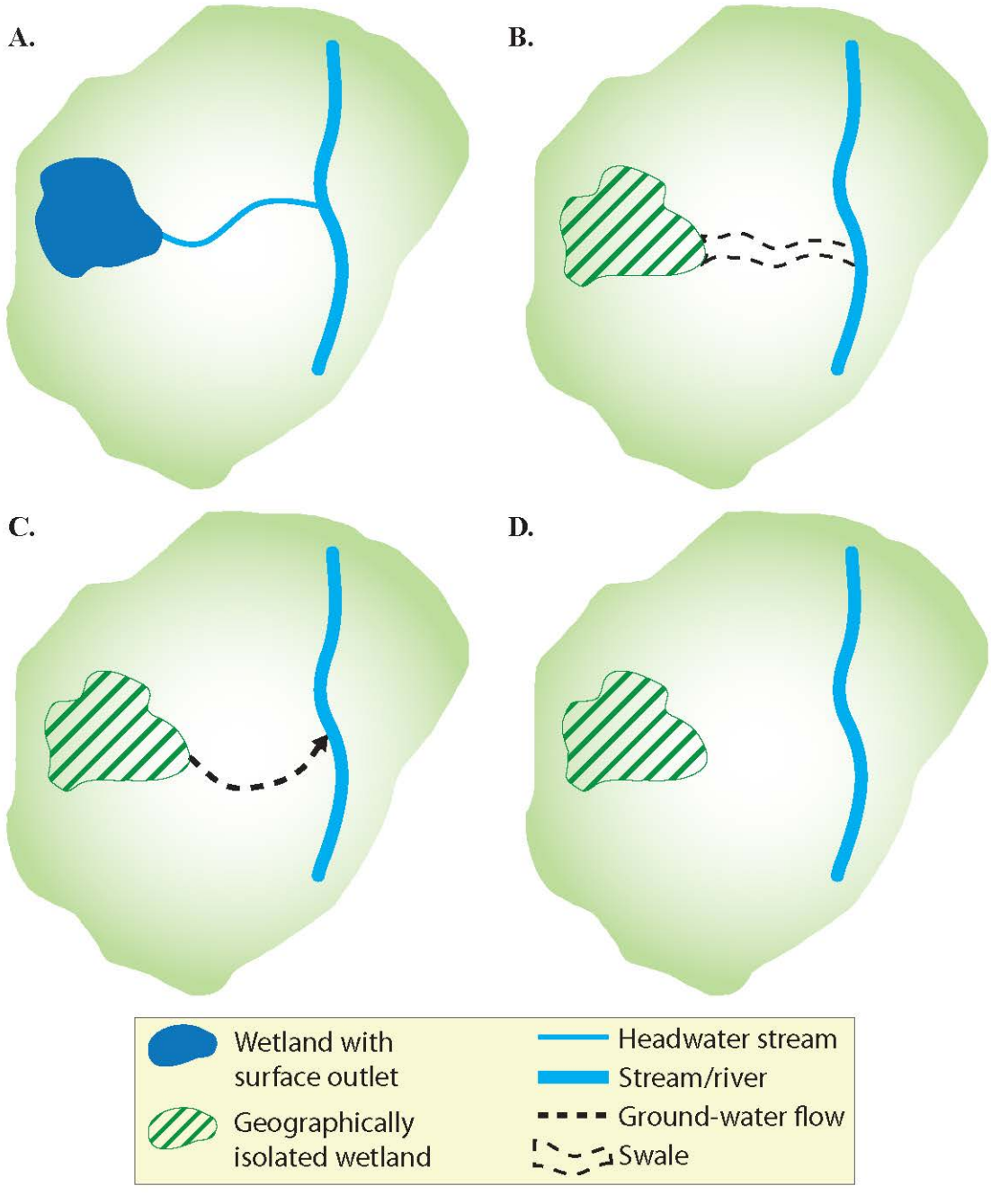
The hydrograph for the Rapidan River in Virginia (Figure 2-15A) illustrates the uniform annual precipitation pattern of the East (with small variations due to increased evapotranspiration in the summer months) interacting with a steep Blue Ridge Mountain watershed comprising metamorphic bedrock with 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 watershed in California (Figure 2-15B) has highly seasonal water surplus because rainfall occurs primarily from November through May and the impermeable bedrock prevents precipitation water from moving to deep ground water. 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 (Figure 2-15C) 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 melting of snow in the basin's higher elevations during the winter and subsequent melting 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 is low (Figure 2-15D), and short, intense rainstorms during the summer monsoons commonly drive hydrologic events (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 (Section B-5). In other San Pedro River

Figure 2-18. Types of hydrologic connections between non-floodplain wetlands and streams or rivers. (A) 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 ground-water flow (flowpath can 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.



mainstem reaches, ground-water flow from regional and alluvial aquifers supports baseflow (Dickinson et al., 2010). Like the Crystal River, the Metolius River in Oregon (Figure 2-15E) 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 near 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 perennial.

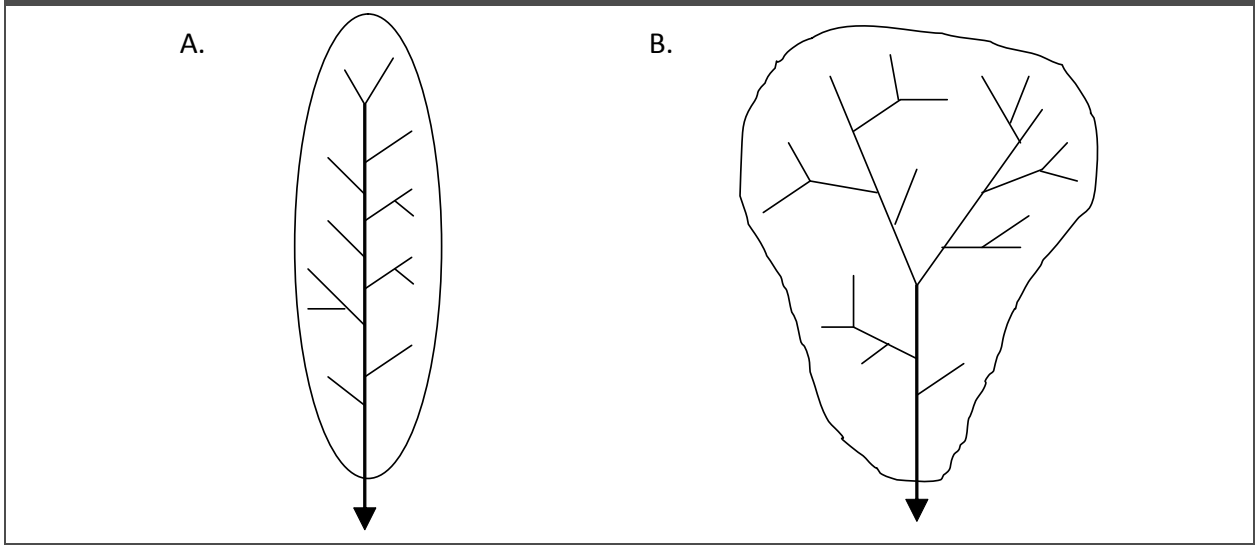
2.4.2 Spatial Distribution Patterns

Climate and watershed characteristics directly affect spatial and temporal patterns of connectivity between streams and wetlands and rivers by influencing the timing and extent of river network expansion and contraction. They also influence 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 eventually would reach the river. Because streams and rivers are not pipes (Section 2.2.3; Bencala, 1993), 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 web (Figure 2-14). Similarly, higher order streams generally are 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 (Section 3.2); 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 (Figure 2-19A); compact basins tend to have dendritic networks with tree-like branching, where streams gradually increase in size before joining the mainstem (Figure 2-19B). This network configuration describes the incremental accumulation of drainage area along rivers, and therefore provides information 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 also is more likely to have a lower stream order

Figure 2-19. Major types of basin shapes and network configurations. (A) A rectangular basin with trellis network, and (B) a compact basin with a dendritic network.



than one in a dendritic network. For example, the lowest reach in the trellis network in Figure 2-19A is a third-order stream, while that of the dendritic network (Figure 2-19B) is a fourth-order stream.

Distance also affects connectivity between non-floodplain 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 non-floodplain wetlands have surface-water outputs (e.g., depressions that experience surface-water spillage or ground-water seeps; Figure 2-18B), the probability that surface water will infiltrate or be lost through evapotranspiration increases with distance. For non-floodplain wetlands connected through ground-water flows, less distant areas are generally connected through shallower flowpaths (Figure 2-5), assuming similar soil and geologic properties. These shallower ground-water flows have the greatest interchange with surface waters (Section 2.2.2) and travel between points in the shortest amount of time. Although elevation is the primary factor determining areas that are inundated through overbank flooding, connectivity with the river generally will be higher for riparian/floodplain wetlands located near the river's edge compared with riparian/floodplain wetlands occurring near the floodplain edge.

Distance from the river network also influences biological connectivity among streams and wetlands. For example, mortality of an organism due to predators and natural hazards generally increases with the distance it has to travel to reach the river network. The likelihood that organisms or propagules traveling randomly or by diffusive mechanisms such as wind will arrive at the river network generally 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 2-20 compares the spatial distribution of wetlands and streams to the river network in six different landscape settings. The figure shows landscape settings ranging from no nearby streams and dense small wetlands (Figure 2-20A), to a few nearby streams with high wetland density (Figures 2-20B and 2-20C), to less spatially uniform wetlands (Figure 2-20D), to areas with higher drainage densities and riparian (Figure 2-20E) or larger, more extensive (Figure 2-20F) wetlands. The maps in Figure 2-20 are single examples of these various settings, so they 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 having many wetlands and relatively low drainage density (Figures 2-20B, 2-20C, and 2-20D), the distances between individual wetlands and the stream can vary greatly. In contrast, the distances in areas having a higher drainage density (Figure 2-20E and 2-20F) are shorter and vary less. All factors being equal, wetlands closer to the stream network will have greater hydrologic and biological connectivity than wetlands located farther from the same network.

2.4.3 Biota

Biological connectivity results from the interaction of physical characteristics of the environment—especially those facilitating or restricting dispersal—and species' traits or behaviors, such as life-cycle requirements, dispersal ability, or responses to environmental cues (Section 1.2.2). Thus, the types of biota within a river system are integral in determining the river system's connectivity, and landscape features or species traits that necessitate or facilitate movement of organisms 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 also can exploit temporary hydrologic connections

Figure 2-20. Examples of different landscapes showing interspersion of wetlands and streams or rivers. (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) might not appear on maps. Source: National Wetlands Inventory Wetlands Mapper (http://www.fws.gov/wetlands/Data/Mapper.html).

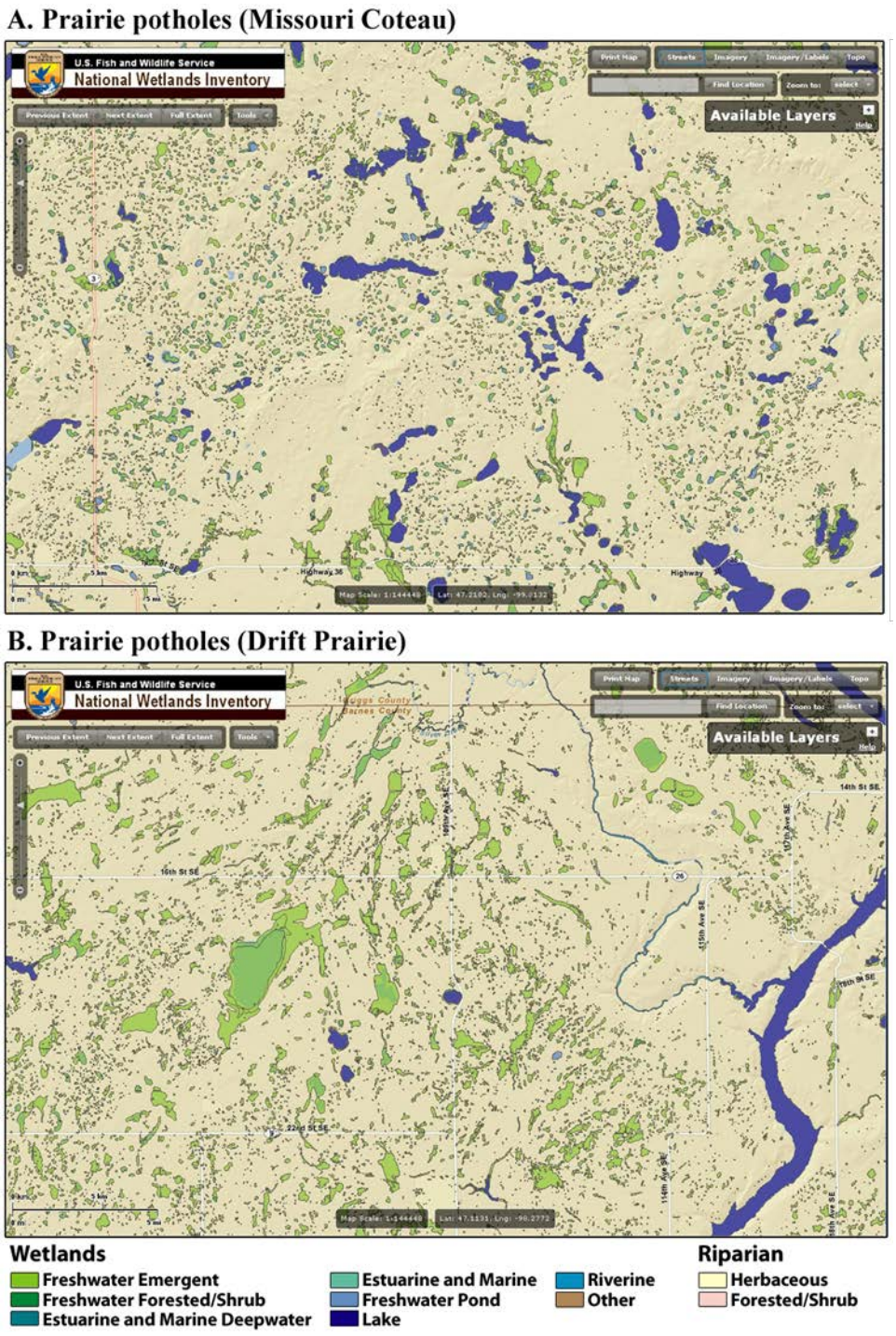
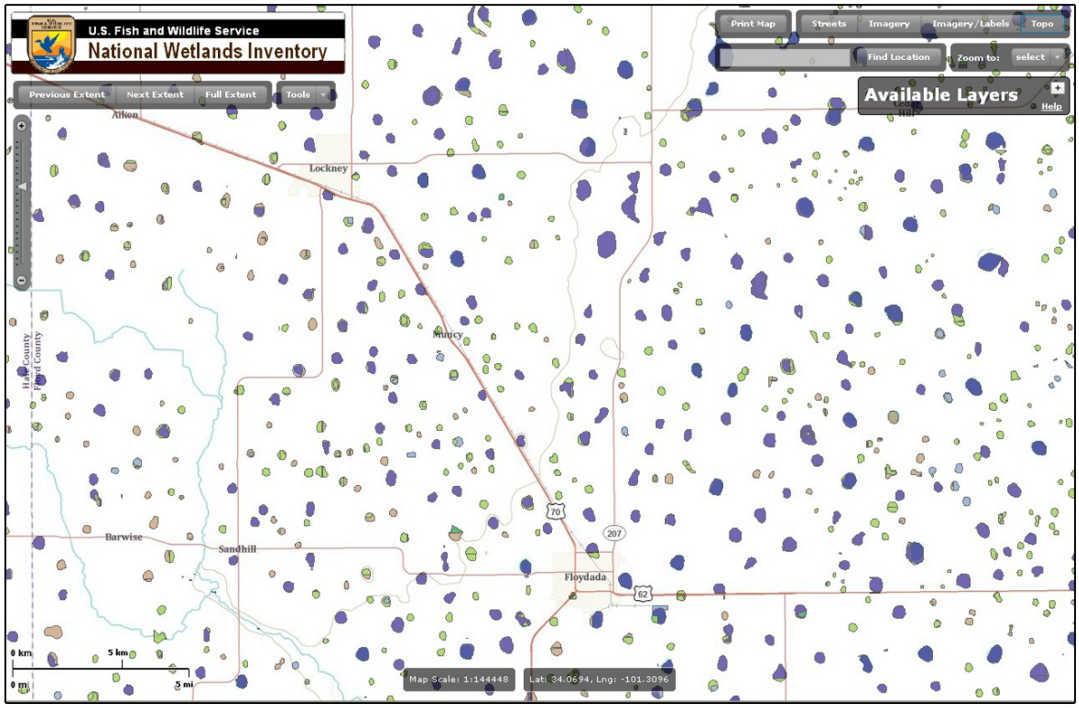
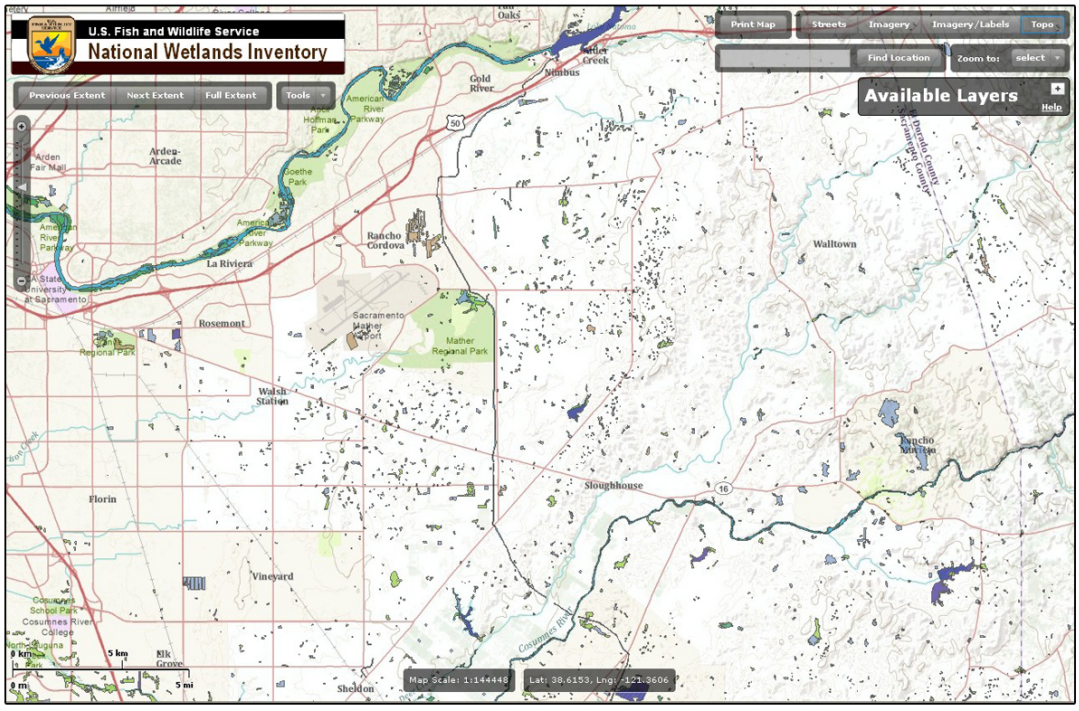


Figure 2–20. Examples of different landscapes showing interspersion of wetlands and streams or rivers (continued).

C. Playa



D. Vernal pools



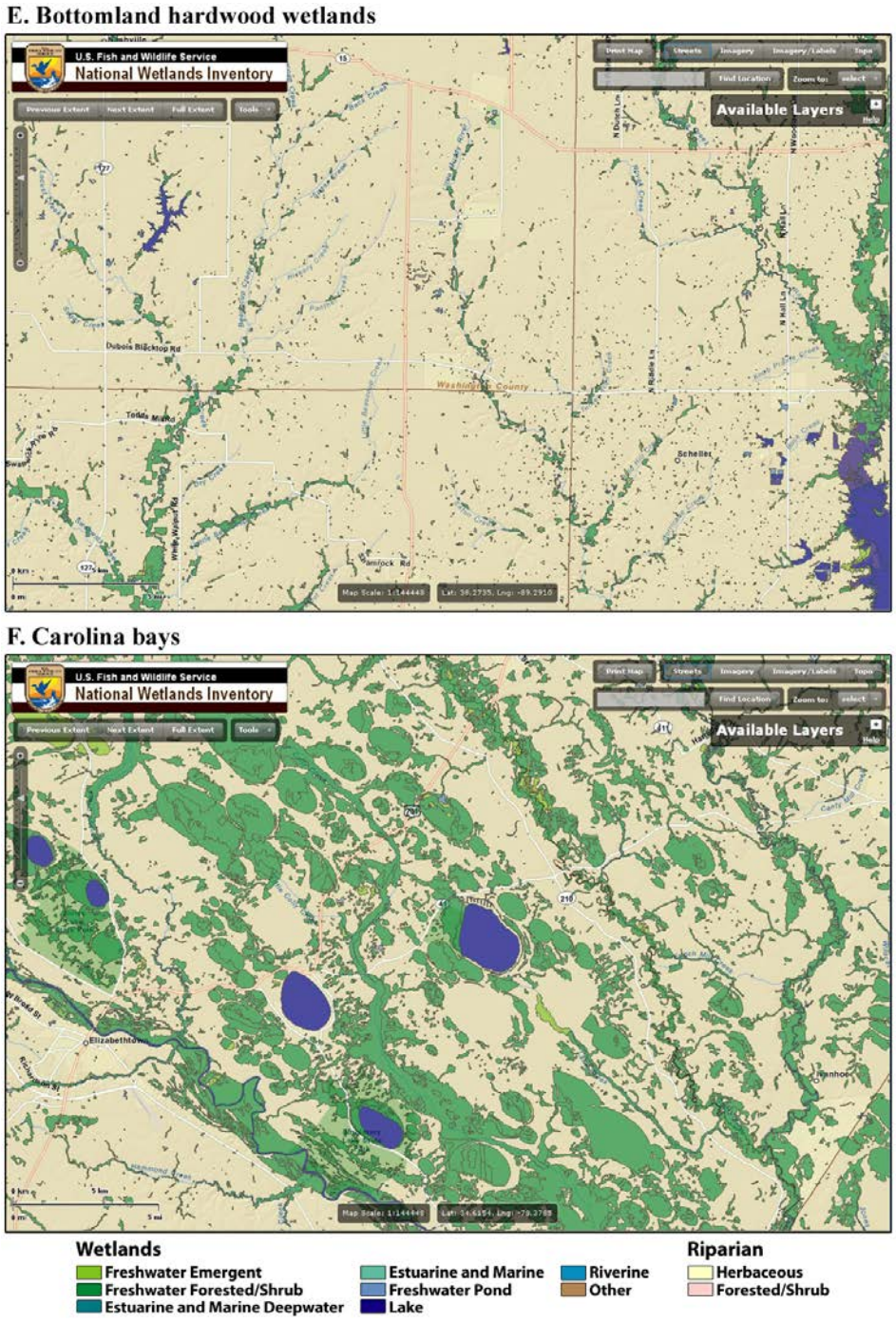
Wetlands

- Freshwater Emergent
- Freshwater Forested/Shrub
- Estuarine and Marine Deepwater
- Estuarine and Marine
- Freshwater Pond
- Lake
- Riverine
- Other

Riparian

- Herbaceous
- Forested/Shrub

Figure 2–20. Examples of different landscapes showing interspersion of wetlands and streams or rivers (continued).



between rivers and floodplain wetland habitats caused by flood pulses (Section 1.2.1; Junk et al., 1989; Tockner et al., 2000), moving into these wetlands to feed, reproduce, or avoid harsh environmental conditions and then returning to the river network (Copp, 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 (Section 1.2.2). 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 move or 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).

The fundamental influence that biological connectivity has on species distributions can last long after a system is disconnected. In a global analysis of freshwater fish diversity, Dias et al. (2014) found that paleoconnected drainage basins (basins that had hydrologic connections during the most recent glacial maximum) currently have greater species richness and lower endemism and beta diversity than paleodisconnected basins. This study indicates that hydrologic connectivity, by allowing dispersal of aquatic organisms, can have a long-lasting legacy effect on the geographic distribution of species.

The examples discussed above illustrate how environmental characteristics provide the physical structure through which biological connectivity occurs, as mediated by biological traits and behavior. The physical structure of the environment is not static, however, and also can be altered by biological behavior. The beaver (*Castor canadensis*) is a keystone species that builds dams that can alter connectivity in several ways. Most obviously, beaver dams reduce hydrologic connectivity by impounding streams and modifying conditions above the dam from lotic to lentic. The area impounded by beaver dams can be large: In the Kabetogama Peninsula of Minnesota, impounded area accounted for up to 13% of the landscape, with an average pond area of about 4 ha (Johnston and Naiman, 1990a, b). In a review of the effects of beaver on stream ecosystems, Collen and Gibson (2001) noted that, although the hydrologic effects of a single beaver dam can be small, the impact of a series of dams on streams can be significant; for example, up to 30% of the water in an Oregon catchment was impounded by beaver dams. Such dams can directly affect material transport (e.g., the ability of the stream to carry sediment is reduced) and alter biogeochemical characteristics (Naiman et al., 1994; Collen and Gibson, 2001). Beaver dams also can affect biological connectivity, for example, by obstructing upstream migration, and cause changes in fish distributions (Collen and Gibson, 2001).

2.4.4 Human Activities and Alterations

Human activities frequently alter connectivity between headwater streams, riparian/floodplain wetlands, non-floodplain wetlands, and downgradient river networks (Sections 1.2.4, 3.2, 4.3, and 4.4). In doing so, they alter 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 become discernible only following human-mediated changes in degree of connectivity. These human-mediated changes can increase or decrease hydrologic and biological connectivity (or,

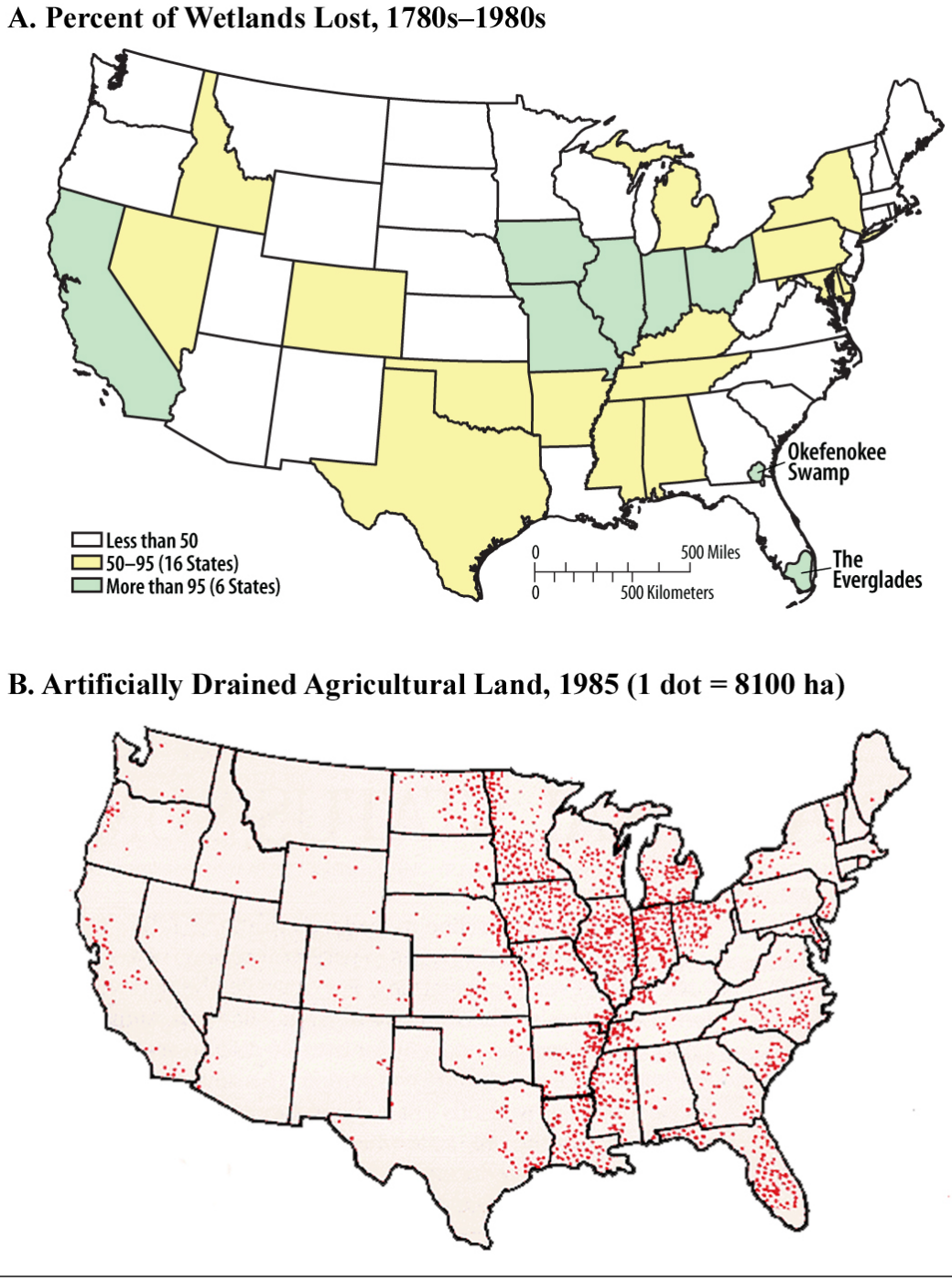
alternatively, decrease or increase hydrologic and biological isolation). For example, activities and alterations such as dams, levees, water abstraction, piping, channelization, and burial can reduce hydrologic connectivity between streams and wetlands and rivers, whereas activities and alterations such as wetland drainage, irrigation, impervious surfaces, interbasin transfers, and channelization can increase hydrologic 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 frequency and magnitude 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, 1984). Dams, however, can have the opposite effect with respect to natural lakes: increasing their biological connectivity with respect to invasive species by adding impoundments that decrease average distances between lakes and serving as stepping stone habitat (Johnson et al., 2008). 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 (via life history, behavioral, and morphological characteristics) 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. Reducing overbank lateral flow can affect downstream water quality, because overbank flow deposits sediment and nutrients that otherwise remain entrained in the river (Hupp et al., 2009).

The greatest human impact on riparian/floodplain wetlands and non-floodplain wetlands has been through wetland drainage (Figure 2-21), primarily for agricultural purposes. Estimates show that, in the conterminous United States, states have lost more than half their original wetlands, with some 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. In the Des Moines lobe of the prairie pothole region, where more than 90% of the wetlands have been drained, a disproportionate loss of smaller and larger wetlands has occurred. Accompanying this loss have been significant decreases in perimeter-area ratios—which are associated with greater biogeochemical processing and ground-water recharge rates—and increased

Figure 2-21. 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).



mean distances between wetlands, which reduces biological connectivity (Van Meter and Basu, In press). Wetland drainage 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). Ground-water withdrawal can have an effect similar to drainage on some wetlands, which can affect wetland connectivity by reducing the number of wetlands. Of particular concern in the arid Southwest is that ground-water withdrawal can decrease regional and local water tables, reducing or altogether eliminating ground-water-dependent wetlands (Patten et al., 2008). Ground-water withdrawal, however, also can increase connectivity in areas where that ground water is applied or consumed.

Particularly noteworthy is that restoration of hydrologic connectivity, especially 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).

2.4.5 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 Sections 5.4 and B.3.

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 km^2 area containing the sites had a temporary surface-water connection to at least one other wetland, including 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 ground water, but ground-water 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 (Section 2.4.4).

Beyond these regional trends in relief and precipitation, local variation in the occurrence of intermittent surface-water connections should be influenced strongly by ground-water dynamics. The ground-water hydrology of prairie potholes has been well investigated at several sites (e.g., Winter et al., 1998; Winter and Rosenberry, 1998). The specific ground-water interactions—and hence the effects of ground-water movement on spillage or mixing, however, are unknown for most prairie potholes. All else being equal, ground-water discharge wetlands should receive more water, and so should have a higher probability of spillage, than ground-water recharge wetlands because 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. Climatic changes that have occurred throughout the Holocene drive these cycles. Evidence, for example, exists for 20-, 22-, 50-, 100-, and 200-year climatic cycles (Ashworth, 1999). Wetland hydrology responds dramatically to these wet-dry cycles as ground-water 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.

2.4.6 Quantifying Connectivity

As previously discussed, watershed connectivity is a dynamic and scalable quantity that occurs along a gradient from highly connected to highly isolated (Ward, 1989; Euliss et al., 2004). Connectivity can be quantified using *structural* metrics of physical landscape features (e.g., watershed topography, the spatial arrangement of habitat patches), or *functional* metrics of system dynamics, which integrate information about processes and interactions that influence hydrologic flows or biological dispersal. Selection of specific metrics for quantifying connectivity depends on the purpose of the assessment, the environmental context (e.g., humid versus arid), type of connection (e.g., hydrologic, chemical, biological), spatial and temporal scale of interest, and available data (Calabrese and Fagan, 2004; Lexartza-Artza and Wainwright, 2009).

2.4.6.1 Hydrologic and Chemical Connectivity

In hydrology, connectivity research has aimed to understand how and when water volume inputs (e.g., precipitation minus water loss through infiltration, evaporation and transpiration) and moisture thresholds trigger surface and subsurface flow, thereby influencing streamflows in a given watershed (Western et al., 2001; Ali and Roy, 2010; Bracken et al., 2013). Because movement of water is the primary mechanism by which chemical substances are transported downstream, quantifying chemical connectivity is closely related to quantifying hydrologic connectivity (Michalzik et al., 2001; Borselli et al., 2008). Hydrologic connectivity research has focused on relating patterns of soil moisture following precipitation events to stream discharge (Western et al., 2001; James and Roulet, 2007; Ali and Roy, 2010) or measuring flow-process connectivity at the hillslope scale (Knudby and Carrera, 2005; Reaney, 2008; Smith et al., 2010). Although this research provides a critical understanding of how water moves through a watershed, it is only indirectly related to connectivity between small streams and rivers, or between wetlands and streams. Metrics for quantifying hydrologic connections between upstream and downstream waters have started to be explored through research characterizing the hydrologic permanence of streams (Fritz et al., 2008; Fritz et al., 2009) or mapping temporal variation in surface connections between wetlands and streams using field (McDonough et al., 2015) or remotely sensed data (Sass and Creed, 2008; Lang et al., 2012; Huang et al., 2014). More commonly, research efforts have focused on data collection methods that could inform measurement of connectivity (e.g., deriving relationships between connectivity and topography or water quality; hydrologic tracers; geostatistical modeling; and watershed, ground-water, or coupled surface water-ground water modeling).

Structural indices derived from topography can be used to predict patterns of watershed wetness. Examples include the Topographic Wetness Index (Quinn et al., 1995), which is quantified using the upslope contributing area and local slope, as well as quasi-dynamic indices that calculate the effective contributing area (**variable source area**) in a watershed (e.g., Barling et al., 1994; Tarboton, 1997; Creed and Beall, 2009). These indices could be used to predict the location of hydrologic flowpaths and areas of a watershed that might be efficient exporters of nutrients, sediment, or pollutants following heavy rainfall or snowmelt periods (Creed and Beall, 2009; Lane et al., 2009). In flatter landscapes, a more dynamic contributing area model is typically required (Shaw et al., 2013). One example is the fill-

and-spill model in which the watershed contributing area expands when wetland storage reaches capacity (fill) and wetlands overflow (spill) onto the land surface and into other surface-water bodies (Tromp-van Meerveld and McDonnell, 2006; Shaw et al., 2013; McCauley and Anteau, 2014). Other researchers have quantified basin-scale hydrologic connectivity as the ratio of flowing stream reaches connected to the outlet to the total potentially flowing stream reaches (Phillips et al., 2011; Spence and Phillips, 2015), or as transport potential in a given direction quantified by a directional connectivity index (Larsen et al., 2012). Similar to this, the volume-to-breakthrough concept quantifies connectivity as actual runoff relative to water inputs, where connectivity decreases with increased infiltration, depression storage, slope length, barriers, or other factors (Bracken and Croke, 2007).

Several other lines of research are contributing to a general understanding of connectivity between water features. Water quality indicators have been used to identify connectivity between wetlands and streams (Johnston et al., 1990; Leibowitz and Vining, 2003). Tracer experiments using ^{15}N, bromide, salt solutions, fluorescing particles, or other conservative compounds have been conducted that can inform flowpaths in aquatic systems (Mulholland et al., 2004; Bencala et al., 2011; O'Brien et al., 2012). Modeling and measuring the mass transfer efficiency of a watershed using a parameter such as the sediment delivery ratio, which describes and predicts the relationship between erosion and sediment yield in a watershed, can indicate the degree of connectivity within a watershed (Atkinson, 1995; Hooke, 2003; Bracken and Croke, 2007). Geostatistical approaches are being developed to consider how connectivity would be quantified within a branched stream network (Fagan, 2002; Ganio et al., 2005; Peterson et al., 2007). In addition, numerous mechanistic modeling and simulation tools can be modified and applied to investigate connectivity dynamics from geographically isolated wetland systems (Golden et al., 2014) and headwaters (e.g., TOPMODEL; Beven and Kirkby, 1979) to downstream surface-water systems.

Although the research community has not reached a consensus regarding the best methods or metrics to quantify or predict hydrologic or chemical connectivity (Lexartza-Artza and Wainwright, 2009; Ali and Roy, 2010; Bracken et al., 2013), future efforts to quantify connectivity using the descriptors discussed in Chapter 1 (frequency, magnitude, duration, timing, and rate of change) or other connectivity metrics will help to further refine and quantify the lines of research summarized above.

2.4.6.2 Biological Connectivity

In the quantification of biological connectivity, species traits (e.g., dispersal mode, habitat requirements, behavior) also must be considered (Calabrese and Fagan, 2004). Structural connectivity can be quantified from the physical landscape (e.g., the size, shape, and arrangement of habitat patches) assuming that the spatial configuration of habitats reflects species' ability to move between them. Functional connectivity directly incorporates information about species' movement obtained from field studies or from models to inform estimates of connectivity (Calabrese and Fagan, 2004; Wainwright et al., 2011).

Indices based on graph theory calculate connectivity using a graph to represent the landscape as a network of nodes (e.g., habitat patches) connected by edges (pathways of movement; Urban and Keitt,

2001). Such connectivity indices include the Minimum Spanning Tree (Urban and Keitt, 2001), Correlation Length (Keitt et al., 1997; Rae et al., 2007), the Integral Index of Connectivity (Pascual-Hortal and Saura, 2006), and the Probability of Connectivity (Saura and Pascual-Hortal, 2007). Graph-theory approaches can be used to assess structural or functional connectivity at multiple spatial scales (Eros et al., 2012). Specific information about habitats and focal species is incorporated by applying node weights (e.g., habitat area or quality, population abundance), edge weights (e.g., Euclidean distance, landscape resistance), or edge characteristics (e.g., direction of movement; Galpern et al., 2011). Indices derived from such graphs seek to characterize connectivity in terms of habitat (e.g., total connected habitat area), dispersal pathways (e.g., relative abundance of individuals using a pathway, path redundancy or vulnerability), or both (Rayfield et al., 2010). The Integral Index of Connectivity, for instance, incorporates patch area, the topological distance between patches and the proportion of connected patches (Pascual-Hortal and Saura, 2006), and has been successfully used to quantify connectivity within a river network at varying spatial scales for otters (Van Looy et al., 2013).

The dendritic nature of stream networks also can be explicitly integrated when considering the biological connectivity for obligate aquatic species, such as fish. The branching structure of a dendritic network (Figure 2-19B), which has a single pathway (the stream channel) between habitat patches (e.g., stream reaches), influences individual movement and population distribution and abundance, and thus the impact of disturbances and fragmentation on connectivity (Fagan, 2002; Grant et al., 2007); this can be reflected in graph-theoretic connectivity indices (Malvadkar et al., 2015). An example of a dendritic metric is the Dendritic Connectivity Index, which uses the number of barriers (e.g., culverts) and the passability of these barriers to quantify the probability that fish can move between two points in a river network (Cote et al., 2009).

2.4.6.3 Summary

This section briefly reviews the growing body of research into testable indices and metrics that represent hydrologic and biological connectivity of functional importance to downstream waters. Data availability is a critical issue, as the information content that connectivity indices provide often is related directly to their data requirements (Calabrese and Fagan, 2004; Bergsten and Zetterberg, 2013). Additionally, the many proposed connectivity indices and approaches discussed in the literature suggest that different metrics are needed to quantify different types of connectivity across diverse environments, scales, and ecosystem functionalities (Rayfield et al., 2010; Galpern et al., 2011; Bracken et al., 2013). With further development and refinement, the utilization of connectivity indices can provide graphical, quantitative assessments of connectivity.





CHAPTER 3. STREAMS: PHYSICAL, CHEMICAL, AND BIOLOGICAL CONNECTIONS TO RIVERS

3.1 Abstract

The physical structure of a river network inherently demonstrates cumulative connectivity (Section 1.2.3) 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, movement of organisms and their products, 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 sediment (clean and contaminated); as transformers of and sinks for nitrogen, carbon, and contaminants; and as providers of essential habitat for migratory animals such as anadromous salmon. Headwater streams as a class provide substantial quantities of water to larger water bodies. For example, first-order streams cumulatively 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 watersheds where headwater streams drain a unique portion of the basin (e.g., hydrology, geology, human alteration). Investigation of connections among river network components continues to be an active area of scientific research, with progress occurring in the development of river network models and connectivity metrics for quantifying connections and their downstream effects. Physical, chemical, and biological connections between headwater streams and downstream waters are fundamental to the structure and function of river networks, and additional empirical data and further breakthroughs that quantify linkages across large spatiotemporal scales will continue to enhance our understanding of river network complexity.

3.2 Introduction

In this chapter, we 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 systems and deep ground-water systems via lateral and vertical connections (e.g., Gray, 1993; Shentsis and Rosenthal, 2003; Walters et al., 2008), we focus here on longitudinal surface-water connections between streams and rivers, and on shallow subsurface-water interactions integral to surface-water connections and downstream water condition. The evidence primarily focuses on the connections between headwater streams and downstream waters, but we draw some evidence from connections of larger streams to rivers, reservoirs, lakes, and coastal waters. We consider the peer-reviewed evidence for connectivity and its consequent effects on downstream rivers in terms of physical (Section 3.3), chemical (Section 3.4), and biological (Section 3.5) connections between upstream and downstream habitats. Although we recognize that many linkages between streams and downstream waters cross physical, chemical, and biological boundaries, we have chosen this format for ease of presentation. In each section we also consider how human alteration of streams affects their connectivity and resulting effects on downstream rivers (Sections 1.2.4 and 2.4.4). In some cases, connectivity and its effects on downstream waters become more discernable with human alteration (e.g., Chin and Gregory, 2001; Wigmosta and Perkins, 2001); however, when human alterations are widespread and relatively uniform (e.g., Blann et al., 2009) attributing downstream effects to particular tributaries or parts of the river network can be more complex. Coupled human-natural systems are an area of active research (Box 3-1). Section 3.6 closes this general section with a discussion on stream-river connections by synthesizing evidence in terms of the conceptual framework (Chapter 2) and viewing streams in a connectivity gradient context (Section 1.2.2). In addition, two case studies on specific types of stream systems are in Appendix B: prairie streams (Section B.4) and southwestern intermittent and ephemeral streams (Section B.5).

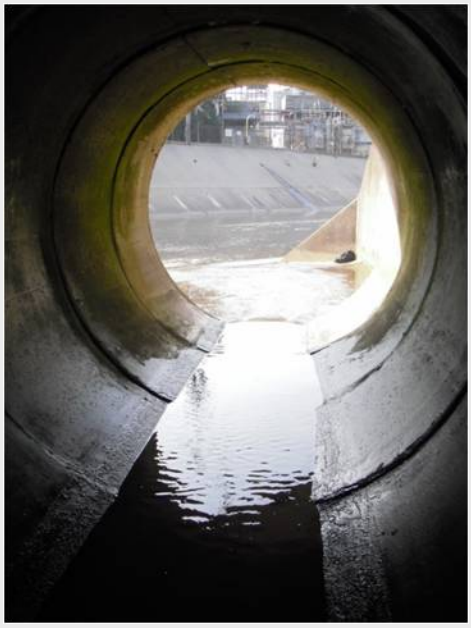
Streams range greatly in size in terms of both drainage area and discharge. In general, their abundance is inversely related to their size. First-order streams typically are most abundant, although individually they have the smallest drainage areas and shortest average stream lengths (Horton, 1945; Schumm, 1956; Ijjasz-Vasquez et al., 1993). When considering drainage area and stream length of headwater streams together, however, they can represent most of the river watershed and network. Thus, despite their small individual size, these headwater streams cumulatively can have a large influence on downstream waters (Section 1.2.3).

Some headwater streams lack channel connections to large downstream water bodies because they drain closed or endorheic basins. Endorheic basins have no surface outflows to oceans, but terminate as inland lakes, seas, playas, or pans (Shaw and Bryant, 2011). Although endorheic streams are common in some areas (Section B.5), endorheic basins represent only approximately 2% of the North American continent (Vörösmarty et al., 2000) and generate 0.15% (9 of 5,892 $km^3\ yr^{-1}$) of its annual discharge (Fekete et al., 2002).

Box 3-1. Urban Streams

Urban development alters the structure and function of stream ecosystems in numerous ways (Paul and Meyer, 2001; Walsh et al., 2005). Although the specific symptoms of what Walsh et al. (2005) referred to as the "urban stream syndrome" depend on numerous factors, including the location, density, type, and age of urban development, common patterns have emerged. For example, urban streams typically experience increased stormflows (from direct runoff to channels), flashier hydrographs, altered baseflows, increased nutrient and contaminant concentrations, and decreased organic matter retention. Many of these attributes are related to changes in connectivity—that is, alteration of the longitudinal, lateral, and vertical connections between the landscape, headwater streams, and downstream waters.

Connectivity and consequences on downstream waters. One pervasive effect of urban development is the alteration of hydrologic connectivity along river networks. The frequency, duration, magnitude, timing, and rate of change of both stormflows and baseflows are altered via multiple pathways. The highly connected, engineered network of impervious surfaces, pipes, and storm drains increases the volume and rapidity of stormwater runoff into urban streams, resulting in increased frequency, magnitude, and rate of change of stormflows within the river network. This quick delivery of stormwater runoff to streams also means that stormflows tend to recede quickly, shortening stormflow duration. Because impervious surfaces reduce infiltration and watershed storage of water, urban development also can reduce baseflow magnitudes. Together, these patterns result in the typical flashy hydrographs of urban streams and altered hydrologic connections throughout urban river networks. Higher stormflow magnitudes and frequencies also can scour sediments from urban channels, which, in combination with engineered channel straightening, can cause urban channels to enlarge via incision and expansion. Direct wastewater discharges to urban streams (e.g., from wastewater treatment plants, industrial facilities, or combined sewer overflows) and water withdrawals for municipal and industrial uses also can affect the frequency, duration, and magnitude of hydrologic connections in urban streams. Vertical hydrologic connections can be augmented by leaky subsurface sewer and water pipes, or diminished by reduced infiltration due to increased impervious surface area and channel incision, straightening, hardening, and simplification.



Stream burial, or the diversion of streams into pipes, culverts, and other conveyances, is common in urban watersheds, and provides another illustration of how urban development alters connections. For example, more than 60% of all streams in Baltimore City, particularly small headwater streams, have been buried (Elmore and Kaushal, 2008). As a result, most lateral and longitudinal connections along urban river networks have been replaced by urban infrastructure, resulting in greatly expanded headwater drainage areas (Kaushal and Belt, 2012).

These changes in hydrologic connectivity have significant consequences for downstream waters in urban areas. Between rain events, urban landscapes accumulate materials such as organic material, nutrients, and contaminants, which then are delivered quickly to urban streams with surface runoff. As natural stream channels are converted to simplified engineered structures, they lose their ability to retain and transform these materials, resulting in reduced storage and lag time before transport to downstream waters (Nedeau et al., 2003; Carey and Migliaccio, 2009; Kaushal and Belt, 2012).

Box 3-1. Urban Streams (continued)



Longitudinal connectivity in urban streams also influences the movement and distribution of organisms in these systems. Urban stream habitats frequently become fragmented and homogenized, as connectivity is disrupted by road crossings, channel incision, and other impacts associated with urban development. Habitat homogenization reduces complexity, which limits the availability of habitats needed throughout species' life cycles (for reproduction, rearing, refuge from disturbance and predation). Fragmentation can result in reduced movement of mobile organisms, most notably fish, through the river network (Perkin and Gido, 2012). Urban streams also can benefit, however, from connectivity with intact, upstream habitats. For example, Waits et al. (2008) found that immigration from less disturbed upstream areas serving as source habitats maintained central stoneroller populations in an urban stream.

Connectivity and restoration of urban streams. Because so many of the adverse effects associated with urban development are related to changes in lateral, longitudinal, and vertical connections along urban riverscapes, restoration of these systems often involves re-establishing connections that existed before urbanization. For example, detention ponds and green infrastructure (rain gardens, bioswales, permeable pavements, green roofs) are designed to slow stormwater runoff into urban streams, thereby increasing retention and processing of water, nutrients, sediment, and contaminants. Ultimately, the slowing of stormwater runoff can re-establish lateral and longitudinal connections as retention and transformation pathways, rather than the primarily export pathway these connections traditionally served in urban river networks.

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. The small size of headwater streams makes distinguishing them from surrounding areas and overlying tree canopies difficult in most regions (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; Roy et al., 2009). Therefore, most streams portrayed on databases and maps as first-order streams are, when ground-truthed, second- or third-order streams. For example, more than 80% of mapped (1:25,000-scale topographic maps) stream terminuses in a Massachusetts watershed 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). Even with this widely known underestimation by databases and maps, first-order streams recognized in the U.S. Geological Survey (USGS) medium-resolution (1:100,000-scale) National Hydrography Dataset (NHD) represent 53% (2,900,000 km) of total stream length (Nadeau and Rains, 2007). Moreover, approximately 50% of these first-order streams were classified as not having year-round flow (i.e., nonperennial; Section 2.2.2; Nadeau and Rains, 2007). Southwestern and prairie streams are predominantly ephemeral and intermittent

(Sections 5.5, 5.6, B.4, and B.5). Thus, despite the shortcomings of existing national maps and hydrographic databases, it is still clear that headwater streams—including ephemeral and intermittent streams—represent a large fraction of river networks in the United States. Combining their overwhelming extent with their high biogeochemical activity (Section 3.4) means that headwater streams, including ephemeral and intermittent channels, have a large cumulative or aggregate effect on the river network (Benstead and Leigh, 2012).

In the following sections, we consider longitudinal connectivity between streams and downstream waters in terms of the physical, chemical, and biological connections between them.

3.3 Physical Connections

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

3.3.1 Water

The recurrent, concentrated surface flow of water from surface runoff and ground water develops and maintains river networks, and water is the primary medium carrying other materials from streams to rivers (Section 2.3). The temporal dynamics of flow (its frequency, duration, magnitude, timing, and rate of change) within and among river networks vary in space and time and influence the physical, chemical, and biological connectivity between streams and downstream waters (Sections 2.2.2, 2.2.3, and 2.3.2.2). Thus, the physical connection of water flow through river networks largely forms the foundation for chemical and biological connections and where along the dynamic connectivity gradient streams are positioned (Section 1.2.2).

Most rivers receive the majority of their water from tributaries rather than from direct precipitation on or ground-water input to river segments (Winter, 2007; Bukaveckas, 2009). Alexander et al. (2007) modeled flow through river 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 cumulatively contribute about 60% of the total volume of mean annual flow to all northeastern streams (Alexander et al., 2007).

Headwater stream contributions to downstream baseflow vary among river networks, based on several large-scale factors (Section 2.4). For example, headwater streams that have stronger connections to ground water or that consistently receive more precipitation relative to downstream reaches have a larger effect on downstream river baseflows. Hydrologic data from 11 nested gages distributed throughout a watershed (176 km^2) 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 ground water as drainage area increased (Shaman et al., 2004). Using geochemical tracers and hydrologic data from 32 nested stations in a watershed (1,849 km^2) of the River Dee in Scotland, Tetzlaff and Soulsby (2008) determined that streams draining the upper 54% of the watershed contributed 71% of baseflow. However, the upper watershed received only 58% of the total annual precipitation, indicating that long residence time ground-water flowpaths from the headwater watersheds were also 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 watershed (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 watershed (Temnerud et al., 2007). Jencso et al. (2009) monitored 24 transects with a total of 84 wells along lower hillslopes, toe-slope, and riparian areas in a northern Rocky Mountains watershed (22.8 km^2) and found that the duration of connectivity from hillslopes to streams was positively correlated (r^2 = 0.95) with the duration of higher than normal downgradient watershed streamflow. This finding demonstrates the strong link between downstream flow conditions and the connectivity of ephemeral and intermittent streamflow from nearby hillslopes, and that the cumulative downstream effect of the hydrologic connections between the hillslope and stream channel is time varying. Hydrologic connections to downstream rivers are often complex, involving longitudinal, lateral, and vertical exchanges that vary over space and time. This means that the flowpath by which headwater streams contribute to downstream waters will vary according to climatic, topographic, and geologic context.

We can also infer the importance of headwater streams from variation in river hydrologic responses over space. Discharge increases with drainage area, and the general assumption, particularly for mesic environments, is that drainage area can be used as a 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 headwater contributions to downstream discharge. Where $c \approx 1$, discharge is generated proportionally with increasing drainage area. Where $c < 1$, upstream portions of the watershed (where headwater streams tend to be most abundant) generate more discharge per unit area than downstream portions, suggesting that rivers with $c < 1$ derive a higher proportion of their flow from headwater streams. Where $c > 1$, downstream portions generate more discharge per area than upstream reaches, suggesting that rivers with $c > 1$ might store more water per unit area in upstream vs. downstream areas. Alternatively, urbanization in the lower portions of the watershed can lead to a similar relationship (Galster et al., 2006). Data from multiple USGS gages along large, unregulated rivers showed that mean and peak annual discharge do 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

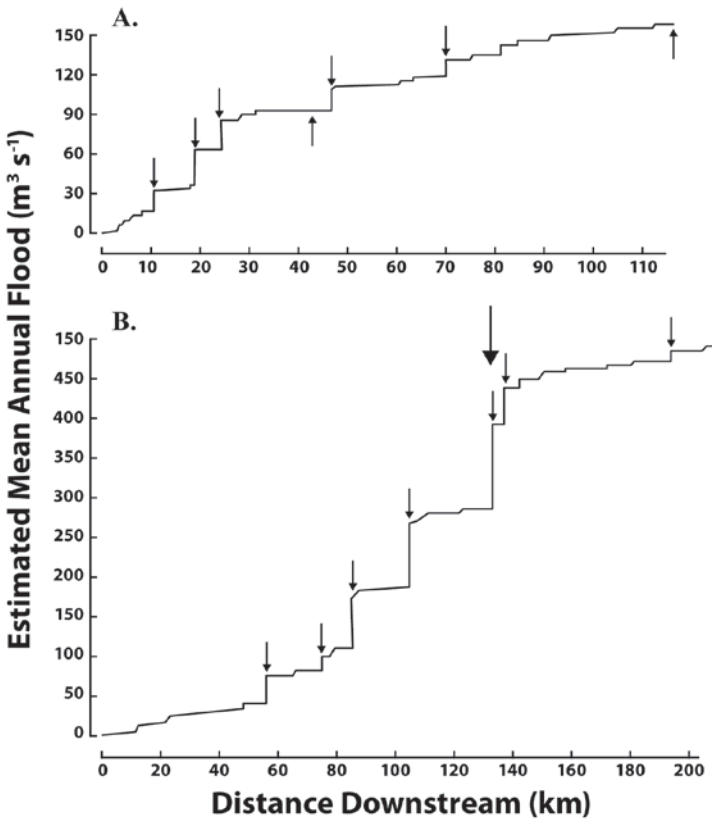
where $c < 1$, three rivers had relationships where $c > 1$, and ten showed changes in the relationship over their period of record.

Despite variability in area-discharge relationships, most mesic watersheds have a value of c between 0.8 and 1 (Galster, 2007), suggesting that drainage area can be used to roughly estimate the proportion of flow that arises from headwater streams. For example, Alexander et al. (2007) found that the watersheds of first-order streams cumulatively accounted for 57% of the total drainage area and 55% of the total annual river flow of the New England states. In more xeric arid and semiarid watersheds where the ground-water table can be below the stream channel and thunderstorms of limited spatial extent dominate runoff, however, c is generally < 1. For instance, in the highly instrumented Walnut Gulch Experimental Watershed (operated by the U.S. Department of Agriculture, Agricultural Research Services [USDA-ARS]) in southeastern Arizona, discharge becomes more nonlinear (c decreases) with increasing watershed area, and a critical transition threshold area occurs roughly within 37–60 ha (Goodrich et al., 1997). The primary causes of increasingly nonlinear response are (1) the increasing role of ephemeral channel infiltration losses to the subsurface, unconsolidated alluvium, and (2) the continual decline of fractional storm area coverage as watershed area increases. Caruso and Haynes (2011) reported that first-order watersheds made up 61% of total drainage area of the Upper Colorado River basin. In this case, the first-order streams produced a lower proportion (41%) of the total annual river flow than suggested by their total drainage area, in part because 84% of the streams were intermittent. Both studies used the 1:100,000-scale NHD, in which first-order watersheds generally correspond to second-order watersheds 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, cumulatively generate a large fraction of the nation's stream and river flows.

The propagation of stormflow through river networks provides clear evidence 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 (Figures 2-8 and 2-11). Timing of the storm and onset of the peak are increasingly delayed with increasing distance down the network (Figure 2-11; see below for further discussion of hydrologic dispersion). Typically, discharge magnitude increases as stormflow accumulates incrementally over the river network (Allan, 1995). The contribution of tributaries to rivers during widespread floods manifests as stepped increases in discharge immediately below confluences, as water flows accumulate through a river network (Figure 3-1).

Such propagation was recorded following a monsoonal storm event through an arid network of ephemeral channels in the Río Grande, NM (Figure 3-2). The high-intensity storm dropped approximately 18–25% of annual rainfall on the stream's approximately 16,000 km^2 drainage area over a 2-day period. Discharge recorded at two gages on the stream and three gages on the Río Grande downstream of the confluence illustrated lag (residence) time and peak hydrograph broadening at least 127 km downstream (Vivoni et al., 2006). Stormflow contributions from the ephemeral stream

Figure 3-1. Longitudinal pattern of flow along (A) River Derwent and (B) River Trent, illustrating stepped increases in flow associated with tributary inflows. Small arrows indicate location of tributary confluences along the mainstem; bold arrow in (B) indicates the confluence of the two rivers. Source: Reprinted from Fluvial Forms and Processes: A New Perspective, (1998) by Knighton with permission of Routledge.

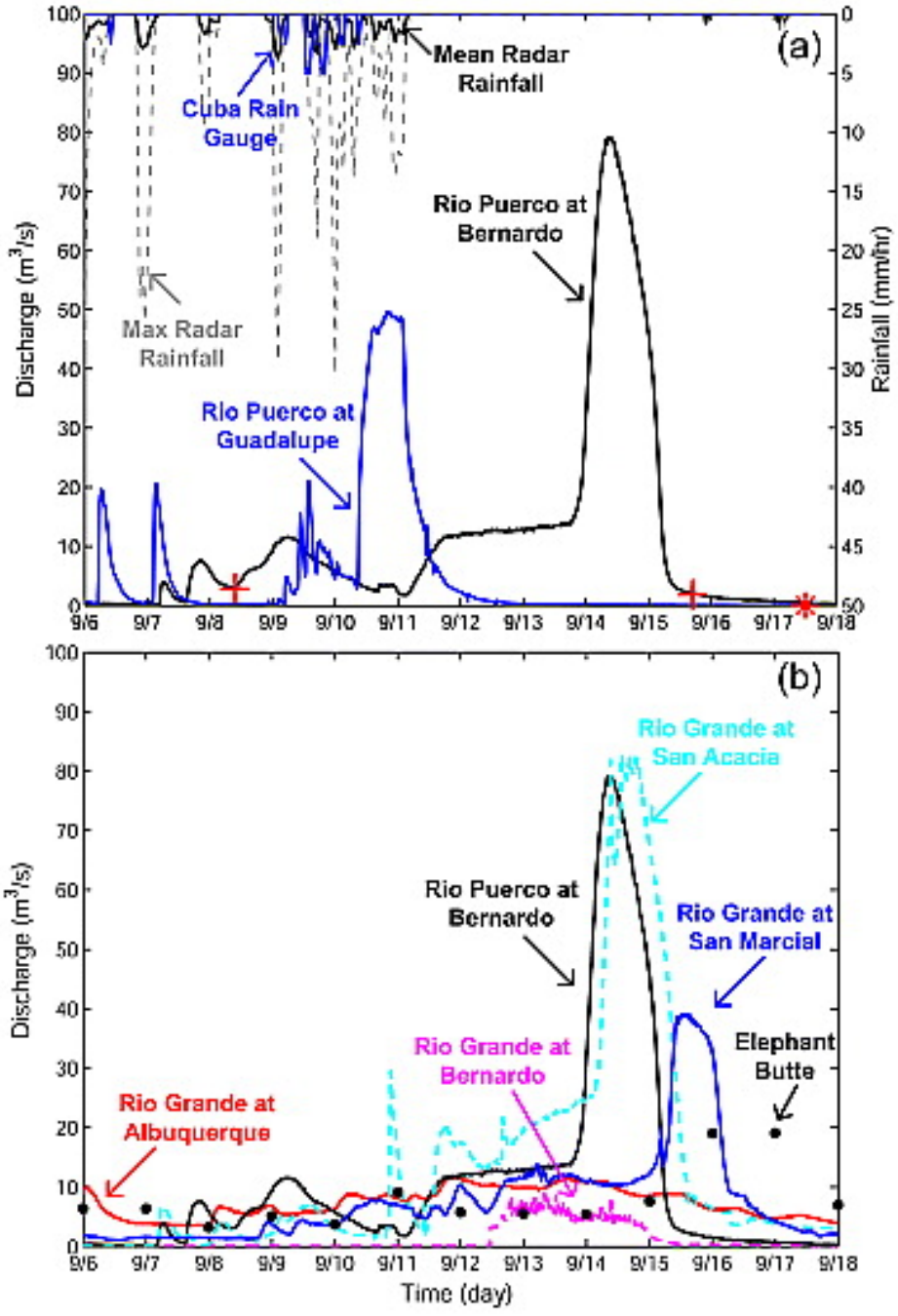


accounted for 76% of flow at the Río Grande, even though these channels were considered to have a flood return interval of 1.11 to 1.84 years across the USGS gages in the network (Vivoni et al., 2006).

How water flows through the streams in river networks shapes hydrologic responses (time to peak flow, peak-flow magnitude, and recession of peak flow) in downstream rivers (also see Sections 2.2, 4.3.2.1, and B.2 for discussion of hydrologic exchange between main channels and floodplains and associated water bodies). A key effect streams in a network structure have on hydrologic responses is dispersion, or the spreading of water output from a drainage basin over time. Hydrologic dispersion is the combined effect of several mechanisms operating across different spatial scales that influence the travel time (or residence 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 water volume move downstream faster than others, rather than as a single, discrete pulse. Hydrodynamic dispersion, which can be visualized by placing a volume

Figure 3-2. Time series of rainfall and streamflow observations in the Rio Puerco and Rio Grande, 6–18 September 2003. Source: Reprinted from Analysis of a monsoon flood event in an ephemeral tributary and its downstream hydrologic effects, (2006) by Vivoni et al. with permission of John Wiley & Sons.



of dye tracer in an upstream location and watching how the dye disperses longitudinally as it moves downstream, takes into account water flowing into and out of recirculating eddies at channel margins, off-channel sloughs, the streambed, and nearby bank sediments (see hyporheic exchange, Section 2.2.2).

These areas, which mix with the main channel flows at relatively slow rates, are collectively part of the stream's transient storage. As streamflow decreases after a storm, water that was temporarily stored in the banks, the floodplain, and other off-channel habitats flows back into the channel and supports stream baseflow (Sections 2.2.3 and 4.3.2.1; Whiting and Pomeranets, 1997; Chen and Chen, 2003; Baillie et al., 2007). Hydrodynamic dispersion is also readily apparent when flow resumes in ephemeral channels. The velocity at the front of flow moving down the dry channel is much slower than upgradient of the front because of higher turbulence and infiltration losses at the front. Flow in these situations, piles up at the front and is reflected as rapid rises in the hydrographs (Figures B-6 and B-10).

Hyporheic flowpaths have been characterized for a variety of situations that affect streambed topography and impede flow across a range of spatial scales (e.g., gravel bars, channel meanders, pool-riffle sequences, and large woody debris; Buffington and Tonina, 2009; Stonedahl et al., 2010; Sawyer et al., 2011) and in varying flow conditions that shift streambed topography (Harvey et al., 2012). The residence time that water spends in the subsurface alluvium before upwelling into streams—that is, the hyporheic residence time—is defined locally by the pressure head, alluvial volume, hydraulic conductivity, bed stability, and near-bed turbulence. For example, because 90% of the stream length in mountainous drainage basins is composed of steep channels with associated bed-form sequencing and limited alluvial volumes, most hyporheic exchange in these systems is expected to be rapid, shallow, and occur over small spatial scales (Buffington and Tonina, 2009). Slower, deeper, and longer hyporheic flowpaths occur in streams in unconfined valleys, with moderate hydraulic gradients and extensive alluvial volumes. In streams of both regions, hydrologic connections exist between shallow ground-water sources and stream channels, but the characteristics of these connections differ. These differences in hydrologic residence time are important, given that residence time reduces downstream flooding, controls various biogeochemical processes, and influences the distribution of stream organisms (Sections 3.4 and 3.5).

Geomorphologic dispersion is the cumulative 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 equidistant from the network outlet, so water simultaneously entering different parts of the network will not simultaneously arrive at the outlet.

Geomorphologic dispersion assumes water flowing through the network moves at a constant velocity or has varying resistance to downgradient transport. Within river networks, however, water velocity and related hydrodynamics change over space and time (e.g., channel slope and dimensions are not uniform across all pathways through the river network; Saco and Kumar, 2002; Paik and Kumar, 2004). Kinematic dispersion is the cumulative effect of spatially variable water velocity as it moves through river networks (Saco and Kumar, 2002). The physical configuration and variable channel form of streams within a river network, which influence components of hydrologic dispersion at varying scales, are the primary controls dispersing flow from streams to rivers over time and thereby cumulatively mediate the arrival time of stormwater pulses in rivers following rainstorms (Saco and Kumar, 2008).

Another factor that influences hydrologic response is channel transmission loss, or the loss of surface-flow volume due to infiltration into unconsolidated alluvium (Section 2.2). Transmission is another process by which streams, particularly in arid and semiarid regions, can slow or divert from the longitudinal flow of water to downstream rivers and thus minimize downstream flooding. Channel transmission losses are readily apparent from a series of hydrographs recorded in the USDA-ARS Walnut Gulch Experimental Watershed (Figure B-10). These hydrographs are the result of several high-intensity thunderstorms in the upper and lower portions of the watershed. As little or no lateral overland or tributary inflow occurs between the two upstream flumes, the decrease in both peak runoff rate and runoff volume is the result of channel transmission losses and dispersion only. As illustrated in this figure, however, even though runoff transmission losses are large there is sufficient runoff to increase flow in the San Pedro River at the downstream Tombstone USGS gaging station. Over relatively short time frames, infiltration or seepage through channel bed and banks typically dominates transmission losses, although evapotranspiration losses can be significant in stream reaches with prolonged surface flows (Hamilton et al., 2005; Costelloe et al., 2007). In many arid areas, precipitation and the potential for runoff are highest in mountainous regions, where small, ephemeral streams are most abundant (Section B.5). Because streams represent the topographic low points in watersheds that collect and concentrate surface water, they tend to have more water available for infiltration, be more permeable (have coarser sediment) than upland soils, have fewer plants, have higher antecedent moisture, and be closer to shallow ground water—all of which are factors that increase the potential for infiltration. In fact, evidence is mounting that ground-water recharge in hot arid and semiarid areas will occur only where water is concentrated and focused, such as in channels, depressions, or areas of high infiltration (e.g., karst; Brahana and Hollyday, 1988; Hughes and Sami, 1992; Sharma and Murthy, 1995; Scanlon et al., 1997; Scott et al., 2000; Constantz et al., 2002; Coes and Pool, 2005). Infiltrated precipitation in upland portions of alluvial drainage basins rarely reaches the ground-water table as recharge due to high potential evapotranspiration, the adaptation of xeric plants to use available soil moisture efficiently, and upward temperature gradients that transport water vapor upward in thick vadose zones. Relative to their cumulative surface area, an inordinate amount of ground-water recharge occurs in headwater ephemeral and intermittent channels within arid drainage basins (Osterkamp et al., 1994; Goodrich et al., 2004).

Channel bed and bank permeability also governs the degree to which infiltration is an important pathway between streams and ground-water 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), suggesting that lateral and vertical hydrologic connections might be especially important in headwater streams. Sand and gravel mining in ephemeral and intermittent channels and other human alterations that increase fine sediment loading and deposition can further slow percolation (Bull and Scott, 1974). Because fine sediments can concentrate in channels following moderate flows, higher flows that scour fine sediments or submerge more permeable floodplains have higher infiltration rates (Lange, 2005). In the Walnut Gulch Experimental Watershed, cumulative transmission losses over 54 km of channel resulted in a 57% decrease in flow volume associated with a storm (Renard and Keppel, 1966). Infiltration losses accounted for up to half the flow

volume along three ephemeral channels in the southwestern United States (Constantz et al., 2002). Chemical and isotopic tracers have confirmed that ephemeral streams are cumulatively important areas for floodwaters to recharge ground-water aquifers in desert regions (Tang et al., 2001). Although transmission losses represent disruptions of surface connectivity between streams and downstream waters, such losses indicate vertical hydrologic connections that reduce downstream flooding and recharge the ground-water aquifers that eventually contribute to flow in downstream waters (Izbicki, 2007).

Human alterations designed to control the spatial and temporal distribution of water have affected the longitudinal, lateral, vertical, and temporal dimensions of hydrologic connectivity in river networks. Structures such as dams, weirs, levees, culverts, and pipes alter longitudinal transport, restrict lateral expansion, and alter vertical exchange (e.g., Gregory, 2006; Hester and Doyle, 2008; Park et al., 2008). Surface-water and ground-water abstraction and diversion can cause tributary segments to dry, thereby severing longitudinal and vertical connectivity and reducing or eliminating lateral connectivity during low-flow periods (e.g., Colvin and Moffitt, 2009; Scanlon et al., 2012). Human alterations that increase fine sediment deposition or microbial biofilm in streambeds also can hamper vertical exchange (Battin and Sengschmitt, 1999; Rehg et al., 2005), causing conditions that can become chronic without periodic floods to flush out deposited sediments and biofilms (Box 3-1).

Human alterations also can affect the temporal dynamics of hydrologic connectivity in river networks. In a predominantly rural river network in central Illinois, the total dispersion of the flow was controlled primarily by geomorphological (~60%) and kinematic dispersion (~35%; Saco and Kumar, 2002). In contrast, hydrodynamic dispersion cumulatively contributed to 72–86% of the total dispersion in highly urbanized watersheds in the Chicago metropolitan area (Cantone and Schmidt, 2011). The rapid hydrologic travel times associated with impervious surface runoff and rapid flow through the sewer and storm drain networks contributed to the predominant influence of hydrodynamic dispersion (Cantone and Schmidt, 2011).

Interbasin water transfer also affects the temporal and spatial dynamics of flow in human-dominated river networks (Meador, 1996). Water is fundamental to human societies for drinking, food production, industry, waste transport and processing, recreation, and aesthetics. Engineered infrastructure moves water (and associated waste products) where and when it is needed (or removes it from where it is unwanted). Many streams in human-dominated watersheds, particularly streams that historically have ephemeral and intermittent flows, receive a significant proportion of their baseflow from municipal and industrial wastewater effluent discharges (Box 3-1). Streams that would be dry in the absence of these discharges are called effluent-dependent streams, whereas those that receive most, but not all, of their flow from effluent are called effluent-dominated streams (Brooks et al., 2006). About 25% of permitted effluent discharges in the United States enter streams with mean annual flows incapable of diluting effluents by more than 10-fold. This percentage of permitted effluent discharges entering streams incapable of diluting effluents by more than 10-fold increases to 60% when low-flow discharge is considered (Brooks et al., 2006). Streams draining human-dominated areas also can derive baseflow

from ground water recharged by over-irrigation and leaky infrastructure (Lerner, 1986; Roach et al., 2008; Townsend-Small et al., 2013).

Ultimately, these alterations can increase the frequency, duration, magnitude, and predictability of baseflows when tributaries might otherwise contain little or no water. Because dry periods in intermittent and ephemeral streams contribute to the key transformation, lag, and refuge functions these systems perform (Sections 3.4 and 3.5), loss of these dry periods has consequences for downstream waters. In addition, when water is stored or imported for human use, it is essentially being "borrowed" from another period or location, which then must contend with reduced water availability. Without careful water management and reuse (e.g., Bischel et al., 2013), any benefits of baseflow augmentation can be overshadowed by potential risks, such as increased contaminant and pathogen exposures (Section 3.4.4) and increased success of introduced species (Jackson and Pringle, 2010).

3.3.2 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 sediment is essential to river systems, excess sediment 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 nearby 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 bedload. Suspended sediment is fine sediment (clay, silt, 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 the variables of sediment flux and sediment grain size on one side, and discharge and channel slope on the other—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 similarly sized sediment; alternatively, less discharge or lower channel slope is needed to move a load of fine sediment than 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 changes in channel dimensions.

The sediment supply-transport capacity balance is particularly relevant to geomorphologic connectivity in river networks, because these variables typically differ as one moves from headwater streams to

downstream rivers (Ferguson et al., 2006; Ferguson and Hoey, 2008). For example, slope and grain size typically decrease, whereas discharge and channel size typically increase, in downstream reaches (Church, 2002). Thus, streams cumulatively and aggregatively affect rivers in part by changing sediment supply or transport capacity locally at confluences over time. Relatively small, local contributions in sediment and discharge from a tributary stream might elicit no detectable change or only a short-lived spike in downstream sediment characteristics, discharge, or channel geometry. In contrast, tributary streams making large relative contributions at mainstem confluences elicit strong, stepped changes in mainstem characteristics. Because headwater streams can make large contributions during infrequent disturbances (e.g., floods, debris flows), the influence of headwater streams on downstream waters can vary significantly over time, and even headwater streams can have long-lasting effects on rivers.

Human alterations can exert considerable influence on the structure and distribution of a watershed's river network, thereby affecting sediment-based connections between headwater streams and downstream waters. For example, road building in steep forested areas in the U.S. Pacific Northwest can cause soil erosion, create concentrated discharge, and increase stream channel network lengths, all of which affect the spatial distribution, intensity, and timing of erosional processes and cumulative sediment delivery to downstream waters (Montgomery, 1994; Wemple et al., 1996; Wemple et al., 2001).

Dams also modify sediment dynamics within river networks. Sediment concentrations and suspended loads can be reduced for hundreds of kilometers downstream of dams, as is especially apparent in the semiarid and arid western U.S. river networks (Williams and Wolman, 1984). The disruption of downstream sediment supply by dams alters the balance between sediment supply and transport capacity (Williams and Wolman, 1984; Kondolf, 1997). Water released from dams lacks sediment load and thus has excess energy. This energy often downcuts channels downstream of dams, causing channel incision and streambed coarsening as finer gravels and sands are transported downstream over time (Williams and Wolman, 1984; Kondolf, 1997). The elimination of floods enables the encroachment of terrestrial vegetation, resulting in channel narrowing and the conversion of complex, multithreaded channels into simple, single-thread channels.

Other human activities also can affect sediment dynamics. Gravel and sand mining locally removes bed sediment and lowers streambed elevation, creating a steep gradient change. Erosion of the streambed can occur both upstream and downstream of the mine. The steep gradient change increases stream power locally, which increases sediment demand and causes the streambed to erode in the upstream direction via headcutting, which often extends far up into tributary channels (e.g., Florsheim et al., 2001; Rinaldi et al., 2005; Rieke-Zapp and Nichols, 2011). Erosion in the downstream direction occurs because most of the sediment being carried by water is deposited in the mining pit, leaving the water that passes over the pit with excess energy that subsequently leads to downstream channel downcutting (Bull and Scott, 1974; Kondolf, 1997). These examples show that the dynamic balance between sediment supply and transport capacity represents a fundamental longitudinal connection along the river network that must be considered to determine the potential repercussions of human alterations.

Streams transport and store sediment. Headwater 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 (e.g., stormflows) that are the dominant means for downstream sediment transport (e.g., Gomi and Sidle, 2003). Because of their abundance and distribution, headwater streams can have a substantial cumulative effect on downstream waters via sediment storage and transport. Poor soil conservation, drainage of wetlands, deforestation, and tributary channelization associated with the development of agricultural land has long been recognized as being detrimental to downstream waters via their connections with headwater streams (Person et al., 1936). To stem further degradation, government agencies encouraged and funded various soil conservation practices and the construction of small impoundments on headwater streams to trap sediment and provide stable water supplies for livestock, irrigation, and recreation (Person et al., 1936; Renwick et al., 2005). Although most such ponds are small (≤1 ha or 2.5 acre) and represent only ~20% of the total impounded area (or 0.4% of the total watershed area), they can cumulatively have a significant effect. For example, Smith and Kraft (2005) estimated that the approximately 2.3 million ponds distributed primarily on headwater streams of the Mississippi River network cumulatively captured 25–50% of the eroded soil from the landscape.

Ephemeral desert streams are another example of sediment connections between headwater streams and downstream waters. These ephemeral streams can exhibit high sediment export efficiency by having higher bedload per unit stream power than that of forested perennial streams (Laronne and Reid, 1993). Despite infrequent flows of short duration, flood waves (bores) in ephemeral desert streams can carry substantial amounts of sediment downstream (Hassan, 1990). The transport distance associated with these floods, however, often is insufficient to link them directly to perennial rivers. For example, a reach-scale study in the Walnut Gulch Experimental Watershed in Arizona estimated sand transport distances of only 401 and 734 m in nine floods over two consecutive years (Powell et al., 2007). Over longer times spans the episodic nature of flow in ephemeral and intermittent channels transfers sediment in a stepwise manner, depositing sediment some distance downstream and then moving it farther downstream by subsequent events. The frequency, timing, and predictability of stream runoff and therefore sediment transport vary widely with significant seasonal, annual, and interannual variations that depend on elevation, climate, channel substrate, geology and the presence of shallow ground water. Over longer time spans, however, sediment will continue to move downstream and affect downstream waters (Brooks and Lemon, 2007).

Despite increasing bank erosion rates with increasing channel size and discharge, sediment yield from watersheds typically decreases with increasing drainage area, due to increased sediment deposition within channels and on nearby floodplains (Walling, 1983). This storage of sediment contributes to the temporal attenuation or lag in the sediment delivery to downstream waters; it also illustrates that headwater streams are important sediment sources for maintaining channels and floodplains.

Streams also can store substantial amounts of sediment that are released only during rare export events. A series of experimental sediment introductions into steep, ephemeral, second-order streams in southwestern Washington showed that between 30 and 45% of the added sediment (ranging from clay

to coarse sand) was exported to the mainstem 95–125 m downstream, during stormflows of 66–69% of bank full discharge (Duncan et al., 1987). Virtually all the added fine clay particles were exported from the ephemeral streams to the mainstem, presumably because this fraction remained suspended at even moderate flows (Duncan et al., 1987). Headwater streams within an Oregon Coastal Range watershed (2.5 km^2 area) stored 23% of total stored sediment within the watershed's river and valley network, compared with only 9% storage within the mainstem channel (May and Gresswell, 2003). Trimble (1999) constructed a long-term sediment budget for the Coon Creek watershed (360 km^2), a Wisconsin stream in the Mississippi River drainage, over periods coinciding with major land-use changes. When agricultural practices caused major soil erosion (1853–1938), streams acted as net sources of sediment (42×10^3 Mg yr^{-1}); after erosion control, streambank stabilization, and revegetation (1975–1993), streams became net sediment sinks (9×10^3 Mg yr^{-1}) (Trimble, 1999).

Several studies identify abrupt changes in sediment size and channel morphology that coincide with stream confluences having sufficiently high symmetry ratios (Knighton, 1980; Rhoads, 1987; Rice and Church, 1998; Rice et al., 2001). Reviews of tributary confluence data have identified that symmetry ratios ranging from 0.2 to 0.7 are needed to create a discernible sediment or channel morphology discontinuity along a mainstem (Rhoads, 1987; 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 flows, 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, but bed particle sizes were similar in the mainstem and stream for the remaining confluences (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 naturally 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) downstream of the dam (Katano et al., 2009). Stream sediment contributions to the river reversed many of the dam-related changes to downstream waters, including restoration of turbidity levels and the proportion of sand and gravel substrate in the river bed (Katano et al., 2009). Other upstream land uses can also have an effect on downstream sediment transport. Numerous modeling studies have shown how land use can affect sediment export from headwater streams to downstream waters. For example, Howarth et al. (1991) used the Generalized Watershed Loading Function model in the Hudson River estuary and its associated watershed and demonstrated that urban, suburban, and agricultural land uses in headwater watersheds produced the highest proportion of downstream sediment and organic carbon delivery to the estuary. More recently, Wilson and Weng (2011) applied the Soil and Water Assessment Tool in the Des Plaines River watershed in Illinois to simulate the cumulative effects of headwater streams on downstream total suspended solids concentrations. Their calibrated model projected that expansion of

medium- and high-density residential development in place of low-density residential development in headwater subwatersheds would decrease downstream total suspended solid concentrations.

3.3.3 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). 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). In-channel wood 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 because 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. Environmental setting, including valley slope, influences the supply of wood to streams and therefore the degree of connectivity between streams and downstream waters.

Wood tends to accumulate in, rather than be exported from, most forested headwater streams, due to their low discharge and relatively narrow channel widths (Keller and Swanson, 1979; Bilby and Ward, 1989; Gurnell, 2003). For example, wood was determined to have entered the channel more than 60 years earlier in a North Carolina headwater stream (Wallace et al., 2001); in some Pacific Northwest streams, wood entered the channel more than a century earlier (Swanson and Bachmann, 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 from 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 Oregon's Coastal Range were delivered downstream from headwater streams by debris flows, rather than originating from the riparian zone next 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); wood export per unit area increased with stream size for headwater streams (6–20 km^2), peaked at intermediate-sized streams (20–100 km^2), and then decreased with stream size for large streams (100–2,370 km^2). The amount of wood in low-gradient midwestern streams was determined to be supply limited mainly because human alteration both depletes large wood sources and results in altered hydrology and channel structure enhancing downstream transport of small wood (Johnson et al., 2006). Topography and topology also govern wood delivery from headwater streams. Downstream segments draining steep, finely dendritic networks 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).

Additional evidence on wood-mediated connections along the river network comes from studies of wood upstream and downstream of tributary confluences. 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 of 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 had insufficient capacity to transport 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 distances 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 $m^3\ m^{-1}\ yr^{-1}$, largely based on 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). Unlike most human-built dams, natural logjams and beaver dams are temporary structures that do not completely restrict transport of water, sediment, and biology across all discharge levels. Although natural wood accumulations act to restrict longitudinal connectivity by slowing the downstream transport, these features enhance lateral and vertical connectivity with the floodplain and hyporheic zone, respectively (Burchsted et al., 2010; Sawyer et al., 2011). The importance of wood in decreasing longitudinal connectivity, while enhancing lateral connectivity, temporary storage, and habitat diversity has been documented not only locally at unit and reach spatial scales (1–100 m stream length) but along entire networks where valley confinement is an important predictor for wood storage (Wohl and Beckman, 2014). Past and ongoing human activities (timber harvest, beaver trapping, road building along streams, placer mining, log floating, desnagging) have so completely removed in-channel wood and availability of near-channel old-growth wood recruitment, that retention of new wood in channels is unlikely (Wohl and Beckman, 2014). 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 additional 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 aggregate over 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, and influential in controlling hydrodynamics and channel morphology of rivers.

3.3.4 Temperature (Heat Energy)

Connections between streams and downstream waters can affect heat transfer, and thus water temperature, throughout river networks (Knispel and Castella, 2003; Rice et al., 2008). Heat is thermal energy transferred across a boundary, whereas temperature is the amount of thermal energy per unit volume (Coutant, 1999; Poole and Berman, 2001). Therefore, the amount of heat and the size of the water body (i.e., volume, discharge) are fundamental controls of water temperature. Because water temperature is such a fundamental property that drives physical (e.g., viscosity and density of water), biological (e.g., organism behavior and physiology), and biogeochemical (e.g., nutrient assimilation and mineralization) characteristics of stream ecosystems, it can cumulatively have significant indirect effects on downstream waters via its effects on other forms of connectivity. This influence can occur over even relatively small spatial scales or patches (Sections 3.4 and 4.5; Allan, 1995). For example, water temperature strongly regulates stream ecosystem respiration, which then drives nutrient uptake (Section 3.4.1; Demars et al., 2011). Warmer temperatures exacerbates eutrophication problems such as fish kills, and heat stress can interact with chemicals synergistically or antagonistically making them more or less toxic to organisms, respectively (e.g., Holmstrup et al., 2010).

The total net heat exchange for a stream has several components, including heat flux from solar radiation, evaporation, convection with air, conduction with the streambed sediments, and advection with direct inputs from precipitation, ground water, tributaries, and effluents (Webb, 1996; Coutant, 1999). Given these diverse thermal energy fluxes, numerous direct and indirect factors can change stream temperature. For instance, riparian vegetation directly affects stream temperature by insulation (shading incoming solar radiation and trapping air, reducing wind; Moore et al., 2005) and indirectly affects stream temperature via its influence on channel morphology (e.g., Trimble, 1997) and degree of hyporheic exchange through input of woody debris (e.g., Sawyer et al., 2012). Channel morphology can directly influence stream temperature by affecting bank shading and altering channel width-to-depth ratio, and indirectly influence stream temperature by affecting hyporheic exchange. Hyporheic exchange influences stream temperature via buffering (reducing the diel temperature range) and lagging (offsetting daily temperature patterns relative to surface-water patterns) effects, due to the extended alluvial flowpath and by the advection or conduction of thermal energy or both (Arrigoni et al., 2008).

Over coarse spatial scales, a nonlinear increase in mean daily water temperature typically occurs from headwater streams to large rivers (Caissie, 2006). A unimodal trend occurs in daily variation (i.e., daily maximum-minimum) of water temperature, as stable ground-water 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 (Caissie, 2006). The steep increase in water temperature immediately downstream of headwater streams is associated with more rapid flux of heat into headwater 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: Some river

networks receive substantial deep ground-water contributions at lower reaches or advective inputs from tributaries along the mainstem. Channel network configurations can influence the length, dominant aspect relative to the sun, and distribution of tributaries, which influence the thermal heterogeneity along a stream that might be associated with inflowing surface and hyporheic water. Callahan et al. (2015) illustrated how topographic, geomorphic, riparian, and hyporheic exchange can interact to influence stream temperature in the Kenai Peninsula, AK. Ground-water inputs played important moderating roles in determining stream temperatures in both low-gradient versus steep headwater streams, despite these streams having different channel morphologies, draining contrasting topographies, and having different riparian canopies (Callahan et al., 2015). Although low-gradient headwater streams had fewer channel margin seeps and lower hyporheic exchange than the steep headwater streams, the subsurface-water temperature entering the low-gradient streams was lower during summer than that entering the steep streams (Callahan et al., 2015).

Although many studies have determined that several direct and indirect factors can alter stream temperature, including those listed above, these effects typically have been documented to carry for only short distances downstream. This is in part because most studies measuring stream temperature changes are conducted over reach or subreach scales (<100 m) and because stream-water temperature equilibrates rapidly (~4 hr) to immediate surrounding conditions (e.g., Zwieniecki and Newton, 1999; Rutherford et al., 2004; Hester et al., 2009). Some studies, however, do provide evidence of thermal connections along river networks. The empirical evidence supporting thermal connections between headwater streams and downstream waters includes studies that have gauged the spatial relationship of water temperature over river 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. Studies of this type have shown that upstream water temperature is significantly related to downstream water temperature, even over relatively long distances. For example, water temperature data collected at 72 locations throughout a Catskill Mountain, NY watershed were used to predict daily mean summer water temperatures spatially 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 watershed was correlated across the river network over an average distance of approximately 5 km (Johnson et al., 2010).

Studies that have detected discontinuities in river temperature associated with stream confluences also provide evidence of thermal connections along river networks. 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 limit 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). A subsequent study in northeastern Oregon determined that tributary

confluences typically provided coldwater (≥3 °C colder than mainstem temperatures) patches during the summer (Ebersole et al., 2015). In addition, 39% of these tributary confluences were with streams that contributed cold hyporheic water even when they lacked surface water—that is, they were ephemeral and intermittent streams that were significantly connected to downstream waters even when the streambed surfaces were dry (Ebersole et al., 2015). Unexpectedly, factors such as tributary size, flow presence, and flowpath length were not important in predicting whether a tributary's confluence would be a cold patch. Rather, the probability of a confluence's being a cold patch was largely explained by amount of available water at the end of the snowmelt season (Ebersole et al., 2015).

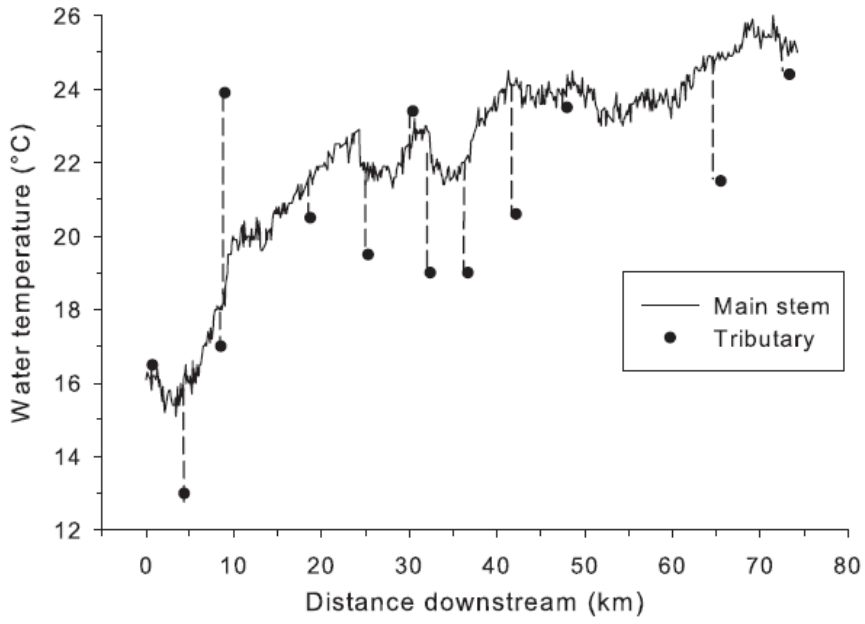
Thermal infrared sensors are a recent remote-sensing tool that can provide snapshots of thermal heterogeneity along river corridors (Torgersen et al., 2001; Torgersen et al., 2008; Cristea and Burges, 2009). Thermal maps and plots of longitudinal profiles overlaid by stream locations show that confluences coincide with distinct peaks and troughs in river temperature (Figure 3-3). The effects of streams were discernible when temperature differences of streams and the mainstem exceeded 1 °C and streams had large symmetry ratios (Cristea and Burges, 2009). In most cases, the effect of the stream on river-water temperature was minor relative 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 persistent coldwater habitats that are less susceptible to meteorological variation than other classes of thermal refuges and therefore are particularly important for aquatic life (Section 3.5.2; Dugdale et al., 2013).

Although headwater stream temperatures are highly responsive to local conditions, they still can have a cumulative effect on downstream waters. The fact that large-scale alteration of headwater streams has been documented to affect downstream water temperature illustrates this point. For example, reductions in baseflow (ground-water inputs) resulting from increased surface runoff from impervious surfaces (Leopold, 1968) and reduced hyporheic exchange through the engineered piping, straightening, and hardening of streambeds contribute to increased average and maximum summer water temperatures and decreased average and minimum winter temperatures in downstream waters. The combination of riparian vegetation removal, increased urban runoff, and storm sewer inputs results in larger temperature swings associated with increased channel width-to-depth ratios and thus air-water surface area available for radiant, evaporative, and convective fluxes (LeBlanc et al., 1997).

3.4 Chemical Connections

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

Figure 3-3. 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 mainstem, 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).



Because water flow is the primary mechanism for downstream transport of chemical substances, chemical connectivity is closely related to hydrologic connectivity (Sections 2.2 and 3.3.1). The movement of water across and through landscapes and into river networks integrates potential solute sources and sinks throughout the watershed. Thus, solute concentrations are an integration of upstream mixing processes and transport processes in the stream channel. In simplest terms, streams generally operate 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 near where they entered the river 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 streams and rivers. Many headwater streams receive pulsed inputs of water, sediment, organic matter, and other materials during rain events. Periodic flows in ephemeral or intermittent streams can have a strong influence on biogeochemistry by connecting the channel to other landscape elements (Valett et al., 2005), and this episodic connection can transmit substantial amounts of material into downstream rivers (Nadeau and Rains, 2007).

The alternation of dry and flowing periods largely drives the temporal dynamics of chemical connections between ephemeral and intermittent streams and downstream waters. The frequency,

duration, magnitude, timing, and rate of change of flow further account for the variable connectivity observed within and across river networks over space and time (Section 1.2.2). Materials accumulate on and within dry streambeds where they are temporarily stored and can undergo transformations (Acuña et al., 2005; Fritz et al., 2006a; Ademollo et al., 2011; Arce et al., 2014). Transmission losses, tributary confluences, various channel forms, and retention structures also can contribute to the spatial distribution of materials and processes in dry streambeds (Marcus, 1987; Graf et al., 1991; Reneau et al., 2004; Taylor and Little, 2013). The onset of flows in ephemeral and intermittent stream channels, particularly those following long dry periods and initiated by floods (i.e., first flushes), are important in transporting and transforming large amounts of unique materials for long distances downstream, which then can have significant effects (e.g., Obermann et al., 2009; Hladyz et al., 2011; David et al., 2012). Human alteration of channel characteristics (e.g., channel shape and depth) and organic matter inputs also affect the ability of streams to temporarily store and cycle materials before transport to downstream waters.

Biogeochemical transformations control the mobility of different chemicals by altering chemical properties, such as form (e.g., dissolved, colloidal, gravitoidal), bioavailability, and toxicity. Thus, transformation is a key process influencing the downstream transport and attenuation of chemicals. Physicochemical (e.g., pH, redox potential, chelator concentration, light, hydrologic residence time) and biological (e.g., extracellular enzymes, physiology, lipid content) conditions control the location, rate, and timing of chemical transformations in streams and downstream rivers. For example, the introduction of stream restoration structures (e.g., small log dams) can affect the spatial distribution of oxic and anoxic zones in streambeds and thus biogeochemical cycling and reaction rates for instream biogeochemical processes throughout the river network (Lautz and Fanelli, 2008). These types of human alterations, in turn, affect the form of chemical substances and the timing of their transport downstream (Box 3-1). Data from the Baltimore Ecosystem Study Long-Term Ecological Research site suggest that increased hydrologic connectivity from urban infrastructure (e.g., pipes, storm drains, ditches) in headwaters increases the frequencies of occurrence and transport rates of nutrients, carbon, and metals to downstream surface waters (Kaushal and Belt, 2012). Urbanization can cause complex downstream responses, however, and sometimes creates longer travel times (i.e., reduced downstream connections). For example, aging infrastructure can leak water and pollutants into ground water rather than transporting these materials directly downstream.

3.4.1 Nutrients

Studies have documented nutrient-based chemical connections along river networks. Alexander et al. (2007) investigated how stream size affected nitrogen transport in a northeastern U.S. river network. 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, which showed that instream nitrogen loss was inversely related to mean stream depth. This finding most likely resulted from the reduced occurrence of denitrification and settling of particulate nitrogen in deeper channels, due to reduced contact and exchange between stream water and benthic

sediments (Alexander et al., 2000). Böhlke et al. (2009) used laboratory-, local-, and reach-scale studies to describe the effect of seasonal and event-based variation of instream properties (e.g., stream depth, flow rates, temperature) on denitrification rates in headwater streams, which can cause interannual variations in rates of nitrate export to downstream waters. A dynamic transport model using a one-dimensional version of the advection-dispersion equation was developed to estimate progressive instream nitrate removal from first- to fourth-order streams (Alexander et al., 2009). Model simulations indicated that denitrification rate constants in headwater tributaries varied strongly by season, based on biogeochemical and hydrologic factors. This in turn had a cumulative effect on downstream nitrate export (Alexander et al., 2009). These studies highlight how stream size affects nitrogen-based chemical connections, with headwater streams within the network affecting downstream water quality.

Phosphorus-based chemical connections also have been documented. Doyle et al. (2003) modeled the relative influence of hydrogeomorphic and uptake processes on longitudinal phosphorus retention through a river network of first- through sixth-order streams. The model revealed greater variation in uptake relative to hydrogeomorphic processes, and the authors concluded that uptake processes influence downstream variation in phosphorus retention at the watershed scale more than hydrogeomorphology.

Research on hydrologic control and seasonality of nutrient export from streams in the Mississippi River basin similarly provides evidence of downstream connectivity (Section B.4.3.2.1). Export of dissolved reactive phosphorus from second- and fourth-order streams in agricultural watersheds occurred mainly during high-discharge conditions, with discharges equal to and greater than the 90th percentile 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 (Bayless et al., 2003). In another study, researchers modeled riverine dissolved reactive phosphorus yield of 73 watersheds within the Mississippi River basin during the January to June period, as a function of nutrient sources and precipitation (Jacobson et al., 2011). Riverine dissolved reactive phosphorus yield was positively related to fertilizer phosphorus inputs, human sources of phosphorus (e.g., sewage effluent), and precipitation, which generates surface runoff that moves fertilizer applied to the landscape into streams and rivers that then transport it 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).

Other environmental and biological processes also can affect nutrient-based chemical connections. The underlying geology of the Mokelumne River in California's central Sierra Nevada Mountains 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 nearby watersheds that were underlain with different rock types (diorite vs. biotite schist) but had similar land-use, vegetation, topography, and watershed 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. A nearby 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. Holloway et al. (1998) concluded that biotite schist streams contributed a disproportionately large amount of total nitrate to downstream reservoirs, despite draining only a small area of the entire watershed.

In another study, nitrate concentrations were measured at 50 sites across the West Fork watershed of the Gallatin River in southwestern Montana's northern Rocky Mountains under different hydrologic conditions and across two seasons, growing and 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 to 2.7 km. This seasonal difference likely resulted from greater biological uptake and use of nitrate during the growing season, which then limited its downstream transport; during the dormant season, downstream transport increased, resulting in greater spatial dependence in nitrate concentrations (Gardner and McGlynn, 2009).

Seasonal variability in chemical connectivity also was observed in Arizona's San Pedro River. Differences in dissolved organic nitrogen concentration were detected among three segments of the river during the dry season, but stream water was well mixed, the system was hydrologically connected, and no differences in dissolved organic nitrogen concentration were detected during the wet season (Brooks and Lemon, 2007). These seasonal differences occur because nitrogen accumulates locally at varying levels during drier periods but is mixed and transported downstream during large, infrequent storm events, making nitrogen concentrations more longitudinally uniform (Fisher et al., 2001).

Peterson et al. (2001) examined chemical connectivity by studying similar network components across different types of river networks. After measuring nitrogen export from 12 headwater streams 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 headwater streams (Peterson et al., 2001). Given the prevalence of headwater streams on the landscape (Section 3.2) and their hydrologic connectivity to other river network components (Sections 2.2 and 3.3.1), headwater stream nitrogen processing can improve water quality in downstream waters. Many other studies also highlight the importance of nitrogen processing 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 in 72 streams across different biomes and used those rates to model how headwater and larger streams in a river network respond to simulated nitrate loading increases. At low loading rates, the biotic removal of dissolved nitrogen from water is high and occurs primarily in headwater streams, which reduces loading to larger streams and rivers downstream. At moderate loading rates, the ability of headwater streams to remove nitrogen is reduced, but larger streams can remove the excess nitrogen. At high loading rates, removal by headwater streams and larger streams in the river 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.

Helton et al. (2011) conducted simulation experiments that illustrated the effects of connectivity in the Ispwich River (MA) and Flat Creek (WY) networks, via the use of river-network models of nitrate dynamics. The nitrate models underpredicted nitrogen removal in many reaches, which was attributed to connections between the river channels and neighboring wetlands that were not characterized by the model and that functioned as nitrogen sinks (Section 4.3.3.2). By not representing the fine-scale variability in nitrogen uptake in river-network models and assuming that nitrogen uptake decreases with depth along a river network, simulations can potentially misrepresent the export of nitrogen from headwater streams to downstream waters (Darracq and Destouni, 2005, 2007). The potential for this misrepresentation, however, depends on the spatial scale of the study and the specific characteristics of the river network.

The influences of headwater and other tributary streams on nutrient concentrations in larger downstream waters, as detailed in the numerous examples above, reflect the combined processes of nutrient cycling and downstream transport that occur throughout river networks, albeit most intensively in headwater streams. The concept of nutrient spiraling provides an approach to quantifying these cycling and transport processes and 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, which stretches the cycle into a helix or "spiral" (Webster and Patten, 1979). The stretch of the spiral, or the openness between its loops, is primarily determined by flow, whereas the diameter of the loops is mainly determined by biological activity (Cummins et al., 2006). Nutrients such as dissolved phosphorus and nitrogen, which enter the stream via ground-water or overland flow, are removed from the water column by algae and microbial organisms. These nutrients are then consumed by organisms at higher trophic levels, transported farther downstream as suspended particles, or returned to the dissolved pool through cell death and lysis. Nutrients flowing through the food web also are regenerated to the dissolved pool via excretion and microbial decomposition. Nutrients in the dissolved, particulate, and living tissue phases of the cycling process are subject to downstream transport, such that each phase transition 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."

Although measurement of total spiraling length requires detailed study of tracer dynamics through multiple compartments of the stream ecosystem, Newbold et al. (1981; 1983a) have shown that it can be approximated by "uptake length" or the distance traveled in the water column before algal and microbial 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 that the three nutrient forms cycle between roughly 8 (nitrate) and 40 (ammonium) times within the length of a first-order stream, and between roughly 8 and 90 times within the respective lengths of first- to fourth-order streams.

Withers and Jarvie (2008) also compared phosphorus uptake lengths among different streams. Shorter uptake lengths are indicative of more rapid phosphorus cycling and greater efficiency of phosphorus retention. The shortest uptake lengths (2–580 m) were in first-order streams that drained "pristine" watersheds. Uptake lengths were longer (26–3,460 m) in second- to fourth-order streams that drained agricultural watersheds, and longest (4,140–367,000 m) in fifth-order rivers that drained a mixture of urban and agricultural land use (Withers and Jarvie, 2008).

These studies highlight the high nutrient-processing potential of headwater streams. This potential results from their low water volume-to-bed sediment area ratio, which enhances conditions for key nutrient uptake processes (e.g., adsorption, precipitation, assimilation) not only at the water-bed interface but within the streambed sediments (Withers and Jarvie, 2008). Downstream ecosystems depend on processes that occur in headwater streams. Given that roughly half the water reaching larger tributaries and rivers originates from headwater streams (Section 3.3.1), 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. This cycling is, fundamentally, a complex of ecosystem processes that intensively uses nutrients and then regenerates them for delivery to downstream waters much in their original form. Because nutrients undergo transformations across various forms (e.g., dissolved, particulate, inorganic, or in living organisms) while being transported downstream (i.e., spiraling), explicitly identifying their exact origin in the network can be difficult.

Although headwater nutrient cycling, or spiraling, functions largely to deliver regenerated nutrients downstream, headwater stream processes measurably alter the delivery of nutrients to downstream waters in many ways. For example, if cycling has been seriously impaired such that nutrient regeneration is inhibited or nutrients are generated in biologically unavailable or toxic forms, the downstream effects could be large. Nutrients taken up as readily available inorganic forms can be released back to the water column as organic forms (Mulholland et al., 1988) that are less available for biotic uptake (Seitzinger et al., 2002). Similarly, nutrients incorporated into particles are not entirely regenerated (Merriam et al., 2002; Hall et al., 2009), but rather accumulate and contribute to longitudinally increasing particulate loads (Whiles and Dodds, 2002). The amount of phosphorus and nitrogen delivered downstream by headwater streams cycles seasonally due to the accumulation of nutrients in temporarily growing streambed biomass (Mulholland and Hill, 1997; Mulholland et al., 2004). Such variations affect downstream productivity (Mulholland et al., 1995) and help explain the seasonality in the spatial correlations of nutrient concentrations described above.

Microbially mediated transformations affect the forms of nitrogen transported from headwater streams to downstream waters, and these transformations can influence—and be influenced by—human alterations of the landscape. Nitrification, or the transformation of ammonium to nitrate, 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 stream-water through transformation to atmospheric nitrogen, is also 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 headwater 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 stream networks of first to third order and first to fifth order, respectively. In headwater agricultural streams, denitrification in stream sediments might not be effective at removing nitrate from stream water because of altered hydrology. In watersheds with tile drains and channelized headwaters, stream nitrate concentration is positively correlated with stream discharge, suggesting that these altered streams are in throughput mode, whereby nitrate inputs 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 and Likens (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, where phosphorus sorbed to metal hydroxide precipitates introduced by mine drainage. These examples further illustrate the potential for headwater streams to absorb nutrient impacts to the benefit of downstream waters.

3.4.2 Dissolved and Particulate Organic Matter

Headwater streams supply downstream waters with dissolved and particulate organic carbon, which support biological activity throughout the river network. Organic carbon enters headwater streams from the surrounding landscape, including wetlands (Section 4.3.3.4 and 4.4.3.1), in the form of terrestrial leaf litter and other seasonal inputs, dissolved organic carbon (DOC) in subsurface and surface runoff, and fine particulate organic matter (including eroded soil) in surface runoff. Headwater reaches also export organic carbon produced within the stream by photosynthesis, both as DOC (Kaplan and Bott, 1982) and suspended particles (Marker and Gunn, 1977; Lamberti and Resh, 1987).

Ågren et al. (2007) determined that headwater streams exported the largest amount of terrestrial DOC on a per unit basis in the Krycklan watershed in Sweden. The amount of organic matter exported from headwater streams to downstream waters varies with multiple factors, including surrounding land use. For example, Schelker et al. (2014) developed a mixing-model approach and quantified that forest harvesting at areal proportions of 11% and 23–25% of a northern Sweden watershed induced stepped

increases in DOC delivery, due to disturbance of shallow forest soils and subsequent transport from headwaters to downstream locations. Similarly, a 20% increase in downstream DOC concentrations was predicted following forest harvesting in the headwater areas of the H.J. Andrews Long Term Ecological Research site, using the VELMA (Visualizing Ecosystems for Land Management Assessments) model (Abdelnour et al., 2013). In southeast Arizona, Meixner et al. (2007) found that DOC consistently doubled to tripled in the San Pedro River during storm events from a flush of terrestrial organic matter and nutrients. This is comparable to the flush response observed by others (Fisher et al., 1982; Brooks et al., 2007) during monsoon precipitation events in the southwestern United States. These examples further demonstrate connectivity of headwater streams and their cumulative effects on downstream water quality.

Fisher and Likens (1973) followed the fate of these inputs in a forested headwater stream in New Hampshire. They concluded that 34% of inputs were mineralized through respiration by consumers and microbes within the headwater stream, which represented the "ecosystem efficiency" of the reach. The remaining 66% was exported downstream and constituted, as Fisher and Likens (1973) observed, "… inputs to the next stream section where they are assimilated, or passed on (throughput) or both." Other studies have reported similar amounts of export. 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 organic matter inputs. A large body of literature has demonstrated that headwater streams modify and export organic carbon that significantly affects ecosystem processes throughout the river network.

Vannote et al. (1980) recognized that exported carbon was not simply the unutilized fraction but was also greatly modified in character. A basic tenet of their River Continuum Concept is that longitudinal variations in the structure of stream ecosystems reflect, in part, the cumulative effects of upstream organic matter processing. 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) account for only 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). Feeding activities of aquatic invertebrates called "shredders" break down leaves that have entered streams (Cummins and Klug, 1979; Cummins et al., 1989). Invertebrate activity is particularly important, as demonstrated by large reductions of fine particle export following 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.

Downstream organisms consume organic carbon exported from headwater streams, supporting metabolism throughout the river network. In part, this results from direct consumption of 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 consumed by other organisms (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). In addition to transformations associated with microbial and invertebrate activity, organic matter in streams can be transformed through other processes such as immersion (Corti et al., 2011) and abrasion (Paul et al., 2006); photodegradation also can be important in ephemeral and intermittent streams where leaves accumulate in dry channels exposed to sunlight (Dieter et al., 2011; Fellman et al., 2013).

The organic carbon turnover length, derived from the nutrient spiraling concept (Section 3.4.1; Newbold et al., 1982b), is a measure of the downstream fate of exported carbon. Carbon turnover length is the ratio of the downstream flux of organic carbon to ecosystem respiration per length of stream. It approximates the average distance that organic carbon would travel before being consumed and mineralized by aquatic organisms. Carbon turnover length for first-order streams is on the order of 1 to 10 km (Newbold et al., 1982b; Minshall et al., 1983), suggesting that organic carbon exported from headwater streams is likely to be used primarily in the somewhat larger streams to 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 organic carbon 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, but a much longer turnover length of 40 km for fine (<1 mm) organic particles. 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. Kaplan et al. (2008) concluded that DOC in a third-order southeastern Pennsylvania stream 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 to carry the carbon to coastal waters.

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

increasingly larger streams and rivers 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 downstream reaches. Studies of transport and mass balance throughout the river network provide such evidence. Shih et al. (2010) applied the SPARROW (SPAtially Referenced Regressions On Watershed attributes) model to organic carbon 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 carbon 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 certain assumptions), we can estimate the amount of organic carbon in river networks that originates from headwater streams. We begin with the proportion of carbon originating from allochthonous sources as 0.78 (Shih et al., 2010). If we assume that the proportion of headwater streams in a drainage area is 0.50 (Section 3.2; 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), the proportion of carbon originating from headwater streams that is delivered downstream is 0.39 × (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 total carbon input to the downstream network (0.88). Thus, 31% (= 0.27/0.88 × 100) of the total carbon supplied to downstream reaches originates from headwater streams.

Most terrestrial organic matter that enters headwater streams 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 headwater 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). The importance of discharge in determining organic matter transport dynamics highlights the interdependence of physical and biological connections within the river network. 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 streams (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 streams can be large, and often depends on factors such as discharge, abiotic retention mechanisms within the channel (Bilby and Likens, 1980), biological communities (Cuffney et al., 1990), and the quality and quantity of riparian vegetation in headwater watersheds (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 coastal headwater streams in Alaska. When debris dams were removed from a New Hampshire headwater stream, export of fine particulate organic carbon increased by 632% (Bilby and Likens, 1980). The longitudinal discontinuities created by logjams and beaver dams slow the downstream transport of organic matter, enabling instream organisms to process the carbon and slowly leak material downstream (Wohl and Beckman, 2014). The strong links among organic matter storage, processing, and downstream transport in ephemeral streams of the southwestern United States can be seen in the distribution of organic matter of varying quality and mobility over periods with varying rainfall intensities (Norton et al., 2007). Arroyos or ephemeral channels in northeastern New Mexico are important in transporting and transforming organic matter that enhances the fertility of agricultural areas along downstream alluvial fans. More frequent but low-intensity rainfall was important in driving biochemical transformations that altered organic matter mobility and quality, which was subsequently transported downstream by larger storms (Norton et al., 2007). Traditional farming practices in the region relied on the temporary storage, transformation, and transport of organic matter from ephemeral streams (Norton et al., 2007; Sandor et al., 2007).

Although organic matter clearly is exported from headwater streams, effects on downstream organisms, and the distance over which these effects propagate are difficult to quantify (Wipfli et al., 2007). Many downstream organisms 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), each with its own transport dynamics, makes tracking sources of downstream contributions difficult. Given the prevalence of headwater streams in both the landscape and the river network (Leopold et al., 1964), and their primacy in organic matter collection and processing, a logical conclusion is that headwater streams exert a strong influence on downstream organic matter dynamics. Benstead and Leigh (2012) estimated that headwater streams, including intermittent and ephemeral channels, result in a global carbon efflux of 1.6 Pg C yr^{-1}, making the overall contributions of rivers and streams about equivalent to all inland lakes and wetlands combined. In addition, headwater streams also serve as a source of colonists for downstream habitats (Section 3.5). For example, headwater springs can provide algae a winter refuge from freezing, then serve as a source of propagules for downstream reaches upon spring thaws (Huryn et al., 2005).

3.4.3 Ions

Measurements of ions and conductivity from nested study designs provide additional evidence for connectivity by various transport mechanisms. Rose (2007) collected data at 52 sampling stations in Georgia's Chattahoochee River basin, which includes the heavily urbanized region of Atlanta, over a 2-year period. The study sought to characterize baseflow hydrochemistry across a rural-to-urban land-

use gradient. A plot of the major ion (sodium, bicarbonate alkalinity, chloride, and sulfate) concentrations versus downstream river distance showed distinct peaks relative to baseflow measurements, 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 headwater streams were transporting ions downstream and affecting downstream conductivity. This spatial pattern in conductivity was consistent between spring and summer surveys of the river network.

In a study in Sweden, measurements of pH from the outlets of seven watersheds were statistically related to headwater pH measurements in those watersheds (Temnerud et al., 2010). As pH at outlets increased under low-flow conditions, so did median pH of the headwater streams. This study illustrates the connectivity between the headwater components of the river network and the outlets of the watersheds and the cumulative effects of headwater streams to downstream waters.

3.4.4 Contaminants and Pathogens

The movement of contaminants—that is, substances that adversely affect organisms when present at sufficient concentrations—and waterborne pathogens provides another line of evidence for chemical connectivity between tributaries and the river network. Existing information typically has been derived from either empirical experiments that release tracer substances into streams to monitor movement along a longitudinal gradient or the use of modeled projections and characterization of contaminants. Studies also have examined trace metal 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, wastewater treatment plant discharges). These studies provide a way to understand sediment transport in streams and rivers and to determine how metals are spatially and temporally dispersed in the watershed (Rowan et al., 1995).

The degree of surface-water and ground-water mixing or exchange in the hyporheic zone influences the transport and uptake of trace metals. In a 7 km perennial stream segment contaminated by copper mining in Arizona, 20% of the dissolved manganese load was removed by microbial activity that was likely stimulated by the physicochemical conditions and increased residence time (compared with surface channel residence time) associated with hyporheic exchange (Harvey and Fuller, 1998). That oxidation of manganese enhanced the uptake of other trace metals and thereby decreased cobalt, nickel, and zinc loads 12–68% over the 7 km reach (Fuller and Harvey, 2000). Modeling the contributions of hyporheic exchange on contaminant dynamics over entire river networks requires further research.

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 streams resulting from coalbed methane extraction activities that are connected to the perennial Powder River, WY. Iron, manganese, arsenic, fluoride, dissolved oxygen, pH, and turbidity differed across sample locations, demonstrating connectivity between wellhead discharge and ephemeral streams. The contribution of ephemeral streams was detected in the Powder River, where pH was consistently elevated downstream of the confluence with a high-pH stream (Patz et al., 2006).

In a broader study, Wang et al. (2007) used retrospective USGS data (1946–2002) to investigate 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. The study indicated that coalbed methane development could have detrimental effects on the Powder River, especially in terms of sodium adsorption ratio (sodicity). Although the authors indicated connectivity and adverse effects in stream quality with increased sodium and stream sodicity, data also revealed inconsistent patterns associated with complex spatial variability within the drainage basin due to the geographic distribution of the coalbed methane wells.

The spatial extent of metal transport has been demonstrated in the upper Arkansas River of 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 cadmium, lead, and zinc concentrations and downstream distance. That same spatial distribution pattern in bed sediment metal concentrations was observed from headwater streams to the downstream 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, bed sediment metal concentrations from river sites were inversely related to downstream distance, and predictions from those models indicated that sediments with metals originating from headwater mining and smelting areas were reaching Lake Pend Oreille, more than 550 km downstream. Hornberger et al. (2009) used a 19–year data set from the Clark Fork River, with sites from the headwater streams to 190 km downstream, and found that bed sediment copper concentrations at downstream sites were positively correlated with concentrations at upstream sites.

Lewis and Burraychak (1979) examined the downstream transport of heavy metals from ephemeral and intermittent streams to a downstream perennial stream, due to the impacts of active and abandoned copper mines. 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 waste from tailings ponds (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 (Lewis and Burraychak, 1979). 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 organisms.

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 web and sediments also were detected below the discharge point (Lewis and Burraychak, 1979).

Lampkin and Sommerfeld (1986) similarly showed that intermittent streams can contribute highly mineralized, acidic waters to a downstream perennial reach, 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. 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 headwater streams. All heavy metal and sulfate concentrations were higher 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.

As discussed in previous sections, headwater streams are connected to downstream waters through the transport of chemicals but also through transformation processes. Boreal river networks, in which headwater streams are sources of DOC and pH increases downstream, provide these transformations. Iron exported from the acidic headwater tributaries is bound to DOC (mobile form). As pH increases, iron-rich ground water enters the channel, and iron transforms to iron (oxy) hydroxides that aggregate and precipitate out of solution (Neubauer et al., 2013). These iron (oxy) hydroxides can function as carriers of toxic metals and metalloids (e.g., arsenic), thereby removing them from solution and temporarily storing them in and along the river network (Neubauer et al., 2013).

Several studies also have projected the cumulative effect of headwater systems on downstream mercury concentrations and loads in response to land use, climate, and atmospheric deposition. The Water Quality Analysis Simulation Program and the Bioaccumulation and Aquatic System Simulator models were used to predict changes in water, sediment, and fish-tissue mercury concentrations across water bodies with varying upstream headwater drainage areas (Knightes et al., 2009). Simulations predicted that watersheds with high headwater drainage densities would exhibit longer lag times for mercury delivery downstream compared to those with low headwater drainage densities. This work suggests that headwater streams can serve a mercury storage function, and that temporally varying connectivity contributes to the transport of mercury from headwater streams to downstream waters.

The cumulative effects of land-cover change on total and methylmercury fluxes from a North Carolina headwater watershed to the Cape Fear River were simulated using the Grid Based Mercury Model (Golden and Knightes, 2011). The simulations estimated a 95% increase in total mercury fluxes from the landscape to downstream waters in response to new suburbanization and a 7% decrease in total and

methylmercury export in response to reforestation. Predicted changes in total mercury fluxes from the landscape to the downstream assessment point resulted primarily from changes in landscape land cover, rather than changes in connections within the river network.

The effects of climate change on total mercury export from headwater tributaries draining a Coastal Plain watershed (79 km^2) in South Carolina were simulated using multiple watershed models (Golden et al., 2014). Results indicated increased total mercury export under the high-precipitation scenario and decreased total mercury export under the low-precipitation scenario, showing that precipitation, and thus hydrologic connections, drive mercury transport from headwater streams to downstream waters.

Contaminants are commonly transported from tributaries to downstream rivers bound to sediments. Using isotopic fingerprinting, Gehrke et al. (2011) identified different tributaries as contributing to downstream mercury contamination of surface sediments in San Francisco Bay. Historic gold mining in the tributary watersheds of the San Joaquin and Sacramento Rivers contributed to contaminated mercury sediments in the northern part of San Francisco Bay, whereas wastes from mercury mine operations were delivered to the southern part of the bay via the Guadalupe River (Gehrke et al., 2011).

Studies of radionuclide (e.g., plutonium, thorium, uranium) distribution, transport, and storage provide convincing evidence for long-distance chemical connections in river networks. Although the natural occurrence of radionuclides is extremely rare, their production, use, and release for military and energy applications have been monitored for more than 50 years. Like metals, radionuclides adsorb readily to fine sediment; thus, the fate and transport of radionuclides in sediment generally mirrors that of fine sediment. From 1942 to 1952, 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 (152 km^2 drainage area), which 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) is 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 plutonium from testing fallout was readily transported to headwater streams in the upper Rio Grande basin via erosion and subsequent overland movement. The distribution of plutonium within the Rio Grande illustrates how headwater streams transport and store contaminated sediment that has entered the basin through both fallout and direct discharge. Although Los Alamos Canyon represented only 0.4% of the drainage area at its confluence with the Rio Grande, its mean annual bedload contribution of plutonium was almost seven times that of the mainstem (Graf, 1994). Much of this contribution occurred sporadically during intense storms that were out of phase with flooding on the upper Rio Grande. Total estimated contributions of plutonium 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 to 1985 is stored in the river and its floodplain; the remaining amount is stored in a downriver reservoir. Similar export of radionuclides through a river network has been traced following the Fukushima Dai-ichi Nuclear Power Plant accident in Japan (Chartin et al., 2013). The highest levels of radionuclide fallout were in areas drained by headwater tributaries. Isotopic analysis of sediment-bound radionuclides collected from throughout the river network over time documented the downstream transfer of contaminated sediment during a succession of summer typhoons and spring snowmelt (Chartin et al., 2013).

Waterborne pathogens (bacteria, viruses, protozoa) are another class of contaminants of concern because of the associated risks to human health and well-being. The principal origins of waterborne pathogens to downstream waters are as point and diffuse sources from livestock and municipal wastes via tributaries (Ferguson et al., 2003). Rainfall events and waterborne disease outbreaks in the United States are strongly correlated, pointing to hydrologic connectivity through tributaries and stormwater drains as a key link in transporting pathogens downstream, where they can overwhelm treatment plants and eventually contaminate drinking water sources (Curriero et al., 2001). Ephemeral and intermittent tributaries also transport waterborne pathogens downstream from livestock and human waste (e.g., Parker et al., 2010; Wilkes et al., 2013). Moist sediments in and near ephemeral and intermittent streams can act as temporary pathogen reservoirs (Chase et al., 2012). Survival of fecal indicator bacteria in dry sediments of an intermittent stream was high and remained constant over 1 month, but declined to unculturable levels after 51 days at 20 °C and 163 days at 5 °C (Chahinian et al., 2012). As for contaminants, various physicochemical (e.g., discharge, nutrient concentrations, temperature, humic acids) and biological (predation, competition) conditions in tributaries can mediate the transport or inactivation of pathogens (Ferguson et al., 2003).

3.5 Biological Connections

Biological connections are linkages throughout the river network, from headwater streams (including those with intermittent and ephemeral flow) to their downstream waters, that are mediated by living organisms or their products (e.g., seeds, exudates, or excreta; Lamberti and Resh, 1987).

Because biological connections often result from passive transport of organisms or their products with water flow, biological connectivity often depends on hydrologic connectivity (Section 3.3.1). Many living organisms, however, also can 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 streams and downstream waters.

Biological connections between upstream and downstream reaches can affect downstream waters via multiple pathways or functions. For organisms capable of significant upstream movement, headwater

streams, including ephemeral and intermittent streams, can increase both the amount and quality of habitat available to those organisms. Many organisms require different habitats for different resources (e.g., food, spawning habitat, overwintering habitat), and thus move throughout the river network—both longitudinally and laterally—over their life cycles (Schlosser, 1991; Fausch et al., 2002). For example, headwater streams can provide refuge habitat under adverse conditions, enabling organisms to persist and recolonize downstream areas once adverse conditions have abated (Meyer and Wallace, 2001; Meyer et al., 2004; Huryn et al., 2005). Headwater streams also 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."

In this section, we consider longitudinal biological connections in terms of both the aquatic organisms—specifically invertebrates and fishes—that move along river networks and their consequent effects on downstream waters (see Section 3.4.2 for discussion of particulate organic matter dynamics and Section 3.4.4 for discussion of waterborne pathogens). We then discuss the importance of organism movement throughout the river network for genetic connectivity in a separate section. We also recognize the many important biological connections between river networks and terrestrial systems (Lamberti and Resh, 1987), but as discussed in Chapter 1, these connections are outside the scope of this document. Lateral biological connections between the river network and riparian and floodplain habitats are considered in Chapter 4.

3.5.1 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 organisms. 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 benthic invertebrate assemblage in downstream waters. Drift, however, has been shown to increase invertebrate mortality significantly (Wilzbach and Cummins, 1989), suggesting that most drifting organisms are exported downstream in the suspended detrital load (Section 3.4.2).

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). This export of invertebrates can be especially high in intermittent and ephemeral streams, as terrestrial invertebrates accumulate in these channels during dry periods and are then transported downstream upon channel rewetting (Corti and Datry, 2012; Rosado et al., 2015). The amount of invertebrate drift often is closely related to stream discharge (e.g., Harvey et al., 2006), as well as 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 through a combination of high productivity and upstream dispersal (Hershey et al., 1993; Humphries and Ruxton, 2002). This dispersal creates downstream to upstream biological connections along the river network; for organisms capable of directed movement over long distances (e.g., winged adult forms of aquatic invertebrate larvae), these connections can occur over significant network distances.

Given this evidence, that headwater streams are biologically connected to downstream waters via the active and passive export of invertebrates is clear, and the cumulative export of invertebrates from numerous headwater streams to downstream waters can be substantial. As with organic matter, however, assessing the effect of headwater invertebrate production and export on downstream waters is difficult, given that these resources enter downstream waters at multiple points and times throughout the river network. Nevertheless, some studies have documented the importance of drifting invertebrates for downstream organisms. Wipfli and Gregovich (2002) estimated that drifting insects and detritus (i.e., particulate organic matter; Section 3.4.2) from fishless headwater streams 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 streams to feed and grow is likely conservative (Section 3.5.2). 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).

Headwater 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). Intermittent streams also can 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. After disturbance, these upstream 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. Dry stream channels also can facilitate dispersal of aquatic invertebrates by serving as dispersal corridors for terrestrial adult forms (Bogan and Boersma, 2012; Steward et al., 2012).

Headwater stream invertebrates also provide critical functional roles in maintaining physical and chemical connectivity to downstream waters (Covich et al., 1999). Invertebrates accelerate the breakdown of coarse particulate organic matter (e.g., leaves) to more mobile fine and dissolved forms (Section 3.4.2; Wallace and Webster, 1996); promote algal productivity and microbial activity (and nutrient uptake) by biofilm grazing (Feminella and Hawkins, 1995); and temporarily store and transfer sediments, nutrients, and contaminants through their trophic and physical activity (e.g., via

bioconsolidation and bioturbation; Pringle et al., 1993; Walters et al., 2008; Statzner, 2012). The contribution of invertebrates in controlling sediment mobilization can be substantial. For example, Statzner (2012) estimated that the discharge necessary to move approximately 0.4 kg of sediment s^{-1} in the Colorado River would increase by an order of magnitude in response to bioconsolidation by net-spinning caddisflies and would decrease by an order of magnitude in response to bioturbation by crayfish.

Diverse and abundant invertebrate assemblages also inhabit the hyporheic zone of river networks (Stanford and Ward, 1988; Boulton, 2000). Hyporheic assemblages are composed of invertebrate species that inhabit shallow subsurface sediments within streambeds to various degrees. Some taxa spend their entire lives in the hyporheic zone (Boulton, 2000). Other taxa spend only part of their life cycles, typically their earliest larval stages or periods of disturbances, in the hyporheic zone, and others spend their entire aquatic stages in the hyporheic zone then migrate out for their aerial adult stages (Boulton, 2000). These hyporheic assemblages make similar contributions to physical and chemical connectivity with downstream waters as benthic invertebrates do, while also enhancing hyporheic exchange (Section 3.3.1) through movements and migration within the hyporheic zone (Boulton, 2000).

3.5.2 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 headwater streams, contributing to regional aquatic biodiversity (e.g., Paller, 1994). As with invertebrates, however, 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 evident for the many diadromous species that migrate between headwater 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 headwater streams and larger rivers.

Through their activities, migratory fish can be important in modifying habitat, and transforming and transporting materials (e.g., Taylor et al., 2006; Hassan et al., 2008). Return migration of diadromous fishes provides a feedback loop in which marine-derived nutrients are transported upstream to headwater streams, for subsequent processing and export (Section 3.4.1). This example illustrates how biological connections also can create chemical connections throughout the river network. Migratory fish also can bioaccumulate and transport contaminants long distances between headwater streams and downstream waters (e.g., Krümmel et al., 2003; Morrissey et al., 2011). Fish also can act as transport vectors of other organisms (e.g., seeds, pathogens, glochidia), moving other organisms against flow or extending their dispersal distances (e.g., Chick et al., 2003; Senderovich et al., 2010; Schwalb et al., 2013). Even nonmigratory taxa can travel substantial distances within river networks throughout their life cycles (Gorman, 1986; Sheldon, 1988; Hitt and Angermeier, 2008). As a result, the distribution and

movement of fish throughout river networks can be highly variable, both spatially and temporally (Schlosser, 1991; Labbe and Fausch, 2000; Fausch et al., 2002).

The importance of connectivity in structuring fish assemblages provides further evidence of biological connections along river networks. Fish assemblages among connected streams tend to be more similar, in that assemblages in reaches located closer together tend to have more species in common than assemblages 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 of fish assemblages (e.g., Osborne and Wiley, 1992; Smith and Kraft, 2005).

The importance of biological connections along river networks is often highlighted by human alterations that affect these connections. For example, fish assemblages within highly connected river networks were more homogeneous, whereas fragmentation by road crossings resulted in greater dissimilarity of fish assemblages between upstream and downstream habitats (Perkin and Gido, 2012). 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), and fragmentation of river networks has been consistently related to local extinction of salmonid populations (Morita and Yamamoto, 2002; Letcher et al., 2007).

For certain taxa, headwater streams—including intermittent and ephemeral streams— provide critical habitat for specific portions of their life cycles. Many fish, both salmonids and nonsalmonids, spawn in headwater 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). Kanno et al. (2014) found that many brook trout moved between mainstem and tributary habitats over their life cycles. Because reproductive success varied across these habitats, this movement resulted in substantial gene movement into tributary habitats (Section 3.5.3).

After spawning, fish using headwater streams 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 headwater streams, 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; Ebersole et al., 2009), perhaps due to warmer temperatures and higher prey and lower predator densities (Limm and Marchetti, 2009).

In prairie streams (Section B.4), the importance of hydrologic connectivity for biological 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). Platania and Altenbach (1998) estimated 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. Adult fish then migrate upstream prior to egg release (Fausch and Bestgen, 1997). Thus, these fishes require hydrologic connectivity to maintain both upstream and downstream 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) and 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 streams often depend on ground-water inputs, temperatures in these ecosystems tend to be warmer in winter (when ground water is warmer than ambient temperatures) and colder in summer (when ground water is colder than ambient temperatures), relative to reaches farther downstream (Section 3.3.4; Power et al., 1999). Thus, these headwater streams 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), again highlighting the spatial and temporal variability of these fish-based biological connections. In some cases, loss of coolwater refuges can facilitate invasion by species more tolerant of warmwater conditions (Karr et al., 1985).

Headwater streams also can provide refuge from flow extremes. Fish can move into headwater streams, including intermittent streams, to avoid high flows downstream (Wigington et al., 2006); fish also can move downstream during peak flows (Sedell et al., 1990), highlighting the bidirectionality of biological connections within these systems. Low flows can cause adverse conditions for organisms, as well, and residual pools that are 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—that is, 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 streams can provide these taxa refuge from other species and enable 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 headwater streams when they were present. The role of headwater streams 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 streams 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). For example, 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).

3.5.3 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 watershed (Hughes et al., 2009; Anderson et al., 2010), and in diapausing organisms, can provide a direct link between distant generations (dispersal through time; Bohonak and Jenkins, 2003).

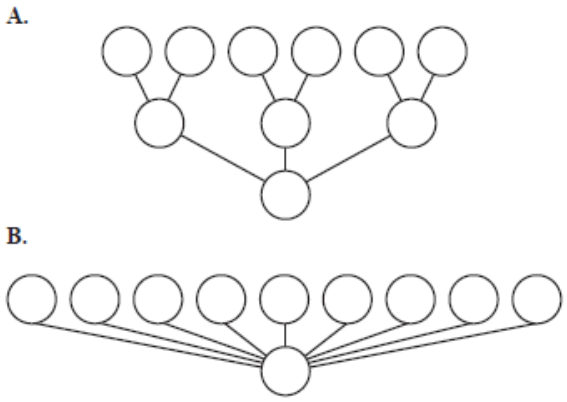
Although physical barriers can protect headwater habitats and populations by isolating them from colonization by and hybridization with invasive species (Section 2.3.2.1), isolation also can have serious adverse effects on native species via reductions in genetic connectivity. For example, Hanfling and Weetman (2006) found that artificial 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 artificial 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 (Section 2.4.2), the direction of dispersal (upstream, downstream, or both), dispersal modes and pathways used (e.g., swimming, flying), and species' life histories (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 (Figure 3-4) 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.

Figure 3-4. (A) A dendritic network with multilevel hierarchical structure, and (B) a uninodal network with all headwater streams feeding directly into a river mainstem. Source: Reprinted from The maintenance of genetic variation due to asymmetric gene flow in dendritic metapopulations, (2009) by Morrissey and de Kerckhove with permission of The Univ of Chicago Press.



Most empirical evidence for the role of headwater streams 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.

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 was strongly correlated with tree cover in first-order (headwater) stream watersheds. 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).

3.6 Streams: Synthesis and Implications

Despite widespread human alterations, rivers are not simple conduits draining watersheds. A river, including the water and material it carries and the organisms living in it, represents the cumulative longitudinal, lateral, and vertical connections of its network of channels integrated over time (Section 1.2.3). Although we recognize that streams also exchange water and other materials with nearby terrestrial and deep ground-water systems via lateral and vertical connections, this chapter focused on longitudinal surface-water connections between streams and rivers, as well as shallow subsurface-water interactions integral to surface-water connections and downstream water condition.

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 (Section 2.2.1). A stream must be linked to a larger, downstream water body by a channel for the two to have a surface-water (hydrologic) connection. Although some streams lack a channel connection to larger water bodies (i.e., small endorheic basins), they are the exception. Streams that link larger water bodies through networks of continuous bed and bank are the rule. The network structure reflects the aggregate and cumulative nature of the connections between distant headwater streams and the downstream river.

Although not comprehensive or equally studied among all stream types, the existing science indicates that connectivity with downstream waters varies among streams and over time. This variation in connectivity to downstream waters can be described as a connectivity gradient, ranging from highly connected to highly isolated (Section 1.2.2). A stream's position on the gradient is influenced not only by distance to downstream waters but also by the frequency, magnitude, duration, timing, and rate of change of fluxes to downstream waters. Connectivity is dynamic: It changes with immediate, seasonal, and interannual or interdecadal (e.g., climate oscillations) conditions that affect the availability and distribution of water, materials, and biota. Because connectivity is dynamic, a complete understanding of a stream's connections and consequences to downstream waters should aggregate connections over relatively long time scales (multiple years to decades; Section 1.2.3). Although distance between streams and downstream waters vary, other factors such as intervening resistance, relative size or chemical load, and species assemblage also influence the degree of connectivity with and level of consequence on downstream waters. Despite being distant from downstream waters, headwater streams make up the majority of stream channels in most river networks and cumulatively supply most of the water in rivers.

Streams are functionally connected to rivers by the movement of water and other materials through this network of channels (Table 3–1). The longitudinal, vertical, and lateral connections within river networks are inextricably tied. Even losing-stream reaches that at times lack sufficient flow for hydrologic 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 (e.g., water, organic matter, organisms) to downstream waters. The most compelling evidence linking headwater streams to downstream habitats supports source, sink (or lag), and transformation functions (Section 2.3.1; Table 2-1). For example, studies that involved sampling throughout river networks have documented headwater streams as sources of water (via floods and baseflow) to rivers (Section 3.3.1). Nitrogen and carbon transported from headwater streams cumulatively contribute to nitrogen and carbon levels in downstream rivers, and headwater streams can function as nitrogen and carbon sinks for river networks (Sections 3.4.1 and 3.4.2). 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 (Section 3.4.4). Many organisms, such as anadromous salmon, have complex life cycles that involve migration through the river network, from headwater streams to downstream rivers and oceans, over the course of their lives (Section 3.5). 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 closely located stream reaches—which numerous studies have documented, for a variety of materials—can be extended over large spatial scales.

Table 3-1. Examples of mechanisms by which streams are connected to and influence downstream waters, by functional type. See relevant section and appendix numbers in parentheses for greater detail. Note that the distinction between types of functions is not always clear. For example, denitrification can be considered a sink or transformation function. Bold letters represent the primary type of connection (B = biological; C = chemical; and P = physical).

Source Function
• Streams supply water downstream through baseflow and floods that influence discharge and habitat (3.3.1, B.4.2.5, B.4.3.1.1, B.5.3, B.5.4.2, B.5.5.1). **P** • Streams supply downstream waters with sediment (3.3.2, 3.4.4, B.4.3.1.3, B.5.3, B.5.4.2). **P** • Streams supply downstream waters with nutrients and other ions (3.4.1, 3.4.3, B. 4.3.2.1, B.5.4.2). **C** • Streams can transport to downstream waters contaminants and pathogens that adversely affect organisms and human health (3.4.4, B.4.3.1.3). **C** • Streams supply dissolved and particulate organic matter that can fuel heterotrophy in downstream waters and influence physicochemical conditions (3.3.3, 3.4.2, B.4.3.2.2, B.5.4.2). **C** • Organisms actively and passively move between streams and downstream waters, carrying with them nutrients, contaminants, pathogens, and other organisms (3.5, B.4.2.4, B.4.3.3). **B** • Organisms can enhance the supply of materials to downstream waters (3.5.1, 3.5.2). **B**
Sink Function
• Streams can divert surface flow from downstream waters via infiltration into underlying alluvium and evapotranspiration to the atmosphere (3.3.1, B.5.3, B.5.4.2, B.5.5.1). **P** • Streams can divert nitrate from downstream waters via denitrification (3.4.1, B.4.3.2.1). **C** • Streams can prevent sediment and associated contaminants from being transported to downstream waters through deposition on floodplains (3.3.2, 3.4.4, B.5.3). **C**
Refuge Function
• Streams can afford protection from temperature extremes, drying, predators, and competition with nonnative species for organisms that inhabit downstream waters (3.5, B.4.3.3). **B**
Transformation Function
• Streams can mediate the form and mobility of nutrients before they enter downstream waters via nutrient spiraling (3.4.1, B.4.3.2.1). **C** • Streams can mediate the form and mobility of organic matter before they enter downstream waters via carbon spiraling (3.4.2, B.4.3.2.2). **C** • Streams can mediate the form and mobility of contaminants before they enter downstream waters via hyporheic exchange or exposure to other physicochemical gradients that lead to biogeochemical transformations (3.4.4). **C** • Organisms can mediate the transformation of materials through their trophic and physical activities (3.4.1, 3.4.2, 3.5.1, 3.5.2, B.4.3.2.2). **B**
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 (3.3.1, 3.3.3, B.4.3.1.1, B.5.3, B.5.4.2). **P** • Streams can delay sediment from arriving at downstream waters through local and network structures (3.3.2, 3.3.3, 3.4.4, B.5.3). **P** • Streams can delay nutrients from arriving at downstream waters through local and network structures and biological uptake (3.4.1, B.4.2.4, B.4.3.2.1). **C** • Streams can delay organic matter from arriving at downstream waters through local and network structures and biological uptake (3.3.3, 3.4.2, B.4.3.2.2). **C** • Streams can delay contaminants from arriving at downstream waters through local and network structures and exchanges that enhance mineralization and precipitation or adsorption to sediment, or both (3.4.4). **C** • Organisms can delay nutrients, organic matter, and contaminants from arriving at downstream waters through consumption, assimilation, and bioconsolidation (3.4.1, 3.4.2, 3.5.1, 3.5.2, B.4.3.2.2). **B**





CHAPTER 4. WETLANDS: PHYSICAL, CHEMICAL, AND BIOLOGICAL CONNECTIONS TO RIVERS

4.1 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 (i.e., from wetlands to rivers and streams, but not vice versa) of surface water and ground water from upgradient areas (e.g., hillslopes and nearby uplands). In addition, riparian/floodplain wetlands have bidirectional connections to streams and rivers (i.e., from wetlands to streams and rivers and vice versa) through lateral movement of surface and ground water between the channel and riparian/floodplain areas. Connections between riparian/floodplain wetlands and streams or rivers occur over a gradient of connectivity, for example, they 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; Sections 1.2.2 and 2.4.2). 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, store 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 non-floodplain landscape settings lack bidirectional hydrologic connections with channels (i.e., water flows from the wetland to the channel but not from the channel to the wetland). These settings, however, have the potential for unidirectional hydrologic flows from wetlands to the river

network through surface water or ground water. Non-floodplain wetlands can attenuate floods through depressional storage and can recharge ground water and thereby contribute to baseflow. These wetlands can affect nutrient delivery and improve water quality by functioning as sources (e.g., of dissolved organic carbon) and as sinks for nutrients (e.g., nitrogen), metals, and pesticides. Non-floodplain wetlands also can 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 non-floodplain wetlands perform these functions depends on their hydrologic and biological connectivity with downstream waters. Non-floodplain wetlands also occur on a hydrologic gradient, from wetlands having permanent connections with perennial channels, to geographically isolated wetlands having ground-water or occasional surface-water connections, to highly isolated wetlands having minimal hydrologic connection to the river network (but which could include surface and subsurface connections to other wetlands; Section 4.4.2). Non-floodplain wetlands that are connected to the river network through a channel (i.e., wetlands that serve as stream origins) will have an effect on downstream waters, regardless of whether the outflow is permanent, intermittent, or ephemeral. For non-floodplain 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.

This literature review is unable to provide evaluations of connectivity for specific groups or classes of wetlands (e.g., prairie potholes or vernal pools). Evaluations of individual wetlands or groups of wetlands, however, could be possible through case-by-case analysis. We can conclude the following:

1. A non-floodplain 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 influence on downstream waters.

2. Many non-floodplain wetlands interact with ground water, which can travel long distances and affect downstream waters.

3. Even when wetlands lack a hydrologic connection to other water bodies, they can influence downstream water through water and material storage and mitigation of peak flows (flood reduction and flood attenuation). Sink functions of non-floodplain wetlands will have effects on a downstream water when these wetlands are situated between the downstream water and known point or nonpoint sources of pollution, thereby intersecting the flowpath between pollutant source and downstream water. More generally, wetland sink functions are likely to be greatest when the wetland is located downgradient from pollutant sources and upgradient from a stream or river.

4. Within a watershed or wetland landscape setting, 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. Caution should be used in interpreting connectivity for wetlands that have been designated as "geographically isolated."

4.2 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 (Section 1.1): (1) What are the connections to and effects of riparian/floodplain wetlands and open waters (e.g., oxbow lakes) on downstream waters? (2) What are the connections to and effects of non-floodplain wetlands and open waters on downstream waters?

In Chapter 1, we provided the scientific context for concepts and gradients of connectivity in hydrology and ecology (Section 1.2). In Chapter 2, we provided definitions for wetlands, gave a rationale for distinguishing between wetlands in riparian/floodplain and non-floodplain 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 riparian/floodplain wetlands to those occurring in riparian and floodplain settings. Below, we provide a detailed review of the contributions of riparian/floodplain wetlands (Section 4.3) and non-floodplain wetlands (Section 4.4) to rivers, followed by conclusions concerning these wetlands and their effects on rivers (Section 4.5). Examples of some of the functions discussed in these two sections are found in Table 4-1. In addition, four case studies on specific types of wetlands or lentic waters representing different landscape settings and geographic regions are in Appendix B: Carolina and Delmarva bays (Section B.1), oxbow lakes (Section B.2), prairie potholes (Section B.3), and vernal pools (Section B.6).

Much 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) to which the wetland(s) are connected or which they influence. If available, we note this information (e.g., whether riparian areas were located in floodplains or along portions of river networks without floodplains), but often we can discuss only generic connections to streams, rivers, or downstream waters. Given that rivers are connected to all upstream components of the river network, including streams (Chapter 2), and the functional relationships between streams and rivers (Chapter 3), however, we consider any evidence of connectivity with a stream (other than endorheic streams; Sections 3.2 and B.5.5.1) to be evidence of connectivity with the river and other downstream waters.

4.3 Riparian/Floodplain Wetlands

4.3.1 Introduction

This section focuses on the connections and influence of riparian/floodplain wetlands on downstream waters. As previously defined in Section 2.2.1, riparian/floodplain wetlands are locations within riparian areas and floodplains (Figures 1-1A, 2-2, and 2-3), respectively, that meet the Cowardin et al. (1979)

Table 4-1. Examples of mechanisms by which riparian/floodplain wetlands and wetlands in non-floodplain settings influence downstream waters, by functional type. See relevant section and appendix numbers in parentheses for more detail. Note that the distinction between types of functions is not always clear, for example, denitrification could be considered a sink or transformation function.

Source Function
• Riparian/floodplain wetlands and non-floodplain wetlands connected to the stream network by channelized flow—ranging from ephemeral to permanent—are sources of downstream water (4.3.2.1, 4.4.2.1, B.1.2.3, B.2.3.1, B.3.3.1, B.6.3.1). • Wetlands that serve as origins for streams (e.g., seeps) can be sources of ground-water discharge, contributing to stream baseflow (4.4.2.3). • Non-floodplain wetlands lacking a channel outlet can be sources of water via overland flow to the stream network if wetland storage capacity is exceeded (4.4.2.1, B.3.3.1, B.6.3.1.1). They can also provide water via subsurface drains ("tile drains") or surface ditches (4.4.2.1, B.1.3.1, B.3.3.1). • Riparian/floodplain wetlands and non-floodplain wetlands can be sources of nutrients and sediments to downstream waters (4.3.2.2, 4.3.3, 4.4.3.1, B.1.3.2, B.3.3.2). • Riparian areas are a source of allochthonous inputs, the primary energy input into the food webs of small, forested streams (4.3.3.4). They also are sources of woody debris that can affect stream morphology and flow regime, and provide habitat for aquatic organisms (4.3.2.2). • Riparian areas and non-floodplain wetlands can be sources of dissolved organic matter that aquatic food webs use, with additional potential effects on pH and mercury concentrations of downstream waters (4.3.3.4, 4.3.3.6, 4.4.3.1). • Riparian/floodplain wetlands and non-floodplain wetlands can be sources of organisms, including plants, invertebrates, amphibians, reptiles, and fish, to downstream waters transported via passive or active dispersal (4.3.4, 4.4.4, B.2.3.3, B.3.3.3, B.6.3.2). • Riparian/floodplain wetlands can provide feeding habitat for riverine organisms, such as fish, during periods of overbank flow (4.3.4.2, B.2.3.3).
Sink Function
• Riparian/floodplain wetlands and non-floodplain wetlands can be sinks for water by intercepting overland or subsurface flow, if available water storage capacity of the wetlands is not exceeded, which can reduce or attenuate flow to downstream waters and flooding (4.3.2.1, 4.4.2.3, B.3.3.1). • Riparian areas and non-floodplain 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 (4.3.2.2, 4.3.3, 4.4.3.2). • 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 (4.3.2.1, 4.3.2.2, 4.3.3, B.2.3.2). They can also be sinks for seeds and plant fragments deposited via overbank flow (4.3.4.1). • Riparian/floodplain wetlands and non-floodplain wetlands can be sinks for nitrogen by converting oxidized forms of nitrogen to molecular nitrogen through denitrification, which is then lost to the atmosphere (4.3.3.2, 4.4.3.2).
Refuge Function
• Riparian/floodplain wetlands and non-floodplain wetlands can provide refuge for fish, aquatic insects, or other lotic organisms from predators or other environmental stressors, facilitating individual or population survival (4.3.4, 4.4.4). • Riparian/floodplain wetlands and non-floodplain 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 (4.4.4, B.1.3.3, B.6.3.2; Table 4-2); non-floodplain wetlands are additionally nesting and nursery sites for American alligators that otherwise primarily reside in streams (4.4.4).

Table 4-1. Examples of mechanisms by which riparian/floodplain wetlands and wetlands in non-floodplain settings influence downstream waters, by functional type. See relevant section and appendix numbers in parentheses for greater detail. Note that the distinction between types of functions, is not always clear, for example, denitrification could be considered a sink or transformation function (continued).

Transformation Function
• Microbial communities in riparian/floodplain wetlands and non-floodplain wetlands can transform elemental mercury to methylmercury before it enters a stream. Methylmercury is a particularly toxic and mobile form that bioaccumulates in aquatic food webs (4.3.3.6, 4.4.3.1). • Riparian/floodplain wetlands and non-floodplain wetlands can transform nitrate to molecular nitrogen through denitrification (4.3.3.2, 4.4.3.2).
Lag Function
• Riparian/floodplain wetlands can temporarily store water following overbank flow, which then can move back to the stream over time as baseflow (4.3.2.1). • Non-floodplain wetlands can contribute to ground-water recharge under low water table conditions, which ultimately contributes to baseflow (4.4.2.3, B.3.3.1). • Non-floodplain wetlands can increase the time for stream discharge to rise and fall in response to a precipitation event due to wetland storage capacity (4.4.2.3).

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/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 floodplain and riparian literature broadly and include any results and conclusions that we judged pertinent to riparian/floodplain wetlands. This judgment was based, in part, on: (1) the processes described in the integrated systems perspective on interactions of watersheds, streams, wetlands and downstream waters (Sections 2.2.2 and 2.2.3); (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 that the processes and functions discussed occur in water bodies within those areas.

As addressed in Chapter 2, much of the theory developed to explain how river systems function has focused on linkages between system components (Vannote et al., 1980; Newbold et al., 1982a; Newbold et al., 1982b; Junk et al., 1989; Ward, 1989; Power et al., 1995a; Power et al., 1995b; Huggenberger et al., 1998; Ward, 1998; Fausch et al., 2002; Ward et al., 2002b; Wiens, 2002; Benda et al., 2004; Thorp et al., 2006; Humphries et al., 2015). The integral connectivity between rivers and their floodplains and riparian areas is a central tenet of stream hydrology and ecology, as is the substantial influence that this bidirectional exchange has on the physical form, hydrology, chemistry, and biology of the river system (Junk et al., 1989; Abbott et al., 2000; Tockner et al., 2000; Woessner, 2000; Amoros and Bornette, 2002; Ward et al., 2002a; King et al., 2003; Naiman et al., 2005; Church, 2006; Kondolf et al., 2006; Poole et al., 2006; Poole, 2010; Tockner et al., 2010; Vidon et al., 2010; Helton et al., 2011; McLaughlin et al., 2011; Humphries et al., 2015). For example, the flood pulse concept, which Junk et al. (1989) first articulated and Tockner et al. (2000) extended, is a fundamental paradigm in river ecology, depicting the lateral expansion and contraction of the river in its floodplain and the resulting exchange of matter and organisms.

The influence of riparian/floodplain wetlands on downstream waters is especially notable because of the potential magnitude and spatial extent of their interactions with rivers and their locations within river networks. Although floodplains can form in modest size streams (Hughes and Lewin, 1982), they typically form in the lower portion of river networks (Montgomery, 1999; Church, 2002, 2006), where they can provide transient storage and subsequent release of river water and materials (Stanford and Ward, 1993; Squillace, 1996; Mertes, 1997; Winter et al., 1998; Tockner et al., 2000; Fernald et al., 2001; Amoros and Bornette, 2002; Malard et al., 2002; Claxton et al., 2003; Davis et al., 2011). Floodplain patterns and river channel complexity are determined by sediment supply and character, river valley slope, stream power, woody debris, and vegetation (Montgomery, 1999; Church, 2002; Coulthard, 2005; Church, 2006; Osterkamp and Hupp, 2010; Sear et al., 2010; Collins et al., 2012). Circumstances conducive to the formation of complex, rapidly changing channel forms (e.g., anastomosing, braided, meandering) and the deposition of coarse sediment create conditions optimal for river-floodplain interactions (Nanson and Croke, 1992; Mertes et al., 1995; Fernald et al., 2001; Fernald et al., 2006; Poole et al., 2006; Whited et al., 2007).

Wetlands that occur in floodplains are referred to as riverine wetlands within the hydrogeomorphic classification system (Smith et al., 1995). Although floodplain wetlands can occur as marshes (Villar et al., 2001; Lee et al., 2005) or scrub-shrub wetlands (Chipps et al., 2006), these areas are known for supporting forested wetlands. Mitsch and Gosselink (2007) classify floodplain forested wetlands as freshwater swamps—for example, cypress-tupelo swamps (*Taxodium distichum* and *Nyssa aquatica*, respectively) and white cedar swamps (*Chamaecyparis thyoides*)—if water is available throughout most of the growing season, or as riparian ecosystems if the floodplain receives seasonal pulses of flooding. Examples of the latter are bottomland hardwoods in the Southeast—for example, sycamore-sweetgum (*Platanus occidentalis* and *Liquidambar styraciflua*, respectively) and cypress-tupelo forests—or

cottonwood-willow (*Populus* spp. and *Salix* spp., respectively) and alder (*Alnus* spp.) riparian communities in the Southwest (Mitsch and Gosselink, 2007).

This section provides further details on the connections between riparian/floodplain wetlands and streams and rivers, and the resulting effects. Below, we examine the physical (Section 4.3.2), chemical (Section 4.3.3), and biological (Section 4.3.4) effects of riparian/floodplain wetlands on rivers and other downstream waters.

4.3.2 The Physical Influence of Riparian Areas on Streams

4.3.2.1 Hydrology

Riparian areas within and outside of floodplains are an important part of the overall riverine landscape (Ward, 1998). Riparian areas are also connected to streams and rivers by a diverse set of hydrologic inputs and outputs (Figure 2-6A; Junk et al., 1989; Winter and Rosenberry, 1998; Benke et al., 2000; Tockner et al., 2000; Bunn et al., 2006). These inputs and outputs are described in Section 2.2 and have been 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 and rivers by capturing water from overbank flow and by storing excess water from streams (Mertes et al., 1995; Poole et al., 2006; Rassam et al., 2006). 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. Gamble et al. (2007) reported that 12 floodplain wetlands in Ohio stored an average of 3,654 m^3 ha^{-1} of water. The authors 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. As streamflow decreases after hydrologic events, the water temporarily stored in riparian/floodplain 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, nearly all of them have the potential to perform this function.

The potential for hydrologic connectivity between riparian/floodplain wetlands and rivers and streams is high during periods of overbank flow and during periods of lower streamflow. Hyporheic exchange occurs when water moves from river or stream channels into riparian or floodplain alluvial deposits and back to the channels, and it occurs during flooded and non-flooded conditions (Sjodin et al., 2001; Gooseff et al., 2008; Bencala, 2011) and on scales ranging from meters to kilometers (Stanford and Ward, 1988; Bencala, 1993, 2005). Complex floodplains typically are environments with high levels of hyporheic exchange (Woessner, 2000; Poole et al., 2006; Poole, 2010).

Vegetation in riparian/floodplain wetlands can influence hyporheic and river water through transpiration. Phreatophytes (plants that obtain their water from the saturated zone) can intercept ground-water and overland flow before it enters a stream and decrease streamflow by directly taking up stream water through their roots. For example, Meyboom (1964) studied two streams in the prairie region of the United States to understand the effect of floodplain vegetation on streamflow fluctuations. When the two streams decreased in flow, the floodplain vegetation accounted for 20% and 100% of this reduction (Meyboom, 1964).

4.3.2.2 Geomorphology (Sediment-vegetation Interactions)

A bidirectional relationship exists between fluvial geomorphology and riparian and floodplain vegetation (Corenblit et al., 2007). Distributions of vegetation communities often are shaped by river flow dynamics and associated erosional and deposition processes, but the communities also exert controls on geomorphic processes and riverine landforms.

Riparian/floodplain wetlands are key depositional environments for sediment that overland flow carries from erosion of nearby 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., oxbow lakes; Section B.2) and wetlands are effective at retaining eroded clays, silts, and sands that otherwise would 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 and floodplains 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 (Church, 2002, 2006). Heavy particles such as sand are the first to be removed, whereas finer, lighter particles such as clays and silts 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 and floodplains can also be a source of sediment to the stream, particularly through streambank erosion. Although streambank erosion is a natural process, it can be accelerated through vegetational changes because 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). In a study of 748 bends in four southern British Columbia streams, for example, Beeson and Doyle (1995) reported

that bank erosion was 30 times more prevalent on nonvegetated versus vegetated banks. In a comparison of row-crop agricultural, 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).

Riparian vegetation also influences stream and river geomorphology through inputs of woody debris or logs, which in turn shape stream channels (Brummer et al., 2006; Sear et al., 2010; Collins et al., 2012). 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 woody debris 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 3.3.3, 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).

4.3.2.3 Temperature and Sunlight

Riparian areas can modify stream temperatures and the amount of light available for photosynthesis in stream and river environments through stream shading, particularly in forested settings (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, strongly influences 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 on 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 directly influences the instream net primary productivity 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 productivity 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 limit stream productivity (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).

In addition to shading by riparian vegetation, riparian areas and floodplains can influence stream and river water temperature through hyporheic exchange (Brosofske et al., 1997; Naiman and Decamps, 1997; Poole and Berman, 2001; Naiman et al., 2005). Hyporheic cooling of stream and river water during warm summer periods has been observed in a wide range of settings, including large gravel bed rivers in Oregon (Fernald et al., 2006; Burkholder et al., 2008; Seedang et al., 2008), an alpine stream in the mountains of Colorado (Constantz, 1998), a boreal river in Sweden (Nyberg et al., 2008), and small streams in Illinois (Peterson and Sickbert, 2006) and northern California (Loheide and Gorelick, 2006). Important to note, however, is that hyporheic exchange can warm streams (Valett et al., 1990). Arscott et al. (2001) found that hyporheic and other thermal regulating processes can lead to large thermal heterogeneity of water bodies associated with complex floodplains. Hester and Gooseff (2010) argue that, for streams impacted by human activities, restoration of hyporheic zones is essential for the recovery of stream functions and ecosystem services.

4.3.3 The Chemical-nutrient Influence of Riparian Areas on Streams

Riparian areas in and outside of floodplains are instrumental in controlling the biogeochemistry of riverine systems through (1) overbank flooding (flood pulse); (2) internal biogeochemical processes; and (3) hyporheic exchange (Junk et al., 1989; Thurman et al., 1991; Heiler et al., 1995; Tockner et al., 2000; Adair et al., 2004; Noe and Hupp, 2005; Valett et al., 2005; Noe and Hupp, 2007; Helton et al., 2011; Powers et al., 2012; Bennett et al., 2015). All three mechanisms help shape nitrogen, carbon, phosphorus, and pesticide cycling with the riverine environment.

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 flowpaths 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 (Figure 2-6) 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 are essential to microbial respiration and are critical to both defining wetland systems and understanding transformational processes that microbes mediate (Boon, 2006; Reddy and DeLaune, 2008).

4.3.3.1 Hyporheic/Soil Processing of Nutrients

Riparian areas connect upland and aquatic environments through both surface and subsurface hydrologic flowpaths (Figure 2-6; Naiman et al., 2005). 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). These processes do not affect deep ground-water hydrologic flowpaths (Figure 2-5) that enter a river or stream below the active riparian root zone. The focus of this section, however, is on surface and shallow subsurface flows; we do not address deep ground-water flowpaths here.

Riparian areas can significantly influence 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). For instance, Johnston (1993) reported that a floodplain wetland retained, 15.2, 13.7, and 14.2% of the solids, total nitrogen, and total phosphorus fluxes, respectively, from the watershed. The degree to which a riparian area serves as either a source or a sink for nitrogen, phosphorus, organic matter, pesticides, and mercury is controlled largely 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).

4.3.3.2 Nitrogen

Riparian areas can remove dissolved nitrogen (N) 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). One study demonstrated that intact riparian and hyporheic zones are critical in decreasing the amount of dissolved inorganic nitrogen that moves from headwaters to larger, downstream waters (Triska et al., 2007). Vidon et al. (2010) showed that riparian areas remove more than half the nitrogen from surface and shallow subsurface water transporting ammonium and nitrate through the rhizosphere (Vidon et al., 2010). Leaching from nitrogen-fixing plants (e.g., red alder, *Alnus rubra*) in riparian systems, however, also can be a major source of nitrogen to stream systems (Compton et al., 2003).

Denitrification potential in surface and shallow subsurface flows is not homogeneous across the riparian area, increasing markedly in the presence of organic carbon or anoxic conditions that create denitrification "hot spots" (McClain et al., 2003; Orr et al., 2014). 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).

The highest denitrification potentials occur in floodplain systems where high organic matter levels, denitrifying microbes, and saturated soil conditions are present (Vidon et al., 2010). Rates of denitrification are greater in riparian soils nearer to streams (Gregory et al., 1991). Johnston (1993) reported nitrate removal along a floodplain gradient of 6.6 g per 100-m distance from the stream. High soil moisture and deposited organic matter enhance microbial activity, thereby tending to increase denitrification (Reddy and DeLaune, 2008).

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 (NO_3^-) transported from agricultural fields to a Maryland river (Vidon et al., 2010) was removed by riparian forests. Nitrogen was removed at a rate of 45 kg N 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 nitrate 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).

4.3.3.3 Phosphorus

The movement and uptake of phosphorus in riparian areas are a function of phosphorus sources, hydrology, and biogeochemistry (Vidon et al., 2010), with interactions between ground water and surface waters driving the biogeochemical processes (Hoffmann et al., 2009). 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 nearby 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 phosphorus 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 less than 0.5 kg P ha^{-1} yr^{-1} often reported. Studies show, however, significantly higher numbers for the release of dissolved phosphorus: up to 8 kg P ha^{-1} yr^{-1} (Hoffmann et al., 2009).

Although riparian soils generally serve as sources of phosphorus when soils are anoxic or when mineral dissolution releases phosphorus (Baldwin and Mitchell, 2000; Chacon et al., 2008), riparian areas are 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 also serve as phosphorus sinks when upland surface runoff travels through the riparian area or when fine-grained sediment containing phosphorus 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).

4.3.3.4 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 from riparian areas to streams 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 webs 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 affect food availability to aquatic organisms by releasing organic carbon and nitrogen into streams (Wetzel and Manny, 1972; Mulholland and Hill, 1997). For example, 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, also can 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, due to larger stream widths and consequently greater distances from the banks. This decreases 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.

4.3.3.5 Pesticides

The roots in riparian areas can be important in removing 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 surface area contact is high and contact time with roots is sufficient (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 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).

4.3.3.6 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, 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). Because some of this mercury and methylmercury moves from soils to surface waters, however, riparian areas might also be a source of the mercury that ends up in the aquatic food web.

4.3.4 Biological Connections Between Riparian Areas and Streams

The dynamic nature of river systems is most apparent in riparian areas and floodplains, where a shifting landscape mosaic supports diverse communities of aquatic, amphibious, and terrestrial plant and animal species adapted to periodic or episodic inundation of riparian areas and floodplains (Power et al., 1995a; Power et al., 1995b; Galat et al., 1998; Robinson et al., 2002; Toth and van der Valk, 2012; Rooney et al., 2013; Granado and Henry, 2014). In unregulated rivers, floodplain inundation greatly increases the area and diversity of aquatic habitats (Junk et al., 1989; Tockner et al., 2000; Brooks and Serfass, 2013). It also enables rapid cycling of nutrients imported from river channels (Section 4.3.3.2), 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; Bestgen et al., 2000; Schramm and Eggleton, 2006; Sullivan and Watzin, 2009; Alford and Walker, 2013; Magana, 2013), 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) and can be integral to the viability of many riverine species (Bunn and Arthington, 2002). Here, we review examples of adaptation to and exploitation of riparian habitats by aquatic species of plants, fish, mammals, and invertebrates.

4.3.4.1 Vascular Plants and Phytoplankton

Channels and riparian/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 example, 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 for which the seeds were 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 also can dislodge viable plant fragments in riparian/floodplain wetlands, which then are transported down the river network. Fragments of seep monkeyflower (*Mimulus guttatus*) are easily dislodged by the relatively high flow velocities along the riparian-channel interface, and fragments can survive and reestablish downstream at rates exceeding 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). For 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 (Sections 4.3.3.2 and 4.3.3.3). 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 example, seeds of the aquatic emergent bur-reed (*Sparganium emersum*) were 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). Riparian floodplain and wetland vegetation can also 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, feathers, or limbs between riparian/floodplain wetlands and the river network (see Sections 4.3.4.2, 4.4.4, and B.3.3.3 for discussions of animal movement). Many macrophyte species have evolved for dispersal by wind, including some of the most invasive in North America, cattail and reed canary grass (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 example, 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 than 100 seeds m^{-2} yr^{-1} (Middleton, 2000).

Phytoplankton also move 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, a nearby 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 web, which ultimately supports downstream

fisheries, resulted from the high net primary productivity of the floodplain. This observation is particularly noteworthy 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 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.

4.3.4.2 Vertebrates

Animals, including many fish and mammals, move between riparian/floodplain wetlands and the river network. The evidence is strong and abundant that fish can move between the main river channel and riparian/floodplain wetlands when the channel and wetlands are hydrologically connected, even when, in some cases, the connection is seasonal or temporary. Such wetlands provide refuge, feeding, and rearing habitat for many fish species and augment recruitment to the river network (Boltz and Stauffer, 1989); 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, more than 90% of the larval and juvenile fish of six 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 (Section B.2). 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 homogeneous 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). Miyazono et al. (2010), studying floodplain lakes in the Yazoo River Basin, found that conditions that included decreases in habitat connectivity, wetland buffers, and certain water quality parameters led to the increased dominance of environmentally tolerant fish in those lakes. Fish assemblages in riparian wetlands along the semiarid region of the Murray River, Australia showed a large decline in diversity when those wetlands were disconnected from the river through hydrologic modifications. This trend was reversed after a managed inundation treatment restored connections between the wetlands and the river (Vilizzi et al., 2013). 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). In addition, both river otters and beavers have a strong preference for riparian areas that are pond- and lake-dominated (Swimley et al., 1999). Thus, movement of animals,

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 in 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 beaver damming would be expected to reduce hydrologic connectivity through impoundment, their influence can be more complex. For example, 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. They concluded that the main hydrologic effects occurred downstream, however, rather than near the dam (Westbrook et al., 2006). The hydraulic head generated by the dam raised the water level above the 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. Increased overbank flooding increases hydrologic connectivity between riparian areas and streams. In contrast, when no dams were present, flooding was limited to the area immediately near the stream channel. Beaver dams also can affect stream biogeochemistry. For example, beaver dams modify nutrient cycling and decomposition dynamics and can affect downstream transport of materials (Naiman et al., 1988; Naiman et al., 1994). For example, beaver-dam wetlands can serve as a source of methylmercury (Roy et al., 2009). Beaver dams also can affect fish species, such as coho salmon (Pollock et al., 2004).

Vertebrates also 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 cascade 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 increase caused suppression and mortality of riparian willow (*Salix* spp.) communities, ultimately resulting in changes to stream morphology such as bank erosion, decreased sinuosity, 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. These channel alterations, in turn, reduced

the frequency of overbank flows, which decreases hydrologic connectivity between the riparian area and downstream waters.

4.3.4.3 Invertebrates

Stream macroinvertebrates (e.g., insects, crayfish, mollusks) and microinvertebrates (e.g., cladocerans, 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 zooplankton) are the intermediate link between primary producers (e.g., algae), detrital 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 dispersing 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; Yetter, 2013). For example, the species diversity and abundance of macroinvertebrates in the wetlands of a river delta have been found to be positively correlated with a gradient of connectivity (Dou et al., 2015).

Invertebrates have evolved two basic strategies to exploit habitats near streams and rivers: (1) rapid colonization of flooded areas and short life cycles that complete before floodplains dry again, or (2) use of aquatic refuges 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 watershed 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 comprise 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 in 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 also take advantage of flooded riparian habitats. 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. At least 41 genera in 21 families across 7 orders of flight-capable insects colonized floating trays placed in floodplain waters in June, August, November, and April. 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 9 windsocks (sampling devices for aerially dispersing organisms) near temporary rock pools for 1 month, during which 850 viable dormant eggs, larvae, and adults from 17 invertebrate taxa were collected. Results from these studies illustrate that aerial dispersal of multiple taxonomic orders and phyla is a significant source of stream invertebrate colonists in newly inundated floodplain habitats.

4.4 Non-floodplain Wetlands

4.4.1 Introduction

This section focuses on the connections and influence of non-floodplain wetlands (defined in Section 2.2.1) on downstream waters. Brinson (1993), in his hydrogeomorphic classification system, categorized wetlands according to four geomorphic settings. This system subsequently was 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. Non-floodplain wetlands consist of certain depressional, slope, and flats wetlands (although some of these wetlands can occur in riparian and floodplain wetland settings; Section 2.2.1). Depressional wetlands, as their name suggests, occur in topographic depressions and might or might not have a surface water inlet or outlet. Common types of depressional wetlands include kettles, potholes, vernal pools, playa lakes, and Carolina bays (Brinson, 1993). Slope wetlands (also known as seeps) are located in breaks of slopes and are sites of ground-water discharge (Hall et al., 2001a; O'Driscoll and DeWalle, 2010). Slope wetlands include fens, which typically are ground-water 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.

Precipitation dominates the water sources in mineral soil flats, with little ground-water input. Wet pine flatwoods and large playas are examples of this wetland type. Non-floodplain wetlands also include organic soil flats. These contain extensive peatlands, or peat bogs, where the accumulation of partially decayed organic matter dominates (Mitsch and Gosselink, 2007). Precipitation also generally dominates the water inputs to bogs, which 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 also can serve as stream origins (Figure 2-18A).

Below, we examine the physical (Section 4.4.2), water quality (Section 4.4.3), and biological (Section 4.4.4) effects of non-floodplain wetlands on rivers and other downstream waters. We then briefly consider the issue of geographic isolation in non-floodplain wetlands (Section 4.4.5).

4.4.2 The Physical Influence of Non-floodplain Wetlands on Streams

Section 2.4.1 provided a general description of how non-floodplain wetlands can connect to downstream waters via surface and ground-water flow (Figure 2-18). In this section, we provide further details on these connections and discuss how such connections affect streamflow.

4.4.2.1 Surface-water Connections

Non-floodplain 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 stream water during baseflow periods (Morley et al., 2011). In other cases, surface connections between non-floodplain wetlands and streams can be intermittent or ephemeral. Rains et al. (2008) and Rains et al. (2006) showed that California vernal pools, situated on both clay and hardpan soils, connected with streams through channels containing transient water flow (Section B.6). 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 swales and channels for 60% of those days (Rains et al., 2008). McDonough et al. (2015) found that forested Delmarva bays had seasonally intermittent surface water connections to streams; these connections occurred during periods of low evapotranspiration and high water tables, that is, from mid-fall to late-spring. In contrast, surface-water connectivity of restored and prior converted (wetlands converted to agriculture before 1985) bays was ephemeral, that is, it occurred in response to rainfall. The cumulative duration of connections to perennial streams was greater and had fewer transitions between connected and disconnected states for forested bays than for restored and prior converted bays (McDonough et al., 2015). Drainage of wetlands via ditching also can produce surface water outflows from depressional wetlands directly to streams (Section 2.4.4); ditches, however, also can introduce nutrients and ions into downstream waters (Brunet and Westbrook, 2012).

Even non-floodplain 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 (Figure 2-18B). Tiner (2003b) identifies vernal pools as 1 of 10 types of geographically isolated wetlands. Yet, as just discussed, the studies by Rains et al. (2008) and Rains et al. (2006) indicate that

vernal pools can be connected to stream networks 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 nearby 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 a nearby water body, the Armand Bayou (Wilcox et al., 2011). Non-floodplain wetlands also can have temporary hydrologic connections to each other. Such connections can occur through the expansion and contraction of surface water that occur between wet and dry periods (e.g., Figure 2 in Niemuth et al., 2010) and through fill and spill of surface waters. One consequence of fill-and-spill behavior is that the contributing area of such a wetland is dynamic and has a nonlinear relationship to potential storage area (Shaw et al., 2012; Shaw et al., 2013). In the intermontane West, evidence suggests that depressional wetlands can connect to one another via temporary overland or shallow ground-water 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). Le and Kumar (2014) analyzed topographic depressions in five study areas across the United States and found that hydrologic connectivity—as determined by nearest neighbor distances—followed a universal power law distribution. One implication of this distribution is that, although most depressions are connected over short distances, a few are connected by long distances, which could cause rapid increases in hydrologic connectivity as the system wets up (Le and Kumar, 2014). However, the distribution can be altered through wetland drainage (Van Meter and Basu, In press). Although some of these 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 might best be understood as a functional unit (Section 4.4.5).

4.4.2.2 Ground-water Connections

In addition to surface-water connections, ground-water flow can connect non-floodplain wetlands with other water bodies, potentially over great distances (Figures 2-5 and 2-18C). Many studies have shown that non-floodplain wetlands can connect to ground water, either receiving ground-water discharge (flow of ground water to the wetland), contributing to ground-water recharge (flow of water from the wetland to the ground water), 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 ground-water connections as one wetland recharged ground water, one was a flow-through wetland, and one was a discharge system. Hunt et al. (2006) found that benthic invertebrate communities were correlated with amounts of ground-water 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, ground-water connections accounted for the high salinity of the wetland soil. The high salinity is indicative of net ground-water discharge to the wetland (Brinson, 1993). Min et al. (2010) reported that 38% of rainfall that entered

four historically geographically isolated wetlands in Florida was recharged to ground water. A literature survey by Bullock and Acreman (2003) found 69 studies making reference to ground-water recharge from wetlands; of these, 32 studies observed ground-water recharge from a wetland, whereas 18 studies did not.

Ground-water flow-through wetlands are sites of both ground-water discharge and recharge, in essence a surface expression of the ground-water system (Richardson et al., 1992; Kehew et al., 1998; Ferone and Devito, 2004). In these wetlands, ground-water discharge generally flows into the wetland on one side or area, and flows back into the ground water 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), Florida cypress dome systems (Sun et al., 1995), 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 ground-water system (Winter, 1999). The flow-through wetland influences the chemistry of the transiting, shallow ground water. Kehew et al. (1998) found a wetland of this type diluted nitrogen concentrations in the ground water of an agricultural watershed.

Whether a wetland recharges ground water, is a site of ground-water 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 example, concluded that ground water discharged into a bog along Lake Michigan through a breach in the sediments underlying the wetland. In dry periods when water tables are low, water tends to move from wetlands into the ground water, while in wetter periods with higher water tables, water can flow in the opposite direction from shallow ground water into the wetlands (Phillips and Shedlock, 1993; Pyzoha et al., 2008; McLaughlin et al., 2014). Lide et al. (1995) observed both ground-water flow into and from a Carolina bay wetland, with discharge to the wetland when the water table was high and recharge to the ground water when the water table was low. Sun et al. (1995) observed similar phenomena in a Florida cypress dome. This exchange and temporary storage of water represents a lag function that can make wetlands particularly important for ground-water recharge during dry periods. Rosenberry and Winter (1997) indicated that ground-water discharge to a wetland often alternates with flow from the wetland to ground water, and the direction of flow is controlled by the balance of recent precipitation with current evapotranspiration demands.

The magnitude and transit time of ground-water 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, ground water 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 et al., 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 decreased substantially by artificial subsurface drainage pipes, known as tile drains (Section 2.4.4; Schiller et al., 2012). 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 that discharge directly to ditches or streams (Tomer et al., 2010).

In summary, non-floodplain wetlands can have a range of hydrologic connectivity with other waters (Figure 2-18). Non-floodplain 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 ground-water flows. Conversely, a wetland can be isolated hydrologically if it lacks surface water and ground-water connections entirely and evapotranspiration is the dominant form of water loss. A wetland also can be hydrologically isolated from streams and rivers if it recharges a ground-water 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 an endorheic stream (Sections 3.2 and B.5.5.1).

4.4.2.3 Effects of Non-floodplain Wetlands on Streamflow

Non-floodplain wetlands can affect streamflow by altering baseflow or stormflow (Section 2.2.2; Figure 2-8) through several mechanisms, including surface storage and ground-water recharge. Depressional wetlands effectively store water because the aboveground portion of the wetland contains a largely empty volume for water storage, in contrast to belowground water storage where only part of the volume is available for water storage, for example, due to soil particles (i.e., the specific yield; Johnson, 1967; McLaughlin et al., 2014). 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. Rovansek et al. (1996) found snowmelt to be the most important source of water for wetlands and ponds in the Alaskan Arctic Coastal Plain, and that these wetlands and ponds functioned as surface storage, thereby removing water from the snowmelt floods. However, Ford and Bedford (1987) note that in permafrost-dominated areas of Alaska, wetland soils tend to be frozen during snowmelt events, resulting in a significant proportion of these floodwaters running directly to streams, thus rendering these wetlands unimportant in streamflow regulation. Likewise, Roulet and Woo (1986) found that wetlands in the Continuous Permafrost Region of Canada tended to be unimportant for either long-term water storage or streamflow regulation.

Regression equations developed to predict peak flows during flooding events generally use lake and wetland storage areas as variables. Using 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. Johnston et al. (1990) found that small losses of wetlands in watersheds with <10% wetlands could have major effects on flood flow in basins around Minneapolis, Minnesota. Wang et al. (2010) modeled the influence of wetlands on hydrologic processes in Manitoba and Minnesota and found that the loss of 10-20% of the wetlands in the study basins would increase peak discharge by 40%. Similarly, Yang et al. (2010) calculated restoration of 600 ha of wetlands in a 25,139 ha watershed would decrease peak stream discharge by 23%. 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 watershed. In contrast, in a lowland watershed, 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 found that four out of four studies that examined surface water depressions having no direct connectivity to a river system concluded that those wetlands reduced or delayed flooding (Bullock and Acreman, 2003). Findings were more varied for slope wetlands with direct connectivity to a river: 26 of 62 studies found reduced flooding, while 27 of the 62 studies concluded that those wetlands increased flooding.

In addition to wetland type, antecedent moisture conditions and available storage capacity also influence 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 attenuating effect on larger floods because floods commonly occur during saturated conditions.

Besides affecting peak flows and downstream flooding, non-floodplain wetlands can alter baseflow or stormflows during dry periods. Ground-water 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 ground-water recharge and thus might contribute to baseflow. Rains (2011), for example, found that perched and flow-through ponds in southwestern Alaska were sites of net ground-water

recharge. Given the high prevalence of ponds on the landscape (Rains, 2011), these wetland types cumulatively could substantially affect stream baseflow via ground-water inputs.

Other wetlands, however, might 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 can function as a sink in dry periods if storage capacity is not exceeded and evaporation rates surpass ground-water recharge. Where storage capacity is exceeded during storm events in otherwise dry periods, watersheds 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 watersheds with wetlands take longer to fill and exceed water-holding capacity than watersheds without wetlands and so, in this case, they provide a lag function by releasing water downstream more slowly.

Non-floodplain wetlands also can reduce the variability of baseflow through landscape hydrologic capacitance (McLaughlin et al., 2014). McLaughlin et al. (2014) simulated the effects of geographically isolated wetlands on the variation in baseflow and found that the magnitude of this effect increased with total wetland area. Holding area constant and increasing the number of wetlands (while decreasing their size) also increased this capacitance. The effect of these wetlands on baseflow was the result of differences in specific yield (the change in output or input depth from evaporation or rain per change in water level) between wetlands and uplands, which causes flow reversals between them (McLaughlin and Cohen, 2013; McLaughlin et al., 2014). Specifically, water flows from upland areas to wetlands (wetland discharge) during wet periods and from wetlands to uplands (wetland recharge) during dry periods, thereby buffering water tables and baseflow.

4.4.3 Effects of Non-floodplain Wetlands on Water Quality

Non-floodplain 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 4.3.3 for details on specific mechanisms). In some cases, non-floodplain 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 non-floodplain wetlands can lack surface water connections to downstream waters, surface and near-surface

hydrologic connections to downstream waters do occur in many non-floodplain systems (Section 4.4.2; Figure 2-18; Sun et al., 1995; Whigham and Jordan, 2003; Wilcox et al., 2011), providing pathways for materials transformed in non-floodplain wetlands (such as methylmercury or degraded organic matter) to reach and affect other aquatic systems.

Below we show that non-floodplain wetlands are areas where extensive microbially mediated processes occur that can affect downstream waters. In Section 4.4.3.1, we describe how non-floodplain wetlands are sources for dissolved organic matter and entrained elements like carbon, nitrogen, and phosphorus, which are important components of food webs 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 non-floodplain wetlands; mercury can 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 4.4.3.2, we discuss how non-floodplain wetlands serve as sinks by sequestering or transforming 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 non-floodplain wetlands. Pesticides, metals, and other potential pollutants also can be sequestered or assimilated in non-floodplain wetlands.

4.4.3.1 Non-floodplain Wetlands as Sources for Downstream Waters

Like all wetlands, non-floodplain 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 example, 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 non-floodplain wetlands can affect streams, rivers, and lakes when compounds that are transformed in wetland environments move to downstream waters through overland flow or shallow ground water (Section 4.4.2; Winter et al., 2003). Two processes that occur in non-floodplain wetlands (and in riparian/floodplain wetlands) are useful to illustrate the influence of non-floodplain wetlands on downstream waters: the methylation and transport of the bioaccumulating pollutant mercury, and the breakdown and transport of organic compounds to receiving waters.

Freshwater wetlands/peatlands are areas of active methylmercury (MeHg) production (Grigal, 2002). Ullrich et al. (2001) noted that methylmercury production was linked to low pH, low salinity, and presence of decomposable organic matter in reducing environments. Sulfate-reducing bacteria are primarily responsible for biological mercury methylation and thrive in the reduced conditions at wetland aerobic/anaerobic boundaries (Benoit et al., 1999); the addition of sulfate (e.g., through atmospheric acid deposition) increases the formation of methylmercury in peatlands (Branfireun et al., 1999). Once formed through microbial (or other) processes, mercury and methylmercury export 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). Methylmercury can be translocated in watersheds having non-floodplain wetlands by entrainment with organic matter exports. It also can move through near-surface and surface flows from non-floodplain peatlands to downstream

waters. For example, Branfireun et al. (1996) reported 58% of MeHg-laden peat porewater leaving a headwater catchment study area occurred during stormflow, 41% during baseflow, and 1% transported via ground water. St. Louis et al. (1994) found that boreal forest catchments in Minnesota with non-floodplain wetlands reduced total mercury concentrations, but had yields of methylmercury 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 webs. Hurley et al. (1995) contrasted MeHg yields from different land use groups in Wisconsin and found that wetland/forest sites were higher than agricultural/forested and agricultural-only sites. Similarly, Porvari and Verta (2003) found that bioaccumulating methylmercury export from non-floodplain 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 negative effects on downstream waters because contaminants, such as methylmercury 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 dissolved organic compounds 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 dissolved organic carbon (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 non-floodplain wetlands in central Ontario were found to export between 11.4 and 31.5 kg C 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 watershed 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; Detenbeck et al., 1993; Clair et al., 1994; Hope et al., 1994; Dillon and Molot, 1997; Johnston et al., 2008).

The export of dissolved organic compounds from non-floodplain wetlands also can affect 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 non-floodplain 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 ground-water flow. Further linking non-floodplain 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).

4.4.3.2 Non-floodplain 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; Detenbeck et al., 1993; Mitsch and Gosselink, 2007; Reddy and DeLaune, 2008; Kadlec and Wallace, 2009). These functions act on the large pool of pollutants that are available through nonpoint sources. Non-floodplain 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).

Non-floodplain wetlands act as sinks and transformers for various pollutants. For example, high levels of human sewage were applied to a forested non-floodplain wetland site for 4.5 years (Ewel and Odum, 1984 and chapters therein). More than 95% of the phosphorus (P), 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, phosphorus retention in non-floodplain 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 non-floodplain marsh. Similarly, wetlands in the Lake Okeechobee, Florida basin were found to have greater storage of total phosphorus than the uplands in which they were bedded, 236 kg ha^{-1} vs. 114 kg ha^{-1} (Cheesman et al., 2010). These findings were echoed by Dunne et al. (2007), who reported that more phosphorus was stored in wetland plant biomass and soil than in corresponding upland compartments, with wetland surface soils (0–10 cm) representing the largest phosphorus reservoir (>87%) and soil organic matter accounting for >69% of the soil total phosphorus variability. They further suggest that restoring 5–20% of the geographical isolated wetland area in priority basins draining to Lake Okeechobee, Florida, could increase phosphorus storage in geographical isolated wetlands by up to 13 kg P ha^{-1}, mostly through increased soil organic matter with its concomitant phosphorus in wetland soils (Dunne et al., 2007). Marton et al. (2014) found that mean phosphorus sorption was approximately two to three times greater in natural depressional wetlands than in restored wetlands and agricultural fields (297, 114, and 86 mg P kg $soil^{-1}$, respectively). Marton et al. (2014) also found that depressional wetlands sorbed twice as much phosphorus as riparian systems. Craft and Casey (2000) reported similar accretion rates in depression and floodplain wetlands of Georgia for sediment, organic carbon, and nitrogen, and significantly highly floodplain storage of phosphorus. Cohen et al. (2007) found that riparian wetlands had higher phosphorus-sorption capacities than non-riverine wetlands. Non-floodplain 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. Marton et al. (2014) found that depressional wetlands denitrified at twice the rate upland systems did, 12.3 ± 4.5 ng N g^{-1} hr^{-1} versus 5.3 ± 1.7 ng N g^{-1} hr^{-1}. Craft and Chiang (2002) determined that wetland soils stored a disproportionately large share of nitrogen, compared with upland soils, in spite of uniform soil organic matter across the landscape. A non-floodplain 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 removed >80% of the nitrate load via denitrification (Moraghan, 1993). A large non-floodplain prairie marsh removed 86% of nitrate, 78% of ammonium, and 20% of phosphate through assimilation and sedimentation, sorption, and other mechanisms (Davis et al., 1981). Geographically isolated, non-floodplain wetland systems in Michigan were found to remove nitrate-nitrogen (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 ground water in Michigan was reported to average 0.50 mg NO_3-N L^{-1} (Whitmire and Hamilton, 2008). Bhadha et al. (2011) found that infiltration to the ground accounted for 14% of phosphorus loss from two historically isolated wetlands in a Florida study area, suggesting that near-surface flow gradients are important to landscape-level phosphorus dynamics. Together, these studies indicate that sink removal of nutrients by non-floodplain wetlands is significant and geographically widespread.

Other pollutants and compounds can be mitigated by non-floodplain wetland sink and transformation processes. For example, microbial methanogenesis completely removed 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 non-floodplain 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 ground water.

4.4.4 Biological Connections Between Non-floodplain Wetlands and Streams

Many of the same factors that affect movement of organisms between riparian/floodplain wetlands and the river network (Section 4.3.4) govern movement of organisms between non-floodplain wetlands and the river network. Non-floodplain wetlands, however, are generally farther from stream channels than riparian/floodplain wetlands, which reduces hydrologic connectivity. The distance, number, and variety of heterogeneous landscape patches (including barriers) over which organisms must disperse also can be greater. Organisms have evolved numerous complex dispersal strategies to overcome non-floodplain flows, reduced hydrologic connectivity, and increased geographic distance between habitats and spatially subdivided populations. Passive transport (e.g., wind dispersal, "hitchhiking" on other animals) and active movement (e.g., walking, crawling, 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 non-floodplain wetland landscapes, making them more difficult to observe than surface water flows. Their effects on community structure and diversity—including metapopulation effects of wetland-to-wetland connectivity—have been well documented (e.g., Wellborn et al., 1996; Snodgrass et al., 2000; Julian et al., 2013), especially for amphibians. Other effects, such as water quality and population or species persistence, are not well understood. Below we review the various dispersal mechanisms that operate in non-floodplain wetland landscapes.

Despite being sessile, 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 non-floodplain 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 non-floodplain 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). Viable seeds or vegetative plant parts also can travel great distances within the guts of or externally attached to migratory birds (Murkin and Caldwell, 2000; Amezaga et al., 2002; Figuerola and Green, 2002), which move between non-floodplain wetlands and river networks, depending on temporally dynamic habitat availability (Murkin and Caldwell, 2000; Haukos et al., 2006 and references therein).

Identifying specific source and recipient populations for any organism over these distances can be challenging, but especially for plants having passively mobile life stages that cannot be precisely tracked. Determining whether wetlands function as sources to or recipients of plant propagules from river networks is especially difficult. Genetic similarity between populations can provide general evidence of connectivity between non-floodplain 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.

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 in structuring non-floodplain 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, zooplankton (i.e., rotifers, ostracods, copepods), and insects (i.e., crane flies, nonbiting midges, 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. Studies have thus shown that migratory birds can passively connect viable plant matter, macroinvertebrates, and zooplankton from disparate habitats across the landscape, with likely—although unresolved—impacts on food web dynamics (Polis et al., 1997).

The scientific literature has many examples of migratory birds—especially migratory waterfowl, including cranes, geese, ducks, and shorebirds—actively moving between and using the different available resources of estuarine, riverine, and riparian systems and non-floodplain wetlands. For example, wood ducks (*Aix sponsa*) are found throughout freshwater deciduous forests of North America. Preferred breeding sites include river floodplains, remote ponds, and woodland pools that receive snowmelt and spring rain, the latter particularly indicative of non-floodplain wetland use (Haramis, 1990). Below we provide several examples of this type of biological connectivity that can connect non-floodplain wetlands to each other and to other aquatic systems.

Approximately 80% of the entire North American population of redhead ducks (*Aythya americana*) winters along coastal Texas and northern Mexico (Weller, 1964). Woodin (1994) identified more than 20,000 redheads using both estuarine systems and freshwater wetlands, reporting that the estuarine systems were exclusively used for feeding, while freshwater coastal pond wetlands were used almost exclusively for drinking water and courting (Mitchell et al., 1992). The coastal ponds redheads used were seasonal basins, which frequently dried completely (Ballard et al., 2010). Ballard et al. (2010) further noted that although the ponds were densely distributed in coastal Texas (up to 4.8 coastal basins per km^2), water availability varied year-to-year. As a result, during dry years redheads would use available coastal ponds up to 8.1 km from the estuarine forging areas, while in wetter years closer ponds would be used (likely to minimize energy expended through flying). Similarly, Adair et al. (1996) reported that lesser scaup (*Aythya affinis*) and redheads avoided salt stress and metabolically expensive osmoregulation through salt-gland excretory functions by feeding in estuaries; drinking, preening, and resting in coastal basins; and then returning to estuaries. Grey teals (*Anas gibberifrons gracilis*) in Australia that feed in saline areas similarly required freshwater to osmoregulate (Lavery, 1972). Mallard ducks (*Anas platyrhynchos*) transiting Iowa during spring migration used seasonally flooded farmed basins in agricultural fields (also known as sheetwater wetlands; LaGrange and Dinsmore, 1989) for feeding and roosted in more permanent emergent wetlands at night. In the study, these shallow sheetwater wetlands provided 19,530 mallard use-days during the daytime compared with 103 use-days for the emergent wetlands.

Nebraska's Rainwater Basin historically had more than 11,000 playas, shallow wind-formed wetland depressions, although human activities over the past 100 years have resulted in the loss of 90% of the

number and approximately 88% of the area (Webb et al., 2010; Uden et al., 2014). Nevertheless, the remaining basins are critical to dependent migratory waterfowl, with 7–10 million waterfowl using the approximately 16,000 km^2 area, including "virtually all of the 600,000 midcontinental greater white-fronted geese (*Anser albifrons*), 500,000 Canada geese (*Branta Canadensis)*, 50% of midcontinent mallards (*Anas platyrhynchos*), and 30% of continental northern pintails (*Anas acuta*)" (Webb et al., 2010, p. 109), 38 shorebird species, and the endangered whooping crane (*Grus americana*). In a 3-year spring migration study of 36–40 playas, Webb et al. (2010) identified 72 migratory species and more than 1.6 million birds actively using these playa basins. The abundance of all wetland bird taxa was related to wetland area within 5–10 km of the study playas, although diving duck abundance (e.g., redhead, canvasback, lesser scaup) was specifically related to riparian area within 5 km, likely due to the presence of open water within these systems (Webb et al., 2010; see their Table 1 for a complete list of taxa found).

Many additional studies have identified Nebraska as an important staging and stopover area for numerous species, perhaps due to its location on the Central Flyway. For example, almost the entire population of midcontinent sandhill cranes (*Grus canadensis*) uses the Central Platte River Valley. Avian researchers reported that cranes roost along both the current and former Platte River channel (Krapu et al., 1984) and forage in grasslands on semipermanent (unconsolidated mud bottom) and temporary palustrine wetlands (Folk and Tacha, 1990) and on frequently inundated soils—especially those within 4.8 km of roost sites (Anteau et al., 2011). Pearse et al. (2010) noted that after feeding in cornfields, sandhill cranes roosted along the Central Platte River Valley in pastures with ponds. These pond systems are likely either playas, as noted above, or palustrine wetlands often surrounded by croplands (Austin and Richert, 2005). Austin and Richert (2005) further stated that the endangered whooping crane was noted as roosting, feeding, and resting in both riverine and palustrine wetlands of the Great Plains. Vrtiska and S.Sullivan (2009) found that lesser snow geese (*Chen caerulescens*) and Ross's geese (*Chen rossii*), which numbered up to 7.3 million in 2001 during peak migration, used wetland habitats in both the Rainwater Basin and Central Platte River Valley, depending on the availability of suitable (e.g., inundated) habitat.

Blanchong et al. (2006) found that this concentrated use of the Rainwater Basin by migratory lesser snow geese resulted in greater contact between individuals, contributing to the spread of *Pastruella multocida*, the bacterium that causes avian cholera. The loss of wetlands within the basin has resulted in higher concentrations of migratory birds within the remaining wetlands, which has led to higher risks of outbreaks of infectious diseases (Blanchong et al., 2006).

The U.S. Fish and Wildlife Service's Subcommittee on Rocky Mountain Greater Sandhill Cranes (SRMGSC, 2007) reviewed the literature on habitat use for the migratory population of Rocky Mountain sandhill cranes. This population, one of five in North America, migrates from wintering areas in Arizona, New Mexico, and central Mexico to breeding areas in Canada, Montana, Idaho, Wyoming, Utah, and Colorado. SRMGSC (2007) reported that this population of sandhill cranes overwintered in multiple riverine, riparian, and non-floodplain habitats, including playas in New Mexico and southeastern Arizona. Areas used in the breeding range include non-floodplain wetlands, such as northern boreal forest bogs, and

other habitat types (e.g., large marsh complexes, smaller, scattered marshes, intermittent streams, beaver ponds, subirrigated wet meadows along riparian zones; SRMGSC, 2007).

Shorebirds also use multiple habitat types during their North American migration. Skagen and Knopf (1993) concluded that dispersion and opportunism, rather than concentration and predictability, characterize movements of shorebirds in the Great Plains. For example, Haig et al. (1998) noted that large population declines of the endangered migratory piping plover (*Charadrius melodus*) along the Missouri River were not actually declines, but a result of the birds moving to the Missouri Coteau (a 7.3 million ha region of the Upper Midwest and Canada replete with closed-basin prairie potholes; Phillips et al., 2005), due to increased flooding along the Missouri. Farmer and Parent (1997) monitored pectoral sandpipers (*Calidris melanotus*) migrating through non-floodplain sheetwater wetlands in Missouri and small depressional wetlands of the Rainwater Basin in Nebraska and found that habitat connectivity affected shorebird movements. Habitat patch density affected movements such that pectoral sandpipers often perceived groups of wetlands as functionally connected and actively exploited the best feeding habitat within that wetland complex. As the landscape became disconnected, however, the monitored species altered their movement behavior, minimizing energy expenditure (Farmer and Parent, 1997).

Other taxa have been reported as linking downstream systems and non-floodplain wetlands. Fish tend to disperse between non-floodplain wetlands and the river network during periodic surficial hydrologic connections or when humans create surface-water connections via ditching (Snodgrass et al., 1996; Langston and Kent, 1997; 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), dispersal between suitable river and non-floodplain wetland habitat over longer distances that is seasonal, climate-induced, and density-dependent has been observed (Serfass et al., 1999; Clark, 2000 and references therein). Spinola et al. (2008) tracked translocated river otters (*Lontra canadensis*) in New York and found that, after release, most otters inhabited a mosaic of isolated aquatic habitats distributed throughout the agriculture-dominated landscape. As noted above for waterfowl, mammals (including muskrats) also can act as transport vectors for hitchhiking organisms like algae (Roscher, 1967).

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 non-floodplain 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 non-floodplain wetlands to satisfy part of their life-history requirements (Table 4-2). For example, Subalusky et al. (2009a) and Subalusky et al. (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 by moving overland 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). Knutson et al. (1999) found that the strongest land-use predictor of anuran richness was urban land use. They speculated that, in addition to urban landscapes being detrimental to anuran habitat quality, their tendency to fragment (i.e., disconnect) anuran habitats is also a factor in the decline of these assemblages. In northwestern Ohio and southern Michigan wetland complexes, the abundance of northern watersnakes (*Nerodia sipedon sipedon*) was positively correlated with wetland size and wetland connectivity, defined by the authors as a wetland's distance to other wetlands (Attum et al., 2007). 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 (Table 4-2; Babbitt et al., 2003; Green, 2005; Hunsinger and Lannoo, 2005; Petranka and Holbrook, 2006).

4.4.5 Geographic Isolation of Non-floodplain Wetlands

In defining non-floodplain wetlands (Section 2.2.1), we noted that this category could include wetlands that are geographically isolated and those that are not. Further, we noted (Section 2.4.1) that certain types of wetlands can be found with or without an outlet and can occur along a gradient of hydrologic connectivity. This gradient can include non-floodplain 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 ground-water 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 (Section 1.2.2) can make determining the degree to which particular non-floodplain 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 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 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 often are 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 a nearby waterway via an intermittent stream. During an almost 4-year study, 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

Table 4-2. Partial list of amphibian and reptile species known to use both streams and non-floodplain 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, floodplain pools, and 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, and floodplain pools (Green, 2005)
Fowler's toad	*Anaxyrus* [=*Bufo*] *fowleri*	Breeds in ponds, temporary pools, streams, ditches, lake shores, and 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 4-2. Partial list of amphibian and reptile species known to use both streams and non-floodplain wetlands or other lentic waters (continued).

Common Name	Scientific Name	Habitat Use
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)

complex serves as the source of water for a headwater stream, and therefore, the complex is not geographically isolated at a larger scale.

Besides the spatial scale of the wetland unit, assessments of non-floodplain wetland to stream connectivity can be affected by the resolution and source of the spatial data that are used. For example, higher connectivity was found in the Tuckahoe Creek watershed in Maryland, when wetland connectivity was evaluated for streams determined from LiDAR compared to streams from both the High Resolution National Hydrography Dataset (NHD) and NHD Plus (Lang et al., 2012). Yang and Chu (2013) found that Digital Elevation Model (DEM) resolution also affected connectivity assessments, with finer DEMs having a higher number of connected areas and less total connected area than coarser DEMs.

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 actually 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 ground-water 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, precisely this isolation is responsible for many of the functions that geographically isolated wetlands provide to downstream waters. In particular, many of the sink and lag functions of these wetlands result from their relative isolation from the river network. This relative isolation, combined with the wetlands' storage capacity, enables 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 also can 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).

4.5 Wetlands: Synthesis and Implications

4.5.1 Riparian/Floodplain Wetlands

Based on our review of the literature, riparian/floodplain wetlands are highly connected to streams and rivers through surface water, shallow ground water, 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 a gradient occurs in the frequency of connectivity within the floodplain (Section 1.2.2), 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 surface water infrequently floods also can be connected to the river more regularly through ground water and the organisms. Key conclusions from our literature review on riparian/floodplain wetlands are summarized in Table 4-3.

4.5.2 Non-floodplain Wetlands

Non-floodplain wetlands consist of depressional, slope, and flats wetlands that lack surface water inlets. Non-floodplain wetlands 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 non-floodplain wetlands indicates that these systems have important hydrologic, water-quality, and habitat functions that affect downstream waters and rivers provided a connection exists between the wetland and downstream water (Table 4-4). The challenge is to identify which non-floodplain wetlands have such a connection. Addressing this issue is difficult, because most wetland studies do not investigate wetland 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 (Chapter 2), hydrologists and ecologists would generally agree that all non-floodplain wetlands are interconnected to some degree and are connected with stream networks, which is why the water-cycle environment is referred to as the hydrosphere. Hydrologists and ecologists also generally agree 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 non-floodplain wetlands and downstream waters.

Non-floodplain wetlands occur along the gradient discussed in Chapter 1, and can be described in terms of the frequency, duration, magnitude, timing, and rate of change of water, material, and biotic fluxes to downstream waters. With respect to hydrologic connectivity, this gradient includes wetlands that have permanent hydrologic connections to the river network through perennial channels; wetlands that have

Table 4-3. Key conclusions on the effects of riparian/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 by releasing stored sediments. • Forested riparian areas provide woody debris that helps shape stream morphology. • Riparian vegetation shades the stream and influences and regulates stream temperature and stream net primary productivity. • Ground water 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 stream-water quality. • The structure of the riparian area (e.g., vegetation, wetlands, redox potential) influences its ability to increase water quality before it reaches the stream. • The near-stream portion of a riparian area is often more important in protecting stream-water quality than is the near-field (near uplands) portion. • Allochthonous inputs generally are 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.

output channels but are isolated from the river network; geographically isolated wetlands (i.e., wetlands completely surrounded by uplands) that have local or regional ground-water 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).

Based on our literature review and basic hydrologic principles, we conclude that non-floodplain wetlands that are connected to the river network through surface water will have an influence on downstream waters, regardless of whether the outflow is permanent, intermittent, or ephemeral. Such non-floodplain wetlands include wetlands that are the origins of streams or are connected downstream to the river network through ditches. They also would include geographically isolated wetlands that are

connected downstream to the river network through upland swales. Further, although the literature review did not address other non-floodplain water bodies to the same extent as wetlands, our overall conclusions also apply to these water bodies (e.g., ponds and lakes that lack surface water inlets) because the same principles govern hydrologic connectivity between these water bodies and downstream waters (Chapter 2).

Non-floodplain 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; that is, 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 ground water. Also included are geographically isolated wetlands that either do not spill, or spill into an upland swale that does not enter the river network. Although such wetlands lack surface-water connections to streams and rivers, they can be connected through local, intermediate, or regional ground-water 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; Sections 2.4.1 and 2.4.2), some of which are identified and discussed in this section. Connectivity also will vary over time, as the river network and water table expand and contract in response to local climate.

It is difficult to generalize about the specific downstream effects of non-floodplain wetlands that lack surface water connections to downstream waters. In Chapter 2 we note that the influence of wetlands and streams on downstream waters depends on two factors: (1) functions that affect material fluxes and (2) connectivity (or isolation) that allows (or prevents) transport of materials between the systems (Section 2.3). The literature we reviewed and summarized provides ample evidence that non-floodplain wetlands provide hydrological, chemical, and biological functions that affect material fluxes. Thus, these wetlands could affect downstream waters if they are connected to (or isolated from) the river network in such a way that it allows (or prevents) transport of materials to downstream waters. However, the more than 200 peer-reviewed references on non-floodplain wetlands we reviewed infrequently evaluated connections between non-floodplain wetlands and river networks and rarely examined the frequency, duration, magnitude, timing, and rate of change of these connections. Even if it is known from an article that the study site is located near a downstream water, connectivity cannot be established without specific information on frequency and magnitude of precipitation events, soil infiltration rate, wetland storage capacity, hydraulic gradients, etc.—information that is only rarely available in publications. Thus, the literature provided no evaluations of connectivity for specific groups or classes of wetlands (e.g., prairie potholes or vernal pools). 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, our review did not reveal 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: It simply means the literature we reviewed does not enable us to distinguish connectivity of these wetland types from each other. Literature that was not included in our review, such as reports

Table 4-4. Key conclusions on the effects of non-floodplain wetlands on rivers.

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

from local resource agencies, could allow the connectivity of these wetlands to be evaluated further, as could analysis of existing or new data or field evaluation.

Further complicating our evaluation is 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 and entrained pollutant removal, water storage) result because of the wetland's ability to isolate material fluxes. As above, to establish that a

wetland influences a downstream water through its isolation, it would have to be known that the wetland intercepted materials that would otherwise reach the downstream water, and this information is typically not provided in publications. The literature we reviewed does provide limited examples of the direct effects of such isolation on downstream waters for some specific wetlands, but not for classes of wetlands (e.g., vernal pools). However, the literature we reviewed allows us to conclude that sink functions of non-floodplain wetlands, which result in part from their relative isolation, will have effects on a downstream water when these wetlands are situated between the downstream water and known point or nonpoint sources of pollution, and thus intersect the flowpath between pollutant source and downstream water. For example, in cases where agricultural land use is a known contributor of sediment to downstream waters, the presence of depressional wetlands along the flowpath between the agricultural land and downstream water will result in reduced sediment loading to the downstream water. These effects would also be realized from sink functions that do not result from the wetland's isolation *per se*, but are emergent wetland properties (e.g., biogeochemical reactivity based on anoxic conditions). Using the same example, if the agricultural land use is a known contributor of nitrogen to downstream waters, depressional wetlands occurring along the flowpath will result in reduced nitrogen loading to the downstream water. In such settings, wetland loss or increased connectivity (e.g., due to ditching or tiling) is likely to reduce the effects of such functions on downstream waters (although functions that depend on connectivity could be increased).

To provide more specific evaluations of the connectivity of non-floodplain wetlands to downstream waters, studies are needed that: (1) further develop and validate methods for assessing wetland and watershed connectivity; (2) apply such methods to different classes of non-floodplain wetlands, especially those that lack channelized surface-water or regular shallow subsurface-water connections; (3) evaluate the frequency, duration, magnitude, timing, and rate of change of water, material, and biotic fluxes to downstream waters; and (4) consider aggregate functions and connectivity of wetland complexes (groups of closely located and interacting wetlands). Such studies are needed throughout the country to cover the breadth of wetlands in non-floodplain settings satisfactorily (e.g., across areas with different climate, geology, and terrain).

Despite these limitations, we can make some conclusions:

1. A non-floodplain 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 influence on downstream waters.
2. Many non-floodplain wetlands interact with ground water, which can travel long distances and affect downstream waters.
3. Even when wetlands lack a hydrologic connection to other water bodies, they can influence downstream water through water and material storage and mitigation of peak flows (flood reduction and flood attenuation). Sink functions of non-floodplain wetlands will have effects on a downstream water when these wetlands are situated between the downstream water and known point or nonpoint sources of pollution, thereby intersecting the flowpath between

pollutant source and downstream water. More generally, wetland sink functions are likely to be greatest when the wetland is located downgradient from pollutant sources and upgradient from a stream or river.

4. Non-floodplain wetlands provide unique and important habitats for many species, both common and rare. Some of these species require multiple types of waters to complete their full life cycles, including downstream waters. Abundant or highly mobile species play important roles in transferring energy and materials between non-floodplain wetlands and downstream waters.

5. Biological connections are likely to occur between most non-floodplain wetlands and downstream waters through either direct or stepping stone movement of amphibians, invertebrates, reptiles, mammals, and seeds of aquatic plants, 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 wetlands and river networks. Migratory birds can be an important vector of long-distance dispersal of plants and invertebrates between non-floodplain wetlands and the river network, although their influence has not been quantified. Whether those connections are of sufficient magnitude to impact downstream waters will either require estimation of the magnitude of material fluxes or evidence that these movements of organisms are required for the survival and persistence of biota that contribute to the integrity of downstream waters.

6. Spatial proximity is one important determinant of the magnitude, frequency and duration of connections between wetlands and streams that will ultimately influence the fluxes of water, materials and biota between wetlands and downstream waters. However, proximity alone is not sufficient to determine connectivity, due to local variation in factors such as slope and permeability.

7. The cumulative influence of many individual wetlands within watersheds can strongly affect the spatial scale, magnitude, frequency, and duration of hydrologic, biological and chemical fluxes or transfers of water and materials to downstream waters. Because of their aggregated influence, any evaluation of changes to individual wetlands should be considered in the context of past and predicted changes (e.g., from climate change) to other wetlands within the same watershed

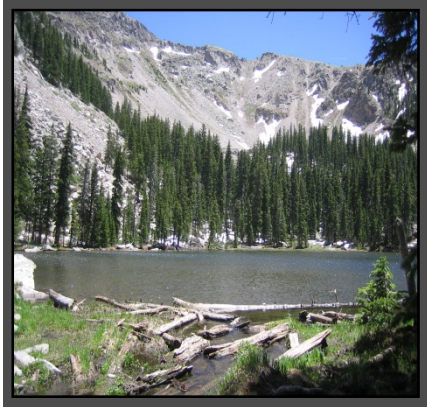
8. Caution should be used in interpreting connectivity for wetlands that have been designated as "geographically isolated" because

    a. the term can be applied broadly to a heterogeneous group of wetlands, which can include wetlands that are not actually geographically isolated (e.g., some vernal pools are not geographically isolated because they have output channels;

    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, 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 ground-water 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 non-floodplain wetlands are summarized in Table 4-4.





CHAPTER 5. APPLICATIONS AND DISCUSSION: CONNECTIVITY CASE STUDIES

5.1 Introduction

Chapters 3 and 4 of this report review evidence from the literature for the physical, chemical, and biological connections of three broad categories of waters—streams, riparian/floodplain wetlands, and non-floodplain wetlands—to, and their resulting effects on, downstream waters. In addition to the three questions in Table 1-1, the EPA's Office of Water asked us to provide detailed information on six specific water body types: Carolina and Delmarva bays, oxbow lakes, prairie potholes, prairie streams, southwestern streams, and vernal pools (Appendix B).

In this chapter, we summarize the results of the six case studies, applying the concepts in Chapters 1 and 2 to the detailed evidence in Appendix B, for each habitat. The full body of evidence and supporting citations, which we omitted here to improve readability, are provided in Appendix B. We summarize evidence from the individual case studies in terms of (1) the descriptors of connectivity (i.e., the frequency, duration, magnitude, timing, rate of change of fluxes to and biological exchanges with downstream waters; Section 1.2.2); (2) the consequences of different systems and degrees of connectivity on downstream waters (Sections 1.2.3 and 2.3); (3) and the effects of typical human alterations (Sections 1.2.4 and 2.4.4). We then use the information from these case studies and from Chapters 3 and 4 to illustrate, hypothetically, where streams, riparian/floodplain wetlands, and non-floodplain wetlands are positioned along a connectivity gradient, highlighting the primary lines of evidence that support that positioning.

5.2 Carolina and Delmarva Bays

Carolina bays are elliptical, ponded, depressional wetlands that occur along the Atlantic Coastal Plain from northern Florida to New Jersey, although they are most abundant in North Carolina and South Carolina (Section B.1). Carolina bays that are geographically specific to the Delmarva Peninsula are often referred to as Delmarva bays. Carolina and Delmarva bays range in size from less than 1 ha to greater than 3,600 ha and are densely concentrated in many areas. In the 1950s, roughly 500,000 bays existed, although the number today is markedly less due to human modification of the landscape. Bays primarily gain water from direct precipitation on their surfaces (with some water deriving from inlet channels, surface runoff, shallow ground water, and natural springs) and lose water through evapotranspiration. As a result, these relatively permanent bays experience fluctuating water levels. Their extensive distribution and wet-dry cycles promote and support a diverse biota.

5.2.1 Connectivity and Consequences on Downstream Waters

Some Carolina and Delmarva bays connect to each other and some connect to downstream waters. Delmarva bays inundate seasonally and connect hydrologically to other bays and to stream networks via intermittent stream channels. Studies also document shallow ground-water connections, via both nearly continuous shallow ground-water recharge and periodic shallow ground-water discharge.

When they occur, hydrologic connections are likely to result in effects on downstream waters. Carolina and Delmarva bays can reduce the amount of nitrate transported between surface-water systems and ground water via denitrification, which is promoted by the periodicity of wetting and drying that occurs in bays, and dilution. Seasonal connections of Delmarva bays to stream networks export accumulated organic matter from wetlands into tributaries of Chesapeake Bay. Hydrologic connections also export methylmercury from these systems (see below).

Although the current published evidence for biological connections is limited and primarily indirect, the potential for movement of organisms between bays and other water bodies is high. These bays provide valuable habitat and food web support for numerous plant and animal species. Fish presence in bays known to dry out periodically indirectly demonstrates that these bays must be connected to other waters. Amphibians and reptiles use bays extensively for breeding and for rearing young. In bays that lack fish, the absence of predators allows abundant amphibian populations to thrive, particularly those with aquatic larval stages. These animals can then disperse many meters across the landscape and colonize downstream waters. Bays also foster abundant aquatic insects, and their emergence can have consequences for nearby waters. Many species documented in Carolina and Delmarva bays are known to live in pond, wetland, and stream environments. As a result, species emerging from bays can become important food sources for organisms in nearby streams after aerial or terrestrial dispersal. Cumulative emergence from thousands of small bays across the landscape could create a significant food source for downstream waters.

5.2.2 Effects of Human Alteration

Human alteration of Carolina and Delmarva bays has affected their physical, chemical, and biological connections to, and effects on, downstream waters. Agriculture, logging, and other human activities have altered the vast majority of Carolina and Delmarva bays, affecting the frequency, duration, magnitude, and timing of hydrologic connections between bays and other waters. Agricultural practices have greatly reduced the number of bays over the past several decades. Channelization and ditching of bays for agriculture is common. Draining bays for agricultural use disrupts or alters numerous wetland functions: sediment and chemical storage and transformation, biological habitat and sources, and organic matter export. Because the ditches commonly connect the surface water of bays that drain agricultural fields to stream networks that drain into downstream water bodies, they serve as conveyances for nutrients, sediment, and contaminants—thereby increasing physical, chemical, and biological connections between bays and the downstream systems. The consequences of this increased connectivity for downstream waters can be especially important in terms of nutrient and contaminant transport. In addition to runoff from farmed fields, periodic drying and flooding of shallow Carolina and Delmarva bays promote the bacteria-mediated methylation of mercury. Subsequent transport of bioavailable methylmercury through ditches can pose a contamination risk to fish and piscivorous birds inhabiting downstream water bodies.

5.3 Oxbow Lakes

Oxbow lakes are natural features of floodplains, originating from curves (meanders) in the river that become cut off from the active river channel (Section B.2). They are located in flat, unconstrained floodplains of river systems.

5.3.1 Connectivity and Consequences on Downstream Waters

The evidence for physical, chemical, and biological connectivity of oxbow lakes to downstream waters is considerable. Because of their location within river floodplains, many oxbows are connected seasonally or episodically to downstream waters during natural flood events via surface and shallow subsurface flows. The frequency, duration, magnitude, and timing of these hydrologic connections depend on river stage, lake geomorphology, and relative position along and distance from the river network. Despite this spatial and temporal variability, oxbow lakes collectively are likely to influence downstream waters.

The frequency, magnitude, and duration of physical connection between oxbow lakes and the river channel have important consequences on the river network. Physical surface connections facilitate biological and chemical exchange between oxbow lakes and rivers. Oxbow lakes function as sinks, because they intercept and store nutrients and other materials from upland runoff that otherwise would flow directly into the river network. In these cases, the lack of a permanent connection between an oxbow lake and a river helps to preserve the chemical integrity of the river network.

When oxbow lakes are connected, the biological material produced within them can subsidize riverine food webs by passive or active transport from the lake to downstream waters. Oxbow lakes are

important areas of biological productivity on floodplains. Periodic surface-water connections between rivers and oxbow lakes facilitate the movement of fish, allowing riverine fish to exploit these productive floodplain water bodies before they move back to the river. In this way, connectivity between oxbow lakes and rivers supports the biological integrity of the river network.

5.3.2 Effects of Human Alteration

Human alterations of the natural flow regime in rivers can influence connectivity between oxbow lakes and the active river channel. In some cases, permanent channels are constructed between oxbows and the river channel and connectivity is increased; in other cases, such as the creation of dikes or levees, connectivity is reduced between oxbows and the altered area of the river network. Practices that alter the natural flow regime of the river (e.g., dams) or inhibit periodic flooding of oxbow lakes (e.g., levees) affect movement of water and sediment and the use of oxbow lakes by riverine fish. When cut off from periodic inundation by the river channel, water in oxbow lakes can evaporate. Over time, these lakes can dry up, be colonized by terrestrial vegetation, and eventually become dry land.

5.4 Prairie Potholes

The prairie pothole region, located in northern-central North America, is named for the abundant, glacially formed wetlands that occur throughout the region, typically as depressions lacking natural outlets (Section B.3). The prairie pothole region covers approximately 777,000 km^2, a vast area that varies in climate, terrain, geology, land use, and human alteration. These variations result in a gradient of connectivity to and effects on downstream waters across the potholes themselves. For instance, the three major physiographic areas within the prairie pothole region (Red River Valley, Drift Prairie, and Missouri Coteau) vary in precipitation, distribution, and density of potholes and streams connecting potholes to downstream waters. Potholes exhibit a wide range of hydrologic permanence, from holding permanent standing water to wetting only in years with high precipitation. Differences in the frequency, duration, and timing of pothole inundation across the region influence wetland function and the diversity and structure of their biological communities.

5.4.1 Connectivity and Consequences on Downstream Waters

Individual prairie potholes span the continuum of isolation from and connection to the river network and other water bodies. In addition to differences among individual potholes, interactions between regional factors (e.g., precipitation) and local factors (e.g., landscape relief) can result in spatial patterns of connectivity across the landscape (Sections 2.4.5 and B.3.2.1) that have consequences for the downstream connectivity and effects of prairie potholes. Considered collectively, unaltered prairie pothole systems have infrequent direct surface-water connections to downstream waters. Evidence of the consequences of these connections on downstream waters is variable. Some studies document measurable effects of water storage capacity of potholes on flood attenuation and maintenance of stream baseflow, whereas other studies show no effect of pothole water storage on streamflows. These differences in observed effects might be explained, in part, by the spatial variation observed within the

prairie pothole region. Potholes can connect to downstream waters via ground-water flows when both are within a continuous zone of a shallow local aquifer. In areas with restricted surface-water and ground-water interactions, the magnitude of effects from such connections will be small.

The chemical connectivity of prairie potholes is largely mediated by their hydrologic connectivity. As depressions on the landscape, potholes tend to accumulate nutrients, sediment, and pesticides that can be chemically transformed and decrease potential effects on downstream waters (e.g., denitrification frequently occurs in saturated pothole sediments). Although chemical sink (storage) functions and periodic source functions of potholes have been documented in the literature, their overall influence on lakes and river networks has been difficult to quantify. This difficulty exists in part because altered and unaltered potholes co-occur in watersheds with different land use and management practices, and many different parts of this complex landscape can affect the integrity of downstream waters. Thus, prairie potholes can have substantial hydrologic and chemical consequences on downstream water levels and flows, but this type of connectivity and its downstream effects are difficult to predict, demonstrate, and quantify.

Although direct evidence is sparse, indirect evidence suggests that prairie potholes are highly biologically connected. Prairie pothole systems have biological connections to downstream waters via annual bird migrations—especially for migratory waterfowl such as cranes, geese, ducks, and shorebirds, which actively move between and use multiple aquatic habitats, including prairie pothole systems. For instance, the prairie pothole region has been identified as an area of global and regional importance for migratory birds, and at least 15 duck species use prairie pothole wetlands. Mammals and many species of amphibians also use potholes. Plants and invertebrates disperse to and from prairie potholes via "hitchhiking" on waterfowl. That potholes lack an endemic aquatic and semiaquatic flora and fauna indicates that communities in potholes are biologically well connected with other aquatic ecosystems, but evidence for effects of biological connections on downstream waters is limited.

5.4.2 Effects of Human Alteration

Human alterations of the landscape affect the connectivity of prairie potholes. Land use in an upland that drains to a wetland can alter the amount of runoff that wetland receives. Much of Upper Midwest cropland is artificially drained to increase agricultural productivity. Filling potholes and lowering the regional water table through agriculture tile drainage have increased the isolation of remaining potholes by decreasing the density of depressions containing water. In some areas, extensive surface draining and ditching has directly and dramatically increased connectivity between pothole basins and the river network. Ditches create surface-water outlets from potholes, connecting potholes to streams and rivers; drains and underground pipes fitted at the bottoms of potholes often discharge to open ditches or streams. This increased hydrologic and chemical connectivity decreases water retention time, thereby reducing storage and biogeochemical processing of nutrients, sediments, and pesticides. The cumulative influence of human alterations on connectivity between potholes and downstream waters has not been systematically studied or reported across the entire prairie pothole region.

5.5 Prairie Streams

Prairie streams drain temperate grasslands in the Great Plains physiographic region of the central United States and Canada (Section B.4). Eventually, these streams drain into the Mississippi River or flow directly into the Gulf of Mexico or the Hudson Bay. Climate in the Great Plains region ranges from semiarid to moist subhumid and intra- and interannual variation in precipitation and evapotranspiration is high. This variation is reflected in the hydrology of prairie streams, which include ephemeral, intermittent, and perennial streamflows. Row cropping and livestock agriculture are the dominant land uses in the region, resulting in the withdrawal of water from stream channels and regional aquifers and its storage in reservoirs to support agriculture.

5.5.1 Connectivity and Consequences on Downstream Waters

Prairie streams typically are connected to downstream waters. Like other types of streams, prairie streams present strong fluvial geomorphic evidence for connectivity to downstream waters, in that they have continuous channels (bed and banks) that make them physically contiguous with downstream waters. Prairie river networks are dendritic and generally have a high drainage density, so they are particularly efficient at transferring water and materials to downstream waters. Their pool-riffle morphology, high sinuosity, and seasonal drying, however, also enhance material storage and transformation. The timing of connections between prairie streams and downstream waters is seasonal and therefore relatively predictable. For example, high-magnitude floods tend to occur in late fall into later spring, although they also occur at other times during the year (Section B.4.2.1); this observation indicates that the magnitude of connections to downstream also varies seasonally.

The frequent and predictable connections between prairie streams and downstream waters have multiple physical, chemical, and biological consequences for downstream waters. Dissolved solids, sediment, and nutrients are exported from the prairie river network to downstream waters. Ultimately, the expansion of the hypoxic zone in the Gulf of Mexico is a downstream consequence of cumulative nutrient loading to the Mississippi River network. Relative to small streams and large rivers draining the moist eastern parts of the Mississippi River basin, small to midsized prairie streams deliver less than 25–50% of their nutrient load to the Gulf of Mexico. Nonetheless, given the large number and spatial extent of headwater prairie streams connected to the Mississippi River, their cumulative effect likely contributes substantially to downstream nutrient loading.

Organisms inhabiting prairie streams have adapted to their variable hydrologic regimes and harsh physicochemical conditions via evolutionary strategies that include rapid growth, high dispersal ability, resistant life stages, fractional reproduction, and life cycles timed to avoid predictably harsh periods. Alterations in the frequency, duration, magnitude, and timing of flows—and thus hydrologic connectivity—are associated with the extinction or extirpation of species in downstream systems. Moreover, many fish species (e.g., Arkansas River shiner, speckled chub, flathead chub) in prairie river networks require sufficient unfragmented (i.e., connected) channel length with adequate discharge to

keep their nonadhesive, semibuoyant eggs in suspension for incubation and early development. When these conditions are not met, the biological integrity of downstream waters is impaired.

5.5.2 Effects of Human Alteration

Human alteration of prairie river networks has affected the physical, chemical, and biological connectivity to and their consequences for downstream waters. Impoundments and water removal, through both surface flow diversions and pumping of ground-water aquifers, are common in this region. These activities have reduced flood magnitude and variability, altered timing, and increased predictability of flows to downstream waters. As a result, physical, chemical, and biological connections to downstream waters have been altered. In addition to the altered land uses and application of nutrients and pesticides for agriculture, human alteration of the river network itself, through channelization, levee construction, desnagging, dredging, and ditching, has enhanced longitudinal connectivity while reducing lateral and vertical connectivity with the floodplain and hyporheic zone, respectively. Pumping from streams and ground water has caused historically perennial river segments to regularly dry during summer months. Changes to the prairie's grazing (from bison to cattle) and burning regimes increase nutrient and suspended sediment loading to downstream waters. Introduced species have extirpated endemic species and altered food web structure and processes in prairie streams, thereby affecting the biological integrity of downstream waters.

5.6 Southwestern Intermittent and Ephemeral Streams

Southwestern streams are predominantly ephemeral and intermittent (nonperennial) systems located in the southwestern United States (Section B.5). Based on the National Hydrography Dataset, 94%, 89%, 88%, and 79% of the streams in Arizona, Nevada, New Mexico, and Utah, respectively, are nonperennial. Most of these streams connect to downstream waters, although 66% and 20% of the drainage basins in Nevada and New Mexico, respectively, are closed and drain into playas (dry lakes). Southwestern streams generally are steep and can be divided into two main types: (1) mountainous streams that drain higher portions of basins and receive higher rates of precipitation, often as snow, compared to lower elevations; and (2) streams located in valley or plateau regions that generally flow in response to high-intensity thunderstorms. Headwater streams are common in both types of southwestern streams.

5.6.1 Connectivity and Consequences on Downstream Waters

Nonperennial southwestern streams, excluding those that drain into playas, are periodically connected to downstream waters by low-duration, high-magnitude flows. In contrast to streams in humid regions where discharge is typically supplemented by ground water as drainage area increases, many southwestern streams lose streamflow to channel transmission losses as runoff travels downstream (Figure B-10). Connection of runoff and associated materials in ephemeral and intermittent streams to downstream waters is therefore a function of distance, the relative magnitude of the runoff event, and transmission losses.

Spatial and temporal variation in frequency, duration, and timing of southwestern stream runoff is largely explained by elevation, climate, channel substrate, geology, and the presence of shallow ground water. In nonconstraining substrate, southwestern rivers are dendritic and their watersheds tend to have a high drainage density. When high flows are present, southwestern streams are efficient at transferring water, sediment, and nutrients to downstream reaches. Due to the episodic nature of flow in ephemeral and intermittent channels, sediment and organic matter can be deposited some distance downstream, and then moved farther downstream by subsequent precipitation events. Over time, sediment and organic matter continue to move downstream and affect downstream waters.

The southwestern streams case study (Section B.5) describes the substantial connection and important consequences of runoff, nutrients, and particulate matter originating from ephemeral tributaries on the integrity and sustainability of downstream perennial streams. Channel transmission losses can be an important source of ground-water recharge that sustains downstream perennial stream and riparian systems. For example, isotopic studies indicate that runoff from ephemeral tributaries like Walnut Gulch, Arizona supplies roughly half the San Pedro River's baseflow through shallow alluvial aquifer recharge.

5.6.2 Effects of Human Alteration

Human alterations to southwestern river networks affect the physical, chemical, and biological connectivity to downstream waters. Impoundments trap water, sediment, and particulate nutrients and result in downstream impacts on channel morphology and aquatic function. Diversion of water for consumptive uses can decrease downstream baseflows but typically does not affect the magnitude of peak flows. Excessive ground-water pumping can lower ground-water tables, thereby diminishing or eliminating baseflows. Urbanization increases runoff volume and flow velocity, resulting in more erosive energy that can cause bank erosion, streambed downcutting, and reduced infiltration to ground water.

5.7 Vernal Pools

Vernal pools are shallow, rain-fed, fishless pools situated on bedrock or low-permeability soils (Section B.6). Vernal pools inundate seasonally and lack continuous surface-water connections to downstream water bodies. Although they can occur in other parts of the United States, this case study focuses on pools in the western states and the glaciated areas of northeastern states. Western vernal pools typically occur in open grasslands; most northern vernal pools are detrital and are fully contained within forest ecosystems. When inundation occurs, vernal pools can fill and overflow through swales or intermittent streams, which connect them to downstream waters.

5.7.1 Connectivity and Consequences on Downstream Waters

Direct surface connection of vernal pools to downstream waters is infrequent. The duration and magnitude of such connections are highly variable and depend on the climate, terrain, and geology of the region and on the location of the vernal pool in the watershed. Vernal pools generally are clustered,

forming wetland complexes. Pools located at the downgradient end of a complex can receive surface water through stepping-stone spillage in addition to precipitation, and generally are inundated longer than upper pools. Because they experience greater inundation and are likely to be located nearer to streams, these downgradient pools are also more likely to be directly connected to streams. Temporary storage of heavy rainfall and snowmelt in individually small vernal pool systems (pools plus soils) can attenuate flooding, provide a reservoir for nearby vegetation during the spring growth period, and increase nutrient availability.

The timing of seasonal inundation and lack of permanent surface connections make vernal pools important biological refuges, which has consequences on the biological health of downstream waters. Vernal pools are highly productive ecosystems that have evolved in a "balance between isolation and connectedness" (Zedler, 2003; page 597). Because they are connected to other aquatic habitats through dispersal, they provide rich reservoirs of genetic and species diversity. Food webs in vernal pools include highly fecund amphibians and insects that convert detrital organic matter into biomass, which is then exported to aquatic ecosystems in other parts of the watershed. 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.

5.7.2 Effects of Human Alteration

Vernal pools have been drained and converted to other land uses (e.g., agriculture, logging, urban development). These activities have increased fragmentation of habitats for amphibians, plants, and invertebrates, and had similar effects on the frequency, duration, magnitude, and timing of inundations, surface-water outflows, and shallow subsurface-water connections to downstream waters as those described in Section 5.2.1 (Carolina and Delmarva bays).

5.8 Synthesis

These case study summaries highlight the key connections between specific water body types and downstream waters. The case study evidence provides further support that the structure and function of downstream waters highly depend on constituent materials and organisms contributed by and transported through water bodies located throughout the watershed. In addition, the studies support that variation in the types and degrees of connectivity determines the range of downstream effects.

These case study summaries illustrate two key points. First, each type of water body addressed here demonstrates variability in connectivity to and effects on downstream waters. Oxbow lakes, for example, are more or less connected to the main river channel based largely on their relative position in the landscape: Systems close to the river channel are highly connected and those farther away are connected less often or the impact on the river takes longer to be realized. Evidence presented in the prairie pothole case study also demonstrates variation in connectivity patterns across the region and shows the consequences of this variability on downstream rivers and lakes. The prairie streams case

study discusses functions and varying degrees of connectivity of streams and their cumulative effects on downstream waters.

Second, the effects of human alteration on the connectivity to and effects on downstream waters depend on the type of water body. Human alteration of different types of streams and wetlands can be complex, either increasing or decreasing connectivity and subsequent effects on downstream waters. For example, evidence shows that ditches in the prairie pothole region increase hydrologic connectivity, and connectivity of oxbow lakes near active river channels can be reduced if that portion of the river is leveed. Coupled human-natural systems are an area of active research and new information about the effects of human activities on connectivity and water integrity is emerging in the peer-reviewed literature.

Positioning the specific water body types in the case studies (Appendix B) along a gradient of connectivity and effect proved to be premature for several reasons. First, the amount of documented evidence (i.e., number of published studies) varied among the water body types. In some instances, a large body of evidence exists and in others, only a few studies exist, limiting sound comparisons. Second, variation in connectivity consistently was reported to be high within some water body types, creating substantial overlap in ranges of connectivity among those water body types. In addition to a need for more studies documenting connectivity in less studied regions, a more refined classification using the descriptors of connectivity described in Chapter 1 (or others) and their controls (e.g., climate, geology, and terrain) within wetland landscape settings are required.

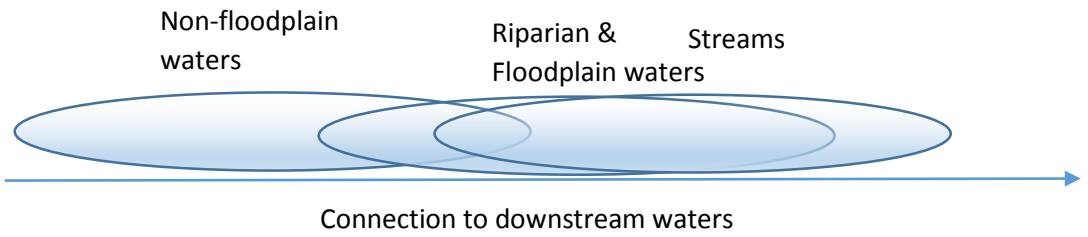
Based on the evidence presented in Chapters 3 and 4, ordering the three broad categories of water bodies considered in this report—streams, floodplain wetlands, and non-floodplain wetlands—along a connectivity gradient (Figure 5-1) is possible. Of these three water body types, streams are, in general, more connected to and have better-documented effects on downstream waters than either wetland category. Floodplain wetlands, in turn, tend to be more connected to downstream waters, and have better-documented downstream effects, than non-floodplain wetlands. This ordering must be recognized as a broad generalization, and considerable overlap can occur among the types, given the spatial and temporal variability in connectivity documented in these habitats (Figure 5-1). Nevertheless, several key lines of evidence support this hypothesized ordering of water body types along the gradient.

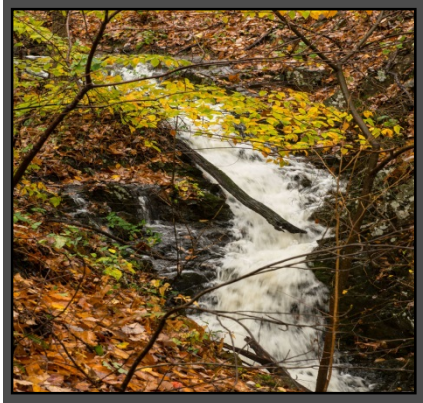
1. Streams are connected to rivers by a continuous channel, which is a physical reflection of surface connectivity. Formation of a channel indicates that connectivity, in terms of its combined descriptors (frequency, duration, magnitude, timing) is sufficiently strong (or "effective") and outweighs terrestrialization processes (e.g., revegetation, wind-mediated processes, soil formation processes).
2. Within-channel flows are more efficient for moving water, sediment, pollutants, and other materials than overland flow; for some aquatic organisms, channels are the only possible transport routes. Channels are places where excess water and materials from the landscape are concentrated as they are transmitted downstream. Recurrent flow of sufficient magnitude over a given area of landscape selects routes with least resistance, which develop into branched

channel networks with a repeating, cumulative pattern of smaller channels that join at confluences to form larger channels.

3. The continuous channels connecting streams to rivers also represent areas of relatively high shallow subsurface connectivity (shallow ground-water recharge and upwelling). Channels are typically more permeable than surrounding soils, lack dense terrestrial vegetation (and thus have lower uptake and evapotranspiration loss), and are topographic low points closer to concentrated shallow ground water.
4. Floodplain wetlands and open waters are connected to rivers by historical and recurrent surface connectivity. Riparian/floodplain wetlands are maintained by the recurrent inundation and deposition of materials from streams and rivers during the peak and recession of flood flows.
5. Riparian/floodplain wetlands and open waters are close to river networks and thus more likely to have strong connectivity with the downstream water than more distant wetlands, when all other conditions are similar.
6. Non-floodplain wetlands are positioned outside the floodplain, and so are not subject to direct flooding from the river or stream. Any hydrologic connections to the river system are therefore unidirectional (from wetland to downstream water and not vice-versa). They are also likely to be more distant from the network, increasing the flowpath lengths and travel time to the network.
7. Because of their large numbers, headwater streams and associated wetlands cumulatively represent a large portion of the landscape interface with a downstream water. These areas provide functions that enhance both exchanges with and buffering of the downstream water, making them critical to mediating the recognized relationship between the integrity of downstream waters and the land use and stressor loadings from the surrounding landscape.
8. Connectivity to downstream waters is reflected in the distribution of aquatic organisms and their dependence on particular aquatic habitats across different stages of their life cycles. For example, the recurrent presence of completely aquatic organisms (i.e., organisms that lack terrestrial life stages, overland dispersal, stages resistant to drying) in streams and wetlands that periodically dry provides indirect evidence for surface-water connections. Because many aquatic species can move and disperse overland, aquatic habitats can be highly connected biologically in the absence of hydrologic connectivity.

Figure 5-1. Relative positioning of streams, riparian and floodplain waters, and non-floodplain waters along a gradient of connectivity. Ellipses are used to illustrate the degree of expected overlap among water-body types based on the range of variation documented in the reviewed literature.







CHAPTER 6. CONCLUSIONS

This chapter presents the five major conclusions of this report, with a summary of key findings from the literature synthesized to develop these conclusions. It also discusses the relative abundance of literature on topics reviewed in this report. Finally, it briefly discusses emerging research that can close some current data gaps and help further clarify the role of connectivity in maintaining the integrity of downstream waters.

Citations have been omitted from the text of the conclusions and key findings to improve readability; please refer to individual chapters for supporting publications and additional information.

6.1 Major Conclusions and Key Findings

Based on our review and synthesis of the literature, we developed five major conclusions, which are presented in this section with a summary of key findings for each conclusion.

6.1.1 Conclusion 1: Streams

The scientific literature unequivocally demonstrates that streams, individually or cumulatively, exert a strong influence on the integrity 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. Streams are the dominant source of water in most rivers, and the majority of tributaries are perennial, intermittent, or ephemeral headwater streams. Headwater streams also convey water into local storage compartments such as ponds, shallow aquifers, or stream banks, and into regional and alluvial aquifers; these local storage compartments are important sources of water for maintaining baseflow in rivers. In addition to water, streams transport sediment, wood, organic matter, nutrients, chemical contaminants, and many of the organisms found in rivers. The literature provides robust evidence that 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 upstream and downstream habitats during one or more stages of their life cycles, or provide food resources to downstream communities. In addition to material transport and biological connectivity, ephemeral, intermittent, and perennial flows influence fundamental biogeochemical processes by connecting channels and shallow ground water with other landscape elements. Physical, chemical, and biological connections between streams and downstream waters interact via integrative processes such as nutrient spiraling, in which stream communities assimilate and chemically transform large quantities of nitrogen and other nutrients that otherwise would be transported directly downstream, increasing nutrient loads and associated impairments due to excess nutrients in downstream waters.

6.1.1.1 Conclusion 1, Key Findings

- Streams are hydrologically connected to downstream waters via channels that convey surface and subsurface water either year-round (i.e., perennial flow), weekly to seasonally (i.e., intermittent flow), or only in direct response to precipitation (i.e., ephemeral flow). Streams are the dominant source of water in most rivers, and the majority of tributaries are perennial, intermittent, or ephemeral headwater streams. For example, headwater streams, which are the smallest channels where streamflows begin, are the cumulative source of approximately 60% of the total mean annual flow to all northeastern U.S. streams and rivers.
- In addition to downstream transport, headwaters convey water into local storage compartments such as ponds, shallow aquifers, or stream banks, and into regional and alluvial aquifers. These local storage compartments are important sources of water for maintaining baseflow in rivers. Streamflow typically depends on the delayed (i.e., lagged) release of shallow ground water from local storage, especially during dry periods and in areas with shallow ground-water tables and pervious subsurfaces. For example, in the southwestern United States, short-term shallow ground-water storage in alluvial floodplain aquifers, with gradual release into stream channels, is a major source of annual flow in rivers.
- 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 help structure stream and river channels by slowing the flow of water through channels and providing substrate and habitat for aquatic organisms.
- There is strong evidence that headwater streams function as nitrogen sources (via export) and sinks (via uptake and transformation) for river networks. For example, one study estimated that rapid nutrient cycling in small streams with no 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 lead to eutrophication and hypoxia, in which over-enrichment causes dissolved oxygen concentrations to fall below the level necessary

to sustain most aquatic animal life in the stream and streambed. Thus, the influence of streams on nutrient loads can have significant repercussions for hypoxia in downstream waters.

- Headwaters provide habitat that is critical for completion of one or more life-cycle stages of many aquatic and semiaquatic species capable of moving throughout river networks. Evidence is strong that headwaters provide habitat for complex life-cycle completion; refuge from predators, competitors, parasites, or adverse physical conditions in rivers (e.g., temperature or flow extremes, low dissolved oxygen, high sediment); and reservoirs of genetic- and species-level diversity. Use of headwater streams as habitat is especially critical 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). The presence of these species within river networks provides robust evidence of biological connections between headwaters and larger rivers; because these organisms also transport nutrients and other materials as they migrate, their presence also provides evidence of biologically mediated chemical connections. In prairie streams, many fishes swim upstream into tributaries to release eggs, which develop as they are transported downstream.
- Human alterations affect the frequency, duration, magnitude, timing, and rate of change of connections between headwater streams, including ephemeral and intermittent streams, and downstream waters. Human activities and built structures (e.g., channelization, dams, ground-water withdrawals) can either enhance or fragment longitudinal connections between headwater streams and downstream waters, while also constraining lateral and vertical exchanges and tightly controlling the temporal dimension of connectivity. In many cases, research on human alterations has enhanced our understanding of the headwater stream-downstream water connections and their consequences. Recognition of these connections and effects has encouraged the development of more sustainable practices and infrastructure to reestablish and manage connections, and ultimately to protect and restore the integrity of downstream waters.

6.1.2 Conclusion 2: Riparian/Floodplain Wetlands and Open Waters

The literature clearly shows that wetlands and open waters in riparian areas and floodplains are physically, chemically, and biologically integrated with rivers via functions that improve downstream water quality, including the temporary storage and deposition of channel-forming sediment and woody debris, temporary storage of local ground water that supports baseflow in rivers, and transformation and transport of stored organic matter. Riparian/floodplain wetlands and open waters improve water quality through the assimilation, transformation, or sequestration of pollutants, including excess nutrients and chemical contaminants such as pesticides and metals, that can degrade downstream water integrity. In addition to providing effective buffers to protect downstream waters from point source and nonpoint source pollution, these systems form integral components of river food webs, providing nursery habitat for breeding fish and amphibians, colonization opportunities for stream invertebrates, and maturation habitat for stream insects. Lateral expansion and contraction of the river in its

floodplain result in an exchange of organic matter and organisms, including fish populations that are adapted to use floodplain habitats for feeding and spawning during high water, that are critical to river ecosystem function. Riparian/floodplain wetlands and open waters also affect the integrity of downstream waters by subsequently releasing (desynchronizing) floodwaters and retaining large volumes of stormwater, sediment, and contaminants in runoff that could otherwise negatively affect the condition or function of downstream waters.

6.1.2.1 Conclusion 2, Key Findings

- Riparian areas and floodplains connect upland and aquatic environments through both surface and subsurface hydrologic flowpaths. These areas are therefore uniquely situated in watersheds to receive and process waters that pass over densely vegetated areas and through subsurface zones before the waters reach streams and rivers. When pollutants reach a riparian or floodplain wetland, they can be sequestered in sediments, assimilated into wetland plants and animals, transformed into less harmful or mobile forms or compounds, or lost to the atmosphere. Wetland potential for biogeochemical transformations (e.g., denitrification) that can improve downstream water quality is influenced by local factors, including anoxic conditions and slow organic matter decomposition, shallow water tables, wetland plant communities, permeable soils, and complex topography.
- Riparian/floodplain wetlands can reduce flood peaks by storing and desynchronizing floodwaters. They can also maintain river baseflows by recharging alluvial aquifers. Many studies have documented the ability of riparian/floodplain wetlands 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.
- Riparian areas and floodplains store large amounts of sediment and organic matter from upstream and from upland areas. For example, riparian areas have been shown to remove 80–90% of sediments leaving agricultural fields in North Carolina.
- Ecosystem function within a river system is driven in part by biological connectivity that links diverse biological communities with the river system. Movements of organisms that connect aquatic habitats and their populations, even across different watersheds, are 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 result in an exchange of matter and organisms, including fish populations that are adapted to use floodplain habitats for feeding and spawning during high water. Wetland and 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 commonly use both streams and riparian/floodplain wetlands to hunt, forage, overwinter, rest, or hide from predators. Birds can spatially integrate the watershed landscape through biological connectivity.

6.1.3 Conclusion 3: Non-floodplain Wetlands and Open Waters

Wetlands and open waters in non-floodplain landscape settings (hereafter called "non-floodplain wetlands") provide numerous functions that benefit downstream water integrity. These functions include storage of floodwater; recharge of ground water that sustains river baseflow; retention and transformation of nutrients, metals, and pesticides; export of organisms or reproductive propagules to downstream waters; and habitats needed for stream species. This diverse group of wetlands (e.g., many prairie potholes, vernal pools, playa lakes) can be connected to downstream waters through surface-water, shallow subsurface-water, and ground-water flows and through biological and chemical connections.

In general, connectivity of non-floodplain wetlands occurs along a gradient (Conclusion 4), and can be described in terms of the frequency, duration, magnitude, timing, and rate of change of water, material, and biotic fluxes to downstream waters. These descriptors are influenced by climate, geology, and terrain, which interact with factors such as the magnitudes of the various functions within wetlands (e.g., amount of water storage or carbon export) and their proximity to downstream waters to determine where wetlands occur along the connectivity gradient. At one end of this gradient, the functions of non-floodplain wetlands clearly affect the condition of downstream waters if a visible (e.g., channelized) surface-water or a regular shallow subsurface-water connection to the river network is present. For non-floodplain wetlands lacking a channelized surface or regular shallow subsurface connection (i.e., those at intermediate points along the gradient of connectivity), generalizations about their specific effects on downstream waters from the available literature are difficult because information on both function and connectivity is needed. Although there is ample evidence that non-floodplain wetlands provide hydrologic, chemical, and biological functions that affect material fluxes, to date, few scientific studies explicitly addressing connections between non-floodplain wetlands and river networks have been published in the peer-reviewed literature. Even fewer publications specifically focus on the frequency, duration, magnitude, timing, or rate of change of these connections. In addition, although areas that are closer to rivers and streams have a higher probability of being connected than areas farther away when conditions governing the type and quantity of flows—including soil infiltration rate, wetland storage capacity, hydraulic gradient, etc.—are similar, information to determine if this similarity holds is generally not provided in the studies we reviewed. Thus, current science does not support evaluations of the degree of connectivity for specific groups or classes of wetlands (e.g., prairie potholes or vernal pools). Evaluations of individual wetlands or groups of wetlands, however, could be possible through case-by-case analysis.

Some effects of non-floodplain wetlands on downstream waters are due to their isolation, rather than their connectivity. Wetland sink functions that trap materials and prevent their export to downstream waters (e.g., sediment and entrained pollutant removal, water storage) result because of the wetland's

ability to isolate material fluxes. To establish that such functions influence downstream waters, we also need to know that the wetland intercepts materials that otherwise would reach the downstream water. The literature we reviewed does provide limited examples of direct effects of wetland isolation on downstream waters, but not for classes of wetlands (e.g., vernal pools). Nevertheless, the literature we reviewed enables us to conclude that sink functions of non-floodplain wetlands, which result in part from their relative isolation, will affect a downstream water when these wetlands are situated between the downstream water and known point or nonpoint sources of pollution, and thus intersect flowpaths between the pollutant source and downstream waters.

6.1.3.1 Conclusion 3, Key Findings

- 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 could be widespread across eastern portions of the prairie pothole region. This work also indicates that reducing water storage capacity of wetlands by connecting formerly isolated potholes through ditching or drainage to the Devils Lake and Red River basins could increase stormflow and contribute to downstream flooding. In many agricultural areas already crisscrossed by extensive drainage systems, total streamflow and baseflow are increased 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 example, 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.
- Non-floodplain wetlands act as sinks and transformers for various pollutants, especially nutrients, which at excess levels can adversely impact human and ecosystem health and pose a serious pollution problem in the United States. In one study, sewage wastewaters were applied to forested wetlands in Florida for 4.5 years; more than 95% of the phosphorus, nitrate, ammonium, and total nitrogen were removed by the wetlands during the study period, and 66–86% of the nitrate removed was attributed to the process of denitrification. In another study, sizeable phosphorus retention (0.3 to 8.0 mg soluble reactive P m^{-2} d^{-1}) occurred in marshes that comprised only 7% of the lower Lake Okeechobee basin area in Florida. A non-floodplain 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 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 onsite nutrient removal by non-floodplain wetlands is substantial and geographically widespread. The effects of this removal on rivers are generally not reported in the literature.

- Non-floodplain wetlands provide unique and important habitats for many species, both common and rare. Some of these species require multiple types of waters to complete their full life cycles, including downstream waters. Abundant or highly mobile species play important roles in transferring energy and materials between non-floodplain wetlands and downstream waters.
- Biological connections are likely to occur between most non-floodplain wetlands and downstream waters through either direct or stepping stone movement of amphibians, invertebrates, reptiles, mammals, and seeds of aquatic plants, 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 wetlands and river networks. Migratory birds can be an important vector of long-distance dispersal of plants and invertebrates between non-floodplain wetlands and the river network, although their influence has not been quantified. Whether those connections are of sufficient magnitude to impact downstream waters will either require estimation of the magnitude of material fluxes or evidence that these movements of organisms are required for the survival and persistence of biota that contribute to the integrity of downstream waters.
- Spatial proximity is one important determinant of the magnitude, frequency, and duration of connections between wetlands and streams that will ultimately influence the fluxes of water, materials, and biota between wetlands and downstream waters. However, proximity alone is not sufficient to determine connectivity, due to local variation in factors such as slope and permeability.
- The cumulative influence of many individual wetlands within watersheds can strongly affect the spatial scale, magnitude, frequency, and duration of hydrologic, biological, and chemical fluxes or transfers of water and materials to downstream waters. Because of their aggregated influence, any evaluation of changes to individual wetlands should be considered in the context of past and predicted changes (e.g., from climate change) to other wetlands within the same watershed.
- Non-floodplain wetlands can be hydrologically connected directly to river networks through natural or constructed channels, nonchannelized surface flows, or subsurface flows, the latter of which can travel long distances to affect downstream waters. 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 hydrologic, chemical, and biological connections to downstream waters.

- Non-floodplain 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 ground-water aquifers; geographically isolated wetlands that have local ground-water or occasional surface-water connections to downstream waters; and geographically isolated wetlands that have minimal hydrologic connection to other water bodies (but which could include surface and subsurface connections to other wetlands). This gradient can exist among wetlands of the same type or in the same geographic region.
- Caution should be used in interpreting connectivity for wetlands that have been designated as "geographically isolated" because (1) the term can be applied broadly to a heterogeneous group of wetlands, which can include wetlands that are not actually 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, 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. For example, a recent study examined hydrologic connectivity in a complex of wetlands on the Texas Coastal Plain. The wetlands in this complex have been considered to be a type of geographically isolated wetland. Collectively, however, they are connected both geographically and hydrologically 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 out through an intermittent stream into downstream waters. Thus, wetland complexes could have connections to downstream waters through stream channels even when the individual wetland components are geographically isolated.

6.1.4 Conclusion 4: Degrees and Determinants of Connectivity

Watersheds are integrated at multiple spatial and temporal scales by flows of surface water and ground water, transport and transformation of physical and chemical materials, and movements of organisms. Although all parts of a watershed are connected to some degree—by the hydrologic cycle or dispersal of organisms, for example—the degree and downstream effects of those connections vary spatially and temporally, and are determined by characteristics of the physical, chemical, and biological environments and by human activities.

Stream and wetland connections have particularly important consequences for downstream water integrity. Most of the materials—broadly defined as any physical, chemical, or biological entity—in rivers, for example, originate from aquatic ecosystems located upstream or elsewhere in the watershed. Longitudinal flows through ephemeral, intermittent, and perennial stream channels are much more efficient for transport of water, materials, and organisms than diffuse overland flows, and areas that

concentrate water provide mechanisms for the storage and transformation, as well as transport, of materials.

Connectivity of streams and wetlands to downstream waters occurs along a continuum that can be described in terms of the frequency, duration, magnitude, timing, and rate of change of water, material, and biotic fluxes to downstream waters. These terms, which we refer to collectively as connectivity descriptors, characterize the range over which streams and wetlands vary and shift along the connectivity gradient in response to changes in natural and anthropogenic factors and, when considered in a watershed context, can be used to predict probable effects of different degrees of connectivity over time. The evidence unequivocally demonstrates that the stream channels and riparian/floodplain wetlands or open waters that together form river networks are clearly connected to downstream waters in ways that profoundly influence downstream water integrity. The connectivity and effects of non-floodplain wetlands and open waters are more variable and thus more difficult to address solely from evidence available in peer-reviewed studies.

Variations in the degree of connectivity influence the range of functions provided by streams and wetlands, and are critical to the integrity and sustainability of downstream waters. Connections with low values of one or more descriptors (e.g., low-frequency, low-duration streamflows caused by flash floods) can have important downstream effects when considered in the context of other descriptors (e.g., large magnitude of water transfer). At the other end of the frequency range, high-frequency, low-magnitude vertical (surface-subsurface) and lateral flows contribute to aquatic biogeochemical processes, including nutrient and contaminant transformation and organic matter accumulation. The timing of an event can alter both connectivity and the magnitude of its downstream effect. For example, when soils become saturated by previous rainfall events, even low or moderate rainfall can cause streams or wetlands to overflow, transporting water and materials to downstream waters. Fish that use nonperennial or perennial headwater stream habitats to spawn or rear young, and invertebrates that move into seasonally inundated floodplain wetlands prior to emergence, have life cycles that are synchronized with the timing of flows, temperature thresholds, and food resource availability in those habitats.

6.1.4.1 Conclusion 4, Key Findings

- The surface-water and ground-water flowpaths (hereafter, hydrologic flowpaths), along which water and materials are transported and transformed, determine variations in the degree of physical and chemical connectivity. These flowpaths are controlled primarily by variations in climate, geology, and terrain within and among watersheds and over time. Climate, geology, and terrain are reflected locally in factors such as rainfall and snowfall intensity, soil infiltration rates, and the direction of ground-water flows. These local factors interact with the landscape positions of streams and wetlands relative to downstream waters, and with functions (such as the removal or transformation of pollutants) performed by those streams and wetlands to determine connectivity gradients.

- Gradients of biological connectivity (i.e., the active or passive movements of organisms through water or air and over land that connect populations) are determined primarily by species assemblages, and by features of the landscape (e.g., climate, geology, terrain) that facilitate or impede the movement of organisms. The temporal and spatial scales at which biological pathways connect aquatic habitats depend on characteristics of both the landscape and species, and overland transport or movement can occur across watershed boundaries. Dispersal is essential for population persistence, maintenance of genetic diversity, and evolution of aquatic species. Consequently, dispersal strategies reflect aquatic species' responses and adaptations to biotic and abiotic environments, including spatial and temporal variation in resource availability and quality. Species' traits and behaviors encompass species-environment relationships over time, and provide an ecological and evolutionary context for evaluating biological connectivity in a particular watershed or group of watersheds.
- Pathways for chemical transport and transformation largely follow hydrologic flowpaths, but sometimes follow biological pathways (e.g., nutrient transport from wetlands to coastal waters by migrating waterfowl, upstream transport of marine-derived nutrients by spawning of anadromous fish, uptake and removal of nutrients by emerging stream insects).
- Human activities alter naturally occurring gradients of physical, chemical, and biological connectivity by modifying the frequency, duration, magnitude, timing, and rate of change of fluxes, exchanges, and transformations. For example, connectivity can be reduced by dams, levees, culverts, water withdrawals, and habitat destruction, and can be increased by effluent discharges, channelization, drainage ditches and tiles, and impervious surfaces.

6.1.5 Conclusion 5: Cumulative Effects

The incremental effects of individual streams and wetlands are cumulative across entire watersheds and therefore must be evaluated in context with other streams and wetlands. Downstream waters are the time-integrated result of all waters contributing to them. For example, the amount of water or biomass contributed by a specific ephemeral stream in a given year might be small, but the aggregate contribution of that stream over multiple years, or by all ephemeral streams draining that watershed in a given year or over multiple years, can have substantial consequences on the integrity of the downstream waters. Similarly, the downstream effect of a single event, such as pollutant discharge into a single stream or wetland, might be negligible but the cumulative effect of multiple discharges could degrade the integrity of downstream waters.

In addition, when considering the effect of an individual stream or wetland, all contributions and functions of that stream or wetland should be evaluated cumulatively. For example, the same stream transports water, removes excess nutrients, mitigates flooding, and provides refuge for fish when conditions downstream are unfavorable; if any of these functions is ignored, the overall effect of that stream would be underestimated.

6.1.5.1 Conclusion 5, Key Findings

- Structurally and functionally, stream-channel networks and the watersheds they drain are fundamentally cumulative in how they are formed and maintained. Excess water from precipitation that is not evaporated, taken up by organisms, or stored in soils and geologic layers moves downgradient by gravity as overland flow or through channels carrying sediment, chemical constituents, and organisms. These channels concentrate surface-water flows and are more efficient than overland (i.e., diffuse) flows in transporting water and materials, and are reinforced over time by recurrent flows.

- Connectivity between streams and rivers provides opportunities for materials, including nutrients and chemical contaminants, to be transformed chemically as they are transported downstream. Although highly efficient at the transport of water and other physical materials, streams are dynamic ecosystems with permeable beds and banks that interact with other ecosystems above and below the surface. The exchange of materials between surface and subsurface areas involves 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 opportunity for transformation of material (e.g., biological uptake, assimilation, or beneficial transformation) in intervening stream reaches increases with distance to the river. Nutrient spiraling, the process by which nutrients entering headwater streams are transformed by various aquatic organisms and chemical reactions as they are transported downstream, is one example of an instream alteration that exhibits significant beneficial effects on downstream waters. Nutrients (in their inorganic form) that enter a 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 into the stream via excretion and decomposition (i.e., in their organic form), 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.

- Cumulative effects across a watershed must be considered when quantifying the frequency, duration, and magnitude of connectivity, to evaluate the downstream effects of streams and wetlands. For example, although the probability of a large-magnitude transfer of organisms from any given headwater stream in a given year might be low (i.e., a low-frequency connection when each stream is considered individually), headwater streams are the most abundant type of stream in most watersheds. Thus, the overall probability of a large-magnitude transfer of organisms is higher when considered for all headwater streams in a watershed—that is, a high-

frequency connection is present when headwaters are considered cumulatively at the watershed scale, compared with probabilities of transport for streams individually. Similarly, a single pollutant discharge might be negligible but the cumulative effect of multiple discharges could degrade the integrity of downstream waters. Riparian open waters (e.g., oxbow lakes), wetlands, and vegetated areas cumulatively can retain up to 90% of eroded clays, silts, and sands that otherwise would enter stream channels. The larger amounts of snowmelt and precipitation cumulatively held by many wetlands can reduce the potential for flooding at downstream locations. For example, wetlands in the prairie pothole region cumulatively stored about 11–20% of the precipitation in one watershed.

- The combination of diverse habitat types and abundant food resources cumulatively makes floodplains important foraging, hunting, and breeding sites for fish, aquatic life stages of amphibians, and aquatic invertebrates. The scale of these cumulative effects can be extensive; for example, coastal ibises travel up to 40 km to obtain food from freshwater floodplain wetlands for nesting chicks, which cannot tolerate salt levels in local food resources until they fledge.

6.2 Strength of Evidence for Conclusions and Data Gaps in the Available Literature

This report synthesizes a large body of scientific evidence to address the questions in Table 1-1 of this report. The major conclusions (Section 6.1) reflect the strength of evidence currently available in the peer-reviewed scientific literature for assessing the connectivity and downstream effects of water bodies identified in Table 1-1.

The conclusions of this report were corroborated by two independent peer reviews by scientists identified in the front matter of this report.

The term connectivity is defined in this report as the degree to which components of a watershed are joined and interact by transport mechanisms that function across multiple spatial and temporal scales (Sections 1.2.2 and 2.3.2.1). Our review found strong evidence supporting the central roles of the physical, chemical, and biological connectivity of streams, wetlands, and open waters—encompassing varying degrees of both connection and isolation—in maintaining the structure and function of downstream waters, including rivers, lakes, estuaries, and oceans. Our review also found strong evidence demonstrating the various mechanisms by which material and biological linkages from streams, wetlands, and open waters affect downstream waters, classified here into five functional categories (source, sink, refuge, lag, and transformation), modify the timing of transport and the quantity and quality of resources available to downstream ecosystems and communities. Thus, the currently available literature provided a large body of evidence for assessing the connections and functions by which streams and wetlands produce the range of observed effects on the integrity of downstream waters.

The body of literature on functions provided by streams and riparian/floodplain wetlands was abundant in all five categories (Table 6-1). The body of literature on functions of non-floodplain wetlands was abundant in two categories (sink and transformation) and moderate in the other three categories (source, refuge, and lag; Table 6-1). The evidence unequivocally demonstrates that the stream channels and wetlands or open waters that together form river networks are clearly connected to downstream waters in ways that profoundly influence downstream water integrity. The body of literature documenting connectivity and downstream effects was most abundant for perennial and intermittent streams, and for riparian/floodplain wetlands (Table 6-2). Although less abundant, the available evidence for connectivity and downstream effects of ephemeral streams was strong and compelling, particularly in context with the large body of evidence supporting the physical connectivity and cumulative effects of channelized flows that form and maintain stream networks.

As stated in Conclusion 3 (Section 6.1.3), the connectivity and effects of wetlands and open waters that are not structurally linked to other waters by stream channels and their lateral extensions into riparian areas and floodplains are more difficult to address solely from evidence available in peer-reviewed studies. One limitation was the relatively small number of published, peer-reviewed studies examining the relationships of non-floodplain wetlands to downstream waters (Table 6-2). The literature on non-floodplain wetlands that is available shows that these systems have important hydrologic, water-quality, and habitat functions that can affect downstream waters where connections to them exist; the literature also provides limited examples of direct effects of non-floodplain wetland isolation on downstream water integrity. Currently available peer-reviewed literature, however, does not identify which types of non-floodplain wetlands have or lack the types of connections needed to convey the effects on downstream waters of functions, materials, or biota provided by those wetlands. These limitations of the literature, considered in context with comments from the Science Advisory Board on an external review draft of this report (U.S. EPA, 2014), are reflected in the lower strength of evidence expressed in the conclusions (Section 6.1.3).

Additional information from other sources not included in this report (e.g., field assessments, analysis of existing or new data, reports from local resource agencies) could be used in case-by-case analysis of non-floodplain wetlands. Importantly, information from emerging research into the connectivity of non-floodplain wetlands, including studies of the types identified in Section 4.5.2 of this report, could close some of the current data gaps in the near future. 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; McDonough et al., 2015), modeling (e.g., Golden et al., 2013; McLaughlin et al., 2014), and landscape classification (e.g., Wigington et al., 2013) 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 and improve the accuracy of connectivity assessments. Emerging research that expands 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 identify waters of national importance and maintain the long-term sustainability and resiliency of valued water resources.

Table 6-1. Relative abundance of literature by functional category. The table shows our confidence, which is based on the relative size of the body of literature documented in the report, in the evidence for source, sink, refuge, lag, and transformation functions of streams and wetlands and their associated effects on downstream waters. A small dot (•) indicates relatively lower confidence, a medium dot (●) indicates relatively intermediate confidence, and a large dot (●) indicates a relatively high level of confidence. The dot size does not necessarily correspond with the number of associated citations in this report because some citations are review articles or meta-analyses, which summarize information for many references. The dot size also does not correspond with the level of confidence in particular conclusions.

Type of water body	Function					Uncertainty discussion (Section)
	Source	Sink (Storage)	Refuge	Lag	Transformation	
Streams	●	●	●	●	●	3.6
Riparian/floodplain wetlands	●	●	●	●	●	4.5.1
Non-floodplain wetlands	•	●	•	•	●	4.5.2

Table 6-2. Relative abundance of literature by review topic area. The table shows the relative size of the body of literature documented in the report that addresses the physical, chemical, or biological connectivity to and effects on downstream waters. A small dot (•) indicates a relatively smaller body of literature, a medium dot (●) indicates a relatively intermediate body of literature, and a large dot (⬤) indicates a relatively large body of literature. The dot size does not necessarily correspond with the number of associated citations in this report because some citations are review articles or meta-analyses, which summarize information from many references. The dot size also does not correspond with level of confidence in particular conclusions.

Topic	Question		Biological		Chemical		Physical	
			Connection	Effect	Connection	Effect	Connection	Effect
Streams	What are the physical, chemical, and biological connections to and effects of ephemeral, intermittent, and perennial streams on downstream waters?	ephemeral	●	•	⬤	●	⬤	●
		intermittent	⬤	●	⬤	●	⬤	●
		perennial	⬤	⬤	⬤	⬤	⬤	⬤
Riparian/ Floodplain Wetlands	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?		⬤	⬤	⬤	⬤	⬤	⬤
Non-floodplain wetlands	What are the physical, chemical, and biological connections to and effects of wetlands and open waters in non-floodplain settings (e.g., most prairie potholes, vernal pools) on downstream waters?		●	•	●	•	•	•





CHAPTER 7. REFERENCES

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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 process 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 Ground Water—Ground water 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. *See* Colluvium.

Anastomosing Channel—A multithreaded stream or river channel in which 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. *See* Hypoxia.

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 ground water that yields ground water to a well, spring, or stream.

Artificial Drainage—Use of constructed 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 months. 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 ground-water discharge in the stream network. Baseflow also can be sustained by human sources (e.g., irrigation recharges to ground water).

Basin—*See* Drainage Basin.

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

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

Braided Channel—A multithreaded channel in which 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.

Colluvium—A layer of unconsolidated soils, sediment and rock fragments deposited by surface runoff and gravitational processes; colluvium generally occurs as a blanket of poorly sorted sediment and rock fragments on the lower parts of hillslopes underlain by bedrock. *See* Alluvium.

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.

Connectivity Descriptors (for streams and wetlands)—The frequency, duration, magnitude, timing, and rate of change of fluxes to and biological exchanges with downstream waters.

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

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

Deep Ground Water—Ground-water flow systems having the deepest and longest flowpaths; also referred to as regional ground-water flow systems, they can occur beneath local and intermediate ground-water flow systems. *See* Local Ground Water, Regional Ground Water.

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. *See* Carolina Bays.

Dendritic Stream Network—A stream network pattern of branching tributaries (see Figure 2-19B).

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 ground water 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 ground water) 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 and river reaches that have flow in one part of the reach but not another part of the reach. *See* Reach.

Dispersal—Movement from natal breeding sites to new breeding sites.

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 drainage area (e.g., per mi^2 or km^2).

Drainage Network—*See* River Network.

Egg Bank—Viable dormant eggs that accumulate in soil or in sediments under water. *See* Seed bank.

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

Endorheic Stream—A stream or river reach that experiences a net loss of water to a ground-water system. *See* Losing Stream or Wetland.

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

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 combined loss of water to the atmosphere due to 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 also can 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 (or greater) magnitude 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—Portions of floodplains 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.

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—Descriptor of flow types in a temporal or magnitude sense (i.e., slow-flow regime, low-flow regime)

Flowpath—*See* Hydrologic Flowpath.

Fluvial—Refers to or pertains to streams; e.g., stream processes (fluvial processes), fluvial landforms, such as fluvial islands and bars, and biota living in and near stream channels.

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

Gaining Stream or Wetland—A wetland or a stream or river reach that experiences a net gain of water from ground water (see Figure 2-5). In this situation, the water table elevation near 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 often is mistakenly understood to mean hydrologically isolated. Geographically isolated wetlands vary in their degree of hydrologic and biotic connectivity.

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

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

Ground-water Discharge Wetland—A wetland that receives ground-water discharge.

Ground-water Flow—Flow of water in the subsurface saturated zone.

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

Ground-water Recharge—The process by which ground water is replenished; a recharge area occurs where precipitation or surface water infiltrates and is transmitted downward to the saturated zone (aquifer). *See* Infiltration, Percolation, Transmission.

Ground-water Recharge Wetland—A wetland that recharges ground water.

Ground-water Reservoir—A saturated body of ground water having loosely definable spatial limits.

Ground-water System—Reference to the ground water and geologic materials comprising the saturated zone; the ground-water system, as a whole, is a three-dimensional flow field.

Ground water–Surface water Interactions—Movement of water between surface-water bodies and ground-water systems. Flows can occur in either direction.

Ground-water 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 medium. 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. *See* 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.

Hydric—An area, environment, or habitat that is generally very wet with plenty of moisture. *See* Mesic, Xeric.

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

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 ground water.

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 beneath 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 ground water.

Hypoxia—The condition in which dissolved oxygen is below the level necessary to sustain most animal life. *See* Anoxic Conditions.

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.

Interfluve—The area of higher terrain between adjacent stream valleys.

Intermediate Ground Water—Ground-water flow systems representative of the wide range of flowpath lengths and depths that occur between local and regional ground-water systems.

Intermittent—This term also can be applied to other surface-water bodies and ground-water 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, ground-water source, or 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 next 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 Ground Water—Ground water with a local flow system. Water that recharges at a high point in the water table that discharges to a nearby lowland. Local ground-water flow is the most dynamic and shallowest of ground-water 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 ground-water system (see Figure 2-5). In this situation, the water table elevation near 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.

Mesic—An area, environment, or habitat with a moderate amount of moisture. *See* Hydric, Xeric.

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

Non-floodplain Wetland—An area outside of the floodplain that meets the Cowardin et al. (1979) three-attribute definition of a wetland (i.e., having wetland hydrology, hydrophytic vegetation, or hydric soils). For the purposes of this report, riparian wetlands that occur outside of the floodplain are not included as non-floodplain wetlands, since these wetlands are subject to bidirectional, lateral hydrologic flows. *See* Floodplain, Wetland.

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 stream or 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 the land surface at any point and runs over the surface to the nearest stream channel.

Oxbow Lakes—Water bodies that originate from the cutoff meanders of rivers; such lakes are common in floodplains of large rivers.

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

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

Perching Water Tables—*See* Perched Ground Water.

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

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

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

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

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

Phreatophyte—Plants that use water from the saturated zone.

Potential Evapotranspiration—The amount of water that would be lost to the atmosphere over a given area through evaporation and transpiration, assuming no limits on the water supply. *See* Evapotranspiration.

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

Prairie Potholes—Complex of glacially formed wetlands, usually lacking natural outlets, 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—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 food web, and provides most of the autochthonous carbon produced in ecosystems. The rate of fixation 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.

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.

Recession [of Flow)—Decrease in flow following a hydrologic event.

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 an organism (or material) to avoid mortality (or loss) in a nearby sink area, thereby preventing the net decrease in material flux that otherwise would have occurred (exports = imports). This term typically refers to organisms but can be used for nonliving materials. *See* Sink Function.

Regional Ground Water—Ground water with a deep, regional-scale flow system; also referred to as deep ground water. These flow systems can occur beneath local and intermediate ground-water flow systems. *See* Local Ground Water, Deep Ground Water.

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 organisms. They are areas through which surface hydrology and subsurface hydrology connect water bodies with their 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, 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, 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., ground water). 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. Can also be expressed as a volume of water (i.e., m^3, $feet^3$, acre-ft).

Saturated Zone—The zone below the land surface where the voids in soil and geologic material are completely filled with water. Water in the saturated zone is referred to as ground water. The upper surface of the saturated zone is referred to as the water table. *See* Ground Water, Unsaturated Zone, Water Table.

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—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.

Seed Bank—Viable dormant seeds that accumulate in soil or in sediments under water. *See* Egg bank.

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 ground-water slope wetland.

Seepage—Water that flows from a seep.

Shallow Ground Water—Ground water with shallow hydrologic flowpaths. *See* Local Ground Water.

Sink Function—Any function within a stream or wetland that causes a net decrease in 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.

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 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 ground water 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 that do not undergo radioactive decay. 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 Burial—The process of incorporating streams—particularly headwaters—into storm sewer systems, usually by routing through underground pipes.

Stream Power—A measure of the erosive capacity of flowing water in stream channels or the rate of energy dissipation against the stream bed or banks per unit of channel length that has the mathematical form: $\omega_a = \rho g Q S$ where ω_a is the stream power, ρ is the density of water (1000 kg/m^3), g is acceleration due to gravity (9.8 m/s^2), Q is discharge (m^3/s), and S is the channel slope.

Stream Network—*See* River Network. A stream network is the same as river network, but typically refers to a smaller spatial scale.

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.

Stream Order (Strahler)—A method for stream classification based on relative position within a river network, when 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). When streams of different order join, the order of the larger stream is retained. Stream-order classifications can differ, depending on the map scale used to determine order.

Streamflow—Flow of water through a stream or river channel. *See* Discharge.

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 trough-like depression that carries water mainly during rainstorms or snowmelt. A swale might or might 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—An 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.

Transport Mechanism—Any physical mechanism, such as moving water, wind, or movement of organisms, which can transport materials or energy. As used in this report, the term specifically refers to physical mechanisms that move material or energy between streams or wetlands and downstream waters.

Tributary—A stream or river that flows into 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 it is consumed and mineralized by aquatic organisms.

Unconfined Aquifer—An aquifer that has a water table; the aquifer is not bounded by lower permeability layers. *See* Confined Aquifer.

Unsaturated Zone— Also referred to as the vadose zone. The zone between land surface and the water table within which the moisture content is less than saturation and pressure is less than atmospheric. Soil pore spaces also typically contain air or other gases. *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)-attribute wetland definition. *See* Wetland.

Uptake Length (for dissolved nitrogen in streams)—The distance traveled in the water column before algal and microbial assimilation occurs.

Valley—A depression of the earth's surface that drains water between two upland areas.

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 influenced by 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 that enters, leaves, and is stored in a hydrologic unit, area, or arbitrarily defined control volume, typically a drainage basin or aquifer, during a specified period of time.

Water Body—Any sizable accumulation of water on the land surface, including streams, rivers, lakes, and wetlands.

Water Surplus—Water that is available for streamflow or recharge of ground water; 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.

Xeric—An area, environment, or habitat that is generally dry with very little moisture. *See* Hydric, Mesic.

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APPENDIX B. CASE STUDIES

B.1 Case Study: Carolina and Delmarva Bays

B.1.1 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 ground water. Bays typically are near each other or near 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 can become part of the downstream food web. 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.

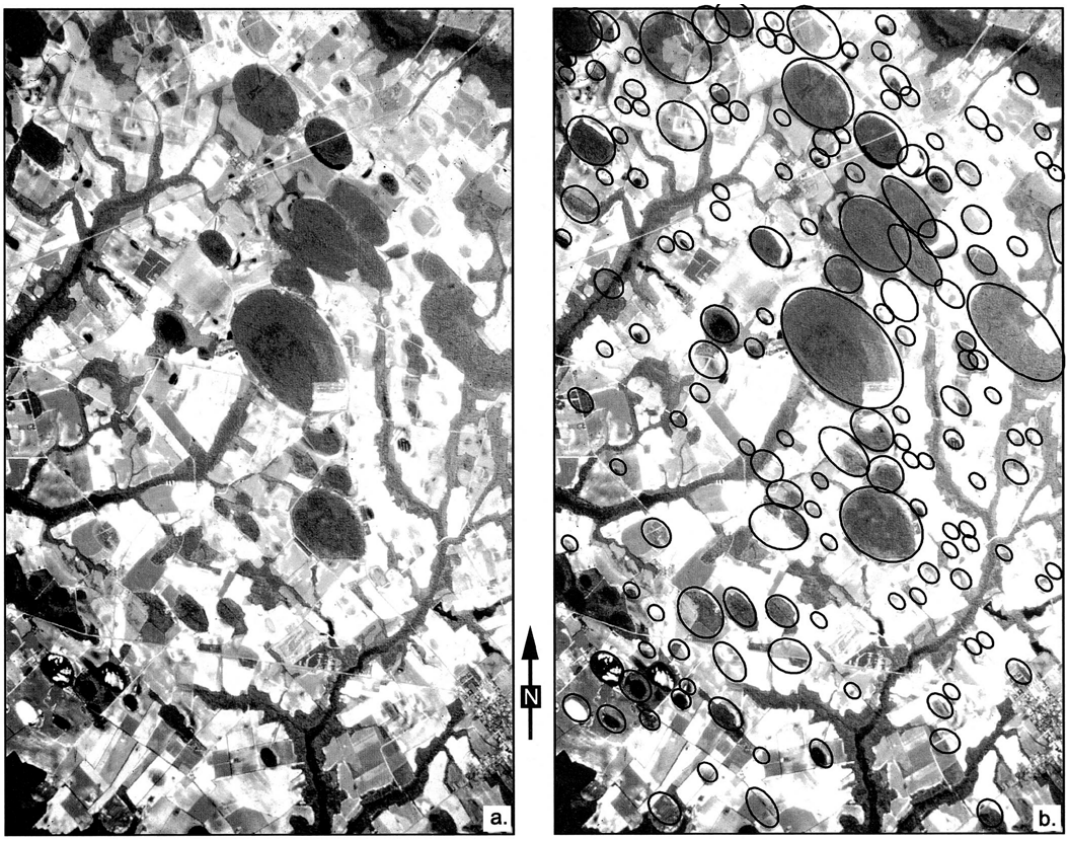
B.1.2 Introduction

B.1.2.1 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, 2003), and range 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 (Figure B-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 number of Carolina and Delmarva bays is likely an underestimation, because many are too small to be readily mapped. The National Wetlands Inventory maps have mapping units of 0.4–1.2 ha, but the Department of Energy's

Figure B-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).



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).

B.1.2.2 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 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).

B.1.2.3 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 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 to bays include artesian wells (Wells and Boyce, 1953), shallow ground water (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 ground water 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).

B.1.2.4 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 ground water 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 ground water (Newman and Schalles, 1990). Phillips and Shedlock (1993) also associated bay water chemistry with shallow ground water; their study found similarities in water chemistry between upland ground water 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.

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 posed a chronic risk to fish (Snodgrass et al., 2000b) and birds that feed on these fish (Brant et al., 2002).

B.1.2.5 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 enables 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 (*Ambystoma cingulatum*) and the gopher frog (*Rana capito*) (Sharitz, 2003).

Sharitz and Gibbons (1982) reported 6 turtle species, 9 lizard species, 19 snake species, and 13 small mammal species in bays. American alligators (*Alligator mississippiensis*) 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).

B.1.3 Evidence of Connectivity

B.1.3.1 Physical Connections

Research is ongoing on the hydrologic connectivity of Carolina and Delmarva bays to surrounding areas via ground-water flows and intermittent surface flows. A few studies have found ground-water connections or indirect evidence of surface-water connections.

A study by Lide et al. (1995) found a ground-water 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 ground-water recharge was present and shallow ground-water discharge occurred periodically.

Phillips and Shedlock (1993) studied three Delmarva bays and also concluded that the bays were connected to local ground water. They studied water table levels and chemistry in transects that ran from uplands through the Delmarva bays. Local ground water strongly influenced the height of the water table in the Delmarva bays. The ground water 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 ground-water 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-water and ground-water 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 ground-water discharge and recharging ground water 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 ground-water 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. Ground-water inflow was the source of 3–26% of water volume into the perimeter of the bays, and ground-water outflow volume (2–21%) was frequent in the center of the bays (Caldwell et al., 2007b).

In addition to ground water, 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 geographic information system methods to determine the nearest river or tributary to Carolina bays (Sharitz, 2003). A geographic information system 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 can exhibit hydrologic connections via overland flow or shallow ground-water 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).

B.1.3.2 Chemical Connections

Few peer-reviewed papers examine chemical connections between Carolina and Delmarva bays and other waters. One, by Phillips et al. (1993), examined ground water in the Delmarva Peninsula and found that the amount of nitrate in ground water 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 nitrate in both ground water 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, Bennett 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 now could 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.

B.1.3.3 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. Of the 39 genera of the family Chironomidae represented, 16 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 fishes, 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. More 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 (Table 4-2). 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. About 90% of Carolina bays located in the Savannah River Site have a tributary or river within 1,600 m (Sharitz, 2003).

B.1.4 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 ground-water inputs and outputs.
- Some Delmarva bays have surface-water connections to the Chesapeake Bay, and the many bays near each other and near permanent waters can be connected during high-precipitation events.
- Human channeling and ditching of the bays are widespread and create surface connections 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 web 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 evaluate fully the influence of Carolina and Delmarva bays on rivers and estuaries at this time.

B.2 Case Study: Oxbow Lakes

B.2.1 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.

B.2.2 Introduction

B.2.2.1 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 in the character and connectivity of individual oxbow lakes within a floodplain often is large.

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 (Crook and Gillanders, 2006), Europe (Hein et al., 2003), North America (Winemiller et al., 2000; Zeug et al., 2005), and South America (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.

B.2.3 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.

B.2.3.1 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 ground-water flow as the dominant surface connections 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 ground-water 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 (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-water and subsurface-water movement between individual lakes and the active river channel, as a study of oxbow lakes on the Loire and Allier Rivers, France, demonstrates. 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 (Section 2.2.3; Figure 1-2).

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 nearby 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 often are 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).

B.2.3.2 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 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 likely were influenced by a combination of river water from surface connections, ground-water 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 effect 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 depends 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 accretion 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 (Mitsch, 1992). An analysis of sediment, carbon, and nitrogen accretion in oxbow lakes on the River Ebro, Spain showed lower recent accumulation (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 (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 (Mitsch, 1992), sediment (Brix, 1994), or pesticides (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).

B.2.3.3 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 cladocerans 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 might 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 the corresponding export of labile phytoplankton from floodplain water bodies to rivers contribute to the food sources of biological assemblages in nearby 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 among 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 mix (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 the migratory fish species from the Mogi-Guaçu 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 (Junk et al., 1989) and low flow (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.

B.2.4 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. The specific local and regional characteristics of both the oxbow lakes and the river influence these connections.
- 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 sources of food and refuges for riverine organisms.
- 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.

B.3 Case Study: Prairie Potholes

B.3.1 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.

B.3.2 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 prairie pothole region (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 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 (Figure 2-21; Dahl, 1990). 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).

B.3.2.1 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 ground-water 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 ground-water recharge. Potholes with ground-water flow-through or with directional reversal of ground-water flow (discharge under some conditions and recharge under others) also have 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 among prairie potholes in response to precipitation, 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 occurred 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 more than 800 mm of average precipitation to northwestern Iowa each year and less than 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 and the 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 organisms (Euliss and Mushet, 2004).

In addition, topography at multiple scales, soil characteristics, and underlying geology influence 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).

B.3.2.2 Chemical Functions

The chemical composition of prairie potholes is determined largely by the degree of connectivity with ground water and the position of the wetland with respect to local and regional ground-water 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 ground-water 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 likely depends 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 effective nitrogen sinks (van der Valk, 2006).

B.3.2.3 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 most 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).

B.3.3 Evidence

B.3.3.1 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 generalization has proved true but in others, it is 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 water storage capacity of wetlands by connecting formerly isolated potholes through ditching or drainage to the Devils Lake and Red River basins could increase stormflow and contribute to downstream flooding. In many agricultural areas already crisscrossed by extensive surface and subsurface drainage systems (Figure 2-21), total streamflow and baseflow are increased 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 affect 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 influence 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 ground-water flows. A high water table and soil pocketed with root pores or fractures from wet-dry cycles promote water movement between wetlands via shallow ground-water 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

ground-water connections to nearby wetlands (Rosenberry and Winter, 1997). Potholes can connect to the river network via ground water 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 ground-water flow (Swanson et al., 1988). Broader, regional movement of ground water is restricted by very low permeability clay-rich tills that can keep deep ground-water 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 near 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 ground water (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).

B.3.3.2 Chemical Connections

The chemical connectivity of prairie potholes is largely mediated by their hydrologic connectivity. Hydrologically isolated potholes tend also to be isolated chemically. 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 (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 (Gleason et al., 2008). Additionally, potholes within agricultural areas that have not been drained or ditched are hypothesized to be nitrogen sinks, transforming nitrate 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 periodically are connected hydrologically 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 influence 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).

B.3.3.3 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 (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, by either 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 (more than 80 ha; van Digglen, 2006) and have been found to colonize, quickly and passively, 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 (less than 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, provided 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, non-pothole 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. Spatial distance is one important factor to consider. 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.

B.3.4 Prairie Potholes: Synthesis and Implications

The key findings for this case study are as follows:

- The degree to which prairie potholes are connected or could 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., Figures 2-20A and 2-20B).
- 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 or low relief, or both. 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 to have important effects on associated rivers and lakes than others are. 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.

B.4 Case Study: Prairie Streams

B.4.1 Abstract

Prairie streams drain temperate grasslands in the central United States. Periods of flooding and drying characterize their hydrology, 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.

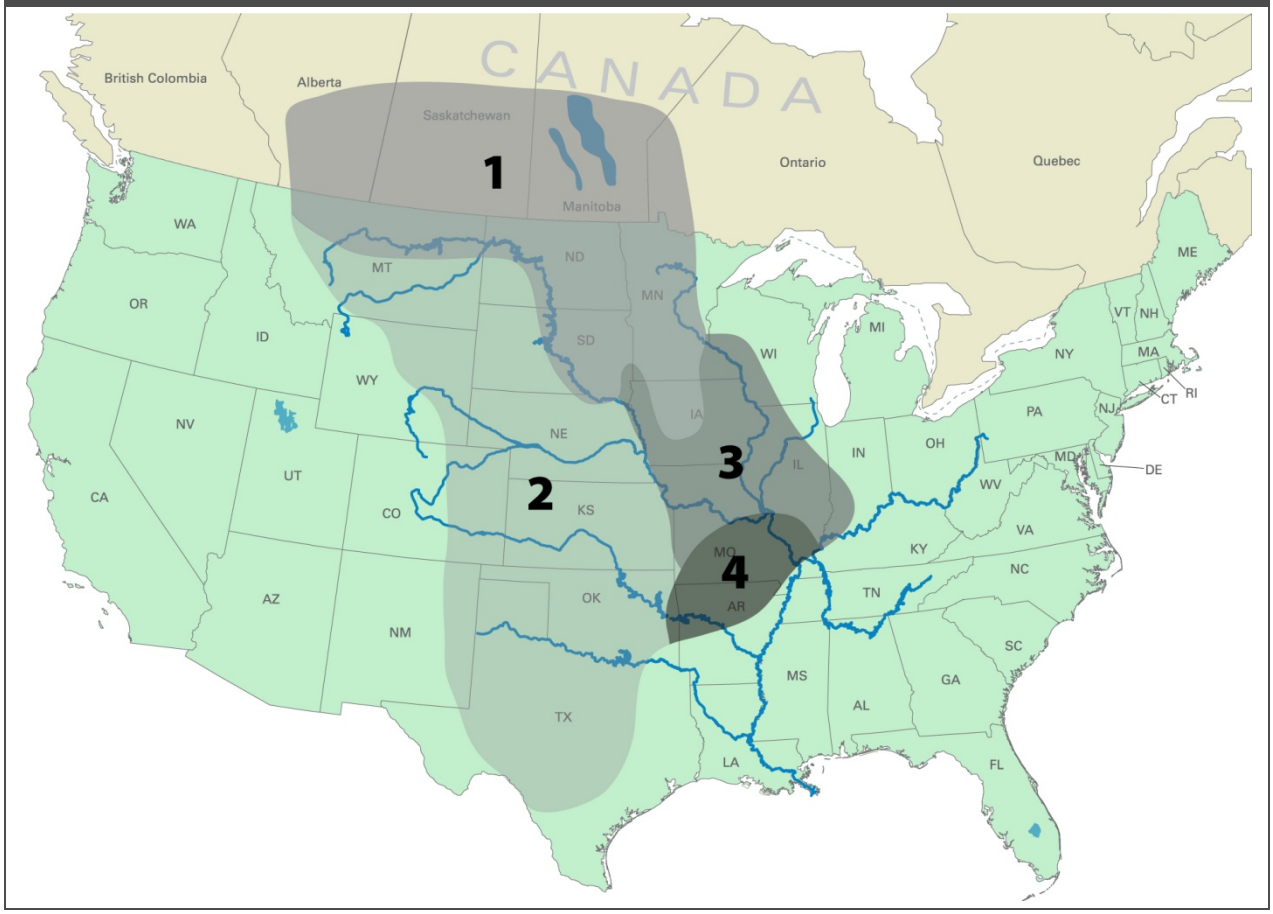
B.4.2 Introduction

B.4.2.1 Geography and Climate

Prairies are temperate grasslands located in the Great Plains physiographic region of the central United States and Canada (Figure B-2). 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 lost almost completely 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, Minnesota), our discussion centers principally on river networks in the high plains subregion of the Great Plains (Subregion 2 in Figure B-2), where drier climate and thin, rocky soil have limited row-crop agriculture.

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 sandstone and shale deposits or unconsolidated sands, silts, and clays characterize other areas (Brown and Matthews, 1995). Soils in the Great Plains are predominantly 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,

Figure B-2. 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).



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 ground water (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).

B.4.2.2 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 (Section 2.4.2), 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 ground-water 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 (Section B.4.2.5). 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 generally receive direct sunlight. 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).

B.4.2.3 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, carbonate, bicarbonate, sodium, 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 (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).

B.4.2.4 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 occasionally can 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 derives mainly from within the channel (autochthonous production), whereas leaf litter and other detritus from nearby 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 be net heterotrophic systems (Mulholland et al., 2001), but those that agricultural activities (e.g., elevated nutrients, channelization) influence can 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 species composition generally highly overlaps, 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 recognized widely in Great Plains river networks (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 have no 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 refuges and providing connectivity between habitats for the dispersal of fish and their eggs in prairie stream networks (Section B.4.3.3; Labbe and Fausch, 2000; Franssen et al., 2006).

B.4.2.5 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; U.S. 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, withdrawn from regional aquifers, and stored in reservoirs. Ground-water withdrawals in the Great Plains are the highest

in the United States (Sophocleous, 2010), causing many once perennial river segments to regularly dry up 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 (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 (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).

B.4.3 Evidence

B.4.3.1 Physical Connections

B.4.3.1.1 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 (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 (Figure B-3). 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 (Figure B-4). 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 (Figure B-4). The subsequent peak at the Wamego gage that occurred 5 days later was associated with a storm mainly affecting 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 (Figure B-4).

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

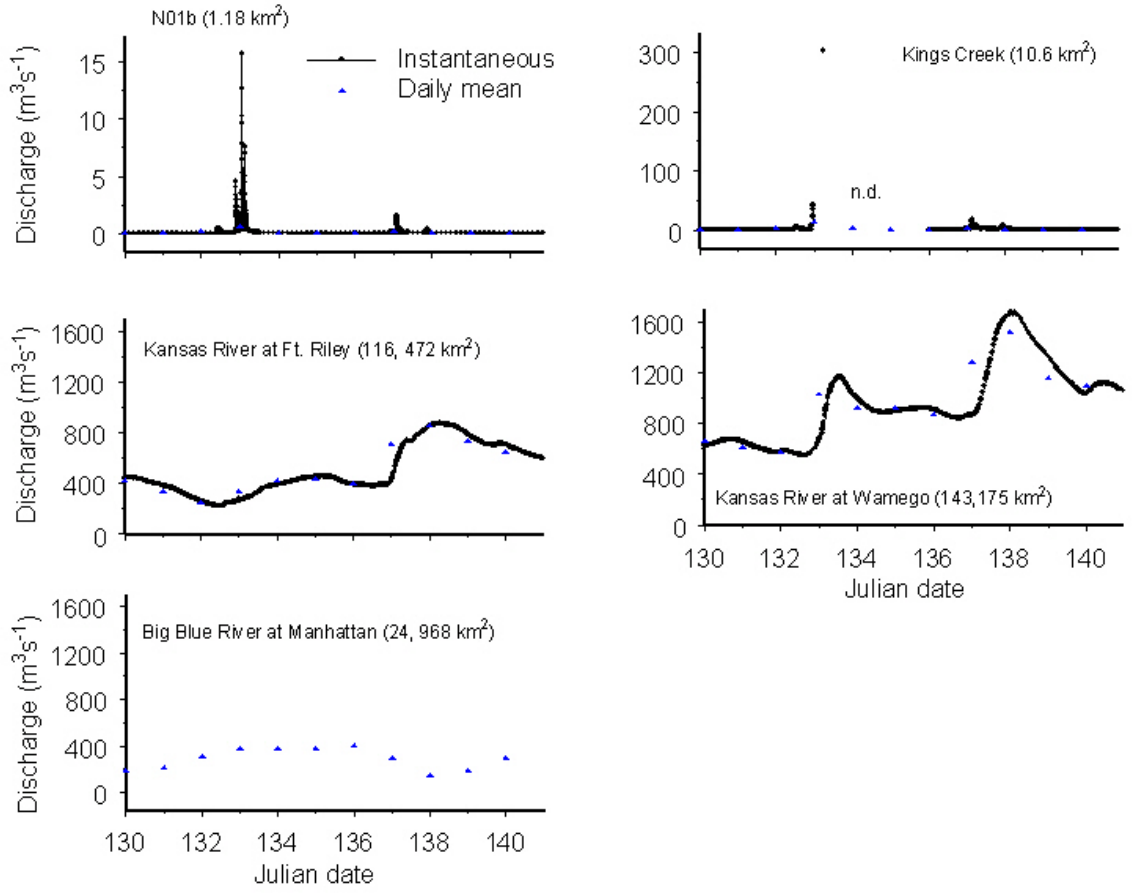
Figure B-3. Map showing the location of Kings Creek and N01B, intermittent tributaries to the Kansas River.



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 of streams offset these reductions by increasing flow from ground water 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, 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).

Figure B-4. Hydrographs (instantaneous and daily mean) showing propagation of the 13 May 1995 (Julian date 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 B-3 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.



B.4.3.1.2 Temperature (heat energy)

Water temperatures represent a substantial stress to biotic communities in Great Plains rivers (Section B.4.3.3). 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 ground water, can provide thermal refuges for avoiding temporary hypothermic and hyperthermic stress (Section B.4.3.3.2). 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 ground water (Wiley et al., 1990).

B.4.3.1.3 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 outlets and nearby 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 near 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 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.

B.4.3.2 Chemical Connections

B.4.3.2.1 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 et al. (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, 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 (Dodds and Oakes, 2006) and across 68 small prairie streams (Dodds and Oakes, 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 ground water. Prairie streams typically are tied closely to ground-water sources (Section B.4.2.2), 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 ground-water influences were minimized.

B.4.3.2.2 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 fine particulate organic matter 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 on suspended POM; Cummins and Klug, 1979) in upstream reaches consumed <1% of suspended POM flux; gatherers that feed on 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., POM and invertebrates) from upstream reaches (in order for downstream predators to consume >100% of locally derived macroinvertebrate production).

As discussed earlier (Section B.4.2.4), 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, 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 also can 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 the rocks 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 POM 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.

B.4.3.3 Biological Connections

B.4.3.3.1 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 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 refuges, 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).

B.4.3.3.2 Fishes

Research on fish assemblages in prairie streams 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 (Perkin 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 (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 ground water fed and maintain permanent pools that can provide habitat during periods of channel drying (Wohl et al., 2009). This ground-water 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 3 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).

B.4.4 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.

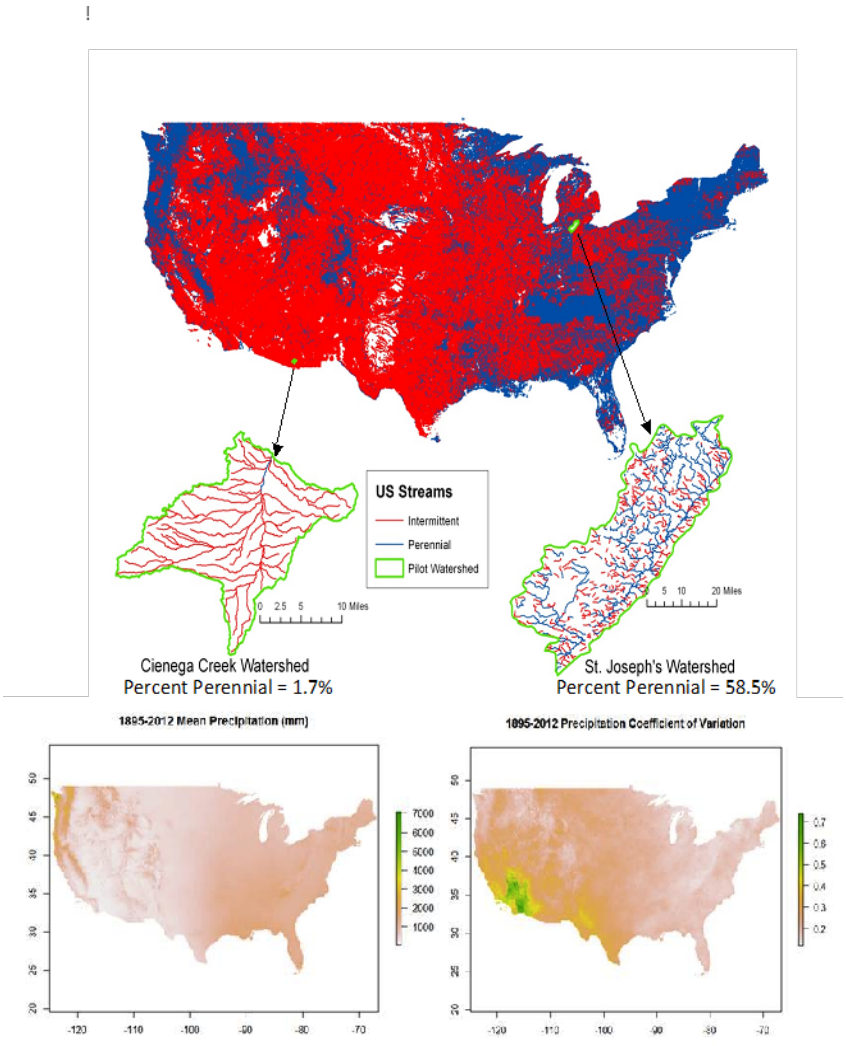
- The most compelling evidence for connectivity along prairie river networks comes from examples of streams as sources of water via flood propagation (Matthai, 1969; Fritz and Dodds, 2004, 2005), sources of contaminated sediment transport (Horowitz et al., 1988; Marron, 1989), sites of nutrient lags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

B.5 Case Study: Southwestern Intermittent and Ephemeral Streams

B.5.1 Abstract

Ephemeral and intermittent streams are abundant in the arid and semiarid landscapes of the West and particularly the Southwest (Figure B-5.). These areas are characterized by low and highly variable precipitation where potential evapotranspiration exceeds precipitation. Based on the National Hydrography Dataset; 94%, 89%, 88%, and 79% of the streams in Arizona, Nevada, New Mexico, and Utah are intermittent or ephemeral (NHD, 2008). The heavily studied Upper San Pedro Basin in southeastern Arizona is discussed in detail because it is 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 streams are also major drivers of the dynamic hydrology of the relatively few perennial reaches in the Southwest. These streams also supply water to mainstem alluvial aquifers and regional ground-water 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 ground water 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), and nutrients, which contribute to river productivity. Several studies found

Figure B-5. Upper: Geographic distribution of intermittent and ephemeral (red) and perennial (blue) streams in the Continental United States and two example watersheds in Arizona and Michigan/Ohio/Indiana from the National Hydrography Dataset (NHD) stream map (http://nhd.usgs.gov/). Lower: maps of mean precipitation and the precipitation coefficient of variation (equal to the standard deviation divided by the mean) of annual precipitation from 1895 to 2012. Note that the NHD might not accurately reflect the total extent of ephemeral or intermittent streams, as it does not include stream segments less than 1.6 km (1 mile) long, combines intermittent and ephemeral streams, and is based on 1:100,000-scale topographic maps.



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).

B.5.2 Introduction

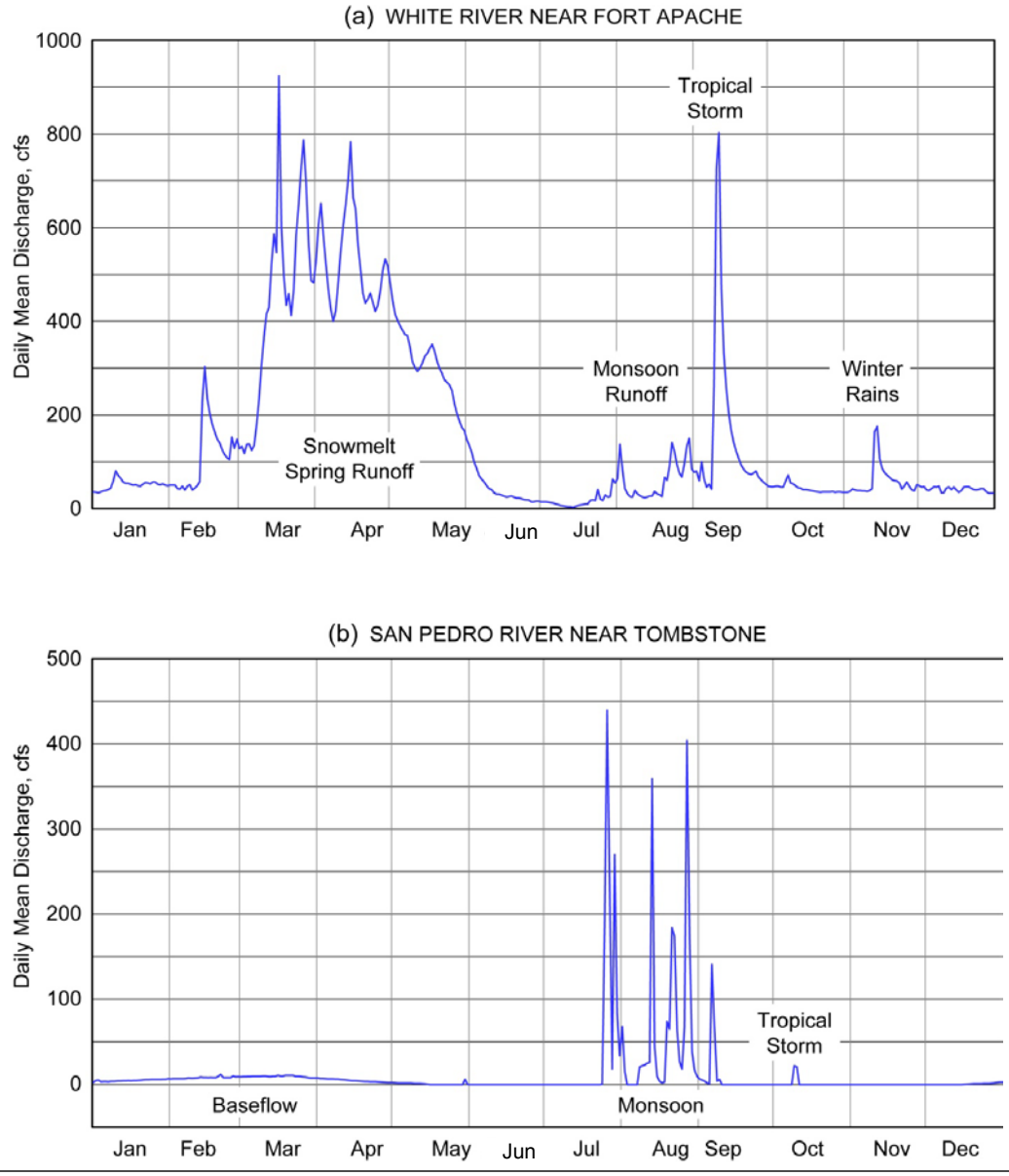
This case study addresses the hydrologic and ecological influence of ephemeral and intermittent streams on perennial or intermittent rivers in the arid and semiarid southwestern United States with

particular emphasis on Arizona and New Mexico. The structure of this case study differs slightly from the other case studies 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.

B.5.3 Southwestern Rivers

Understanding the unique characteristics of southwestern American rivers is necessary to evaluate the connectivity and 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 types, particularly in the Basin and Range geologic province. The first type comprises rivers in the mountainous upper basins that receive more precipitation, often as snow, and the second type comprises those rivers located in the arid or semiarid plateau regions and valley 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. 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 B-6 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 southeastern 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 is 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 ground water dependent, flowing primarily in a baseflow regime and supported by discharge from a connected regional or alluvial aquifer or both. As discussed in more detail below, part of the baseflow is often 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 host a disproportionately greater percentage of the biodiversity than the areas surrounding them (Goodrich et al., 2000; Stromberg et al., 2005). Reservoir construction, irrigation withdrawals, and the cumulative impacts of ground-water pumping have converted many historical, perennially flowing reaches into intermittently flowing reaches (Blinn and Poff, 2005).

Figure B-6. 2003 calendar year hydrographs from (a) the White River near Fort Apache, AZ and (b) the San Pedro River near Tombstone, AZ.



Abrupt changes in streamflow regimes (i.e., a change from perennial to intermittent or ephemeral and back again) can also result from underlying geology. Streams with abrupt changes are often referred to as interrupted streams (Meinzer, 1923; Hall and Steidl, 2007). A constriction and rise in bedrock geology can force regional ground water to the surface resulting in perennial flow while streamflow encountering highly fractured bedrock or a highly porous karst system can virtually disappear over very short distances. Another relatively abrupt transition in arid and semiarid stream hydrology and morphology occurs where steep mountain slopes transition into lower valley slopes. At this transition, watersheds with high sediment transport out of the mountainous portion often form alluvial fans. The stream channel system above the transition is typically dendritic and below the transition, the channel

system often becomes a diffusive set of shallow braided channels. Runoff over alluvial fans typically becomes less concentrated or confined to a single large channel but more diffuse and shallower turning into broad sections of sheet flow (Parker et al., 1998). The diffuse runoff is more likely to infiltrate into the alluvial fan. Very large flows may be required for runoff to cross the alluvial fan and connect to downstream waters.

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 ground water 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 ground-water recharge in the southwestern 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 ground-water recharge at the basin scale" (Phillips et al., 2004).

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 ground water (Wilson and Guan, 2004; Blasch and Bryson, 2007; Wahi et al., 2008). Mountains with shallow soils and more consolidated rock will shed stormflow and shallow ground water off the mountain block onto the valley, which often consists of deep alluvium, particularly in the basin and range geologic province. This area 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 ground-water flow (Blinn and Poff, 2005; Blasch and Bryson, 2007; Yuan and Miyamoto, 2008).

Runoff generation in arid and semiarid valley floors and lowlands where basin alluvium is relatively porous and deep is dominated by the infiltration-excess mechanism in which precipitation rates exceed infiltration rates. In the arid and semiarid Southwest, high-intensity convective thunderstorms typically trigger this situation. 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 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 ground water (Tang et al., 2001; Constantz et al., 2002; Harrington et al., 2002; Goodrich et al., 2004; 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 alluviums under and next to streams begin 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; Baillie et al., 2007; Dickinson et al., 2010).

The magnitude of aquifer recharge is highly temporally variable 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 the El Niño/Southern Oscillation (Woolhiser et al., 1993) at interannual time scales. Over decadal climate cycles, winter precipitation also is 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 and 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).

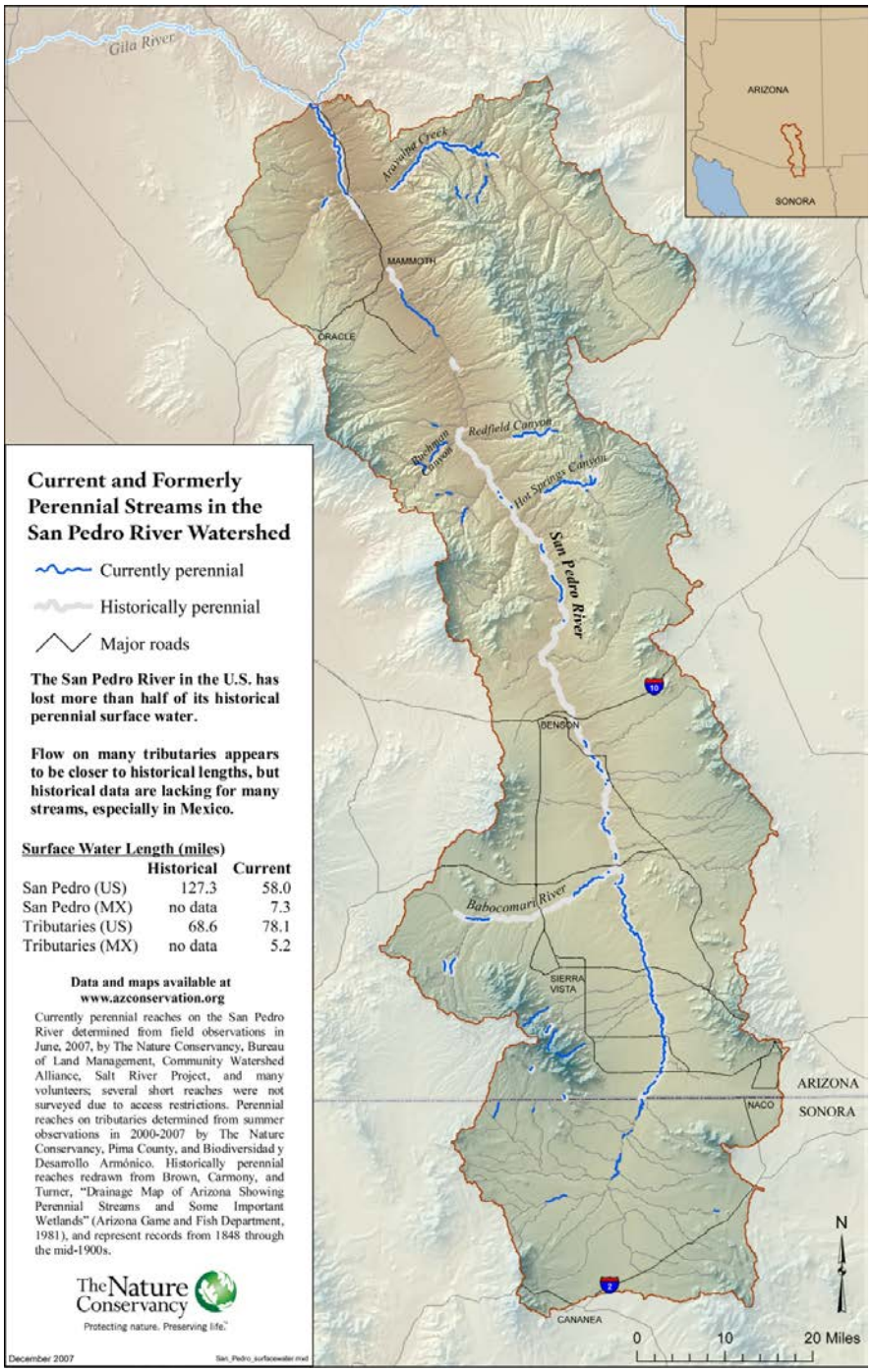
B.5.4 San Pedro River

B.5.4.1 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 is the only significant un-impounded river in Arizona and the last remaining stream in southern Arizona with long perennial reaches (Figure B-7; Kennedy and Gungle, 2010). 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. The San Pedro Basin consists of 93% nonperennial reaches (including ephemeral and intermittent), 6.3% artificial path (canals, diversions, pipeline, connectors), and 0.7% perennial reaches in the U.S. portion of the basin as derived from the USGS NHD[1] (Figure B-8). The percentage of streams types is not static but varies from year-to-year. The Nature Conservancy and its partners annually map the wet and dry reaches along the San Pedro mainstem and several large tributary streams since 2007

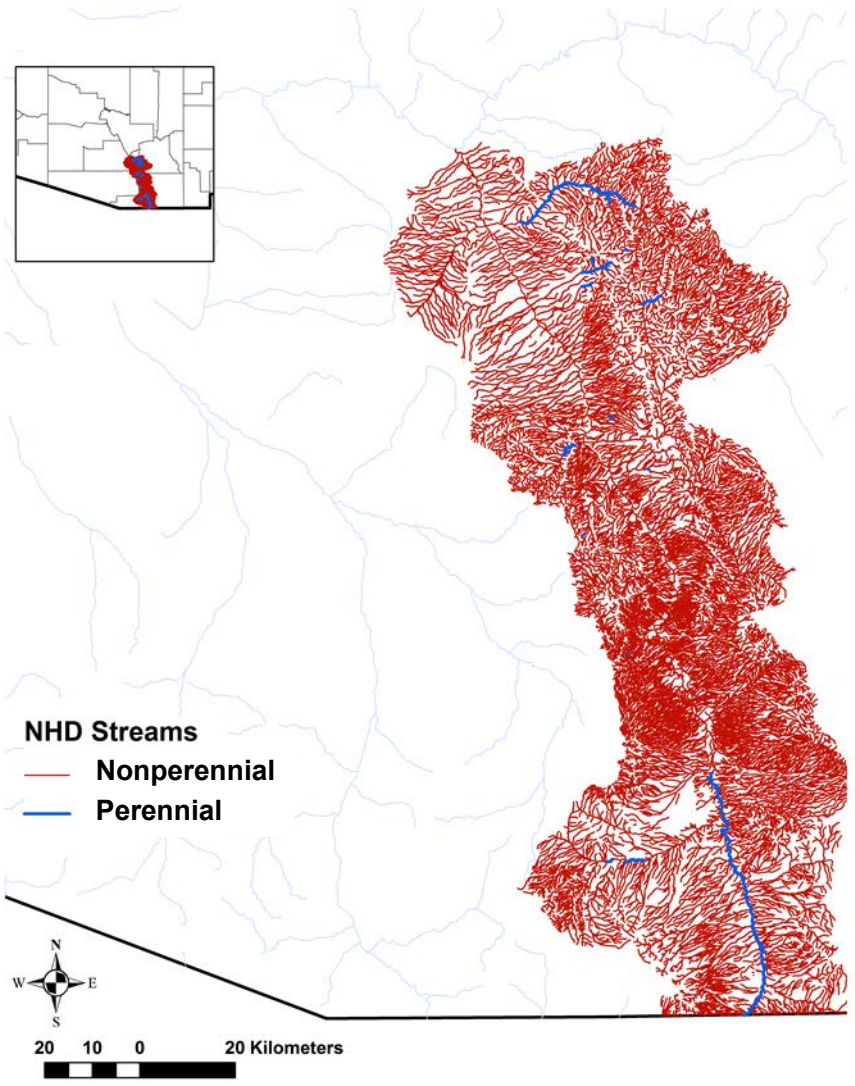
[1]Based on USGS National Hydrography Dataset (NHD) stream map (http://nhd.usgs.gov/). Note that the NHD might not reflect the total extent of ephemeral or intermittent streams accurately, as it does not include stream segments less than 1.6 km (1 mile) long, combines intermittent and ephemeral streams, and is based on 1:100,000-scale topographic maps.

Figure B-7. 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.



(Turner and Richter, 2011). The wet-dry mapping is conducted roughly in the middle June, historically the time of lowest streamflow, prior to the onset of the monsoon. For 2014, about 25% (54.1 km) of the 214 km surveyed were found to be wet (214 km is ~1.1% of the stream length plotted in Figure B-8).

Figure B-8. Perennial (blue) and nonperennial (red) streams in the San Pedro Basin from the U.S.-Mexico border to its confluence with the Gila River based on USGS National Hydrography Dataset (NHD) stream map (http://nhd.usgs.gov/).



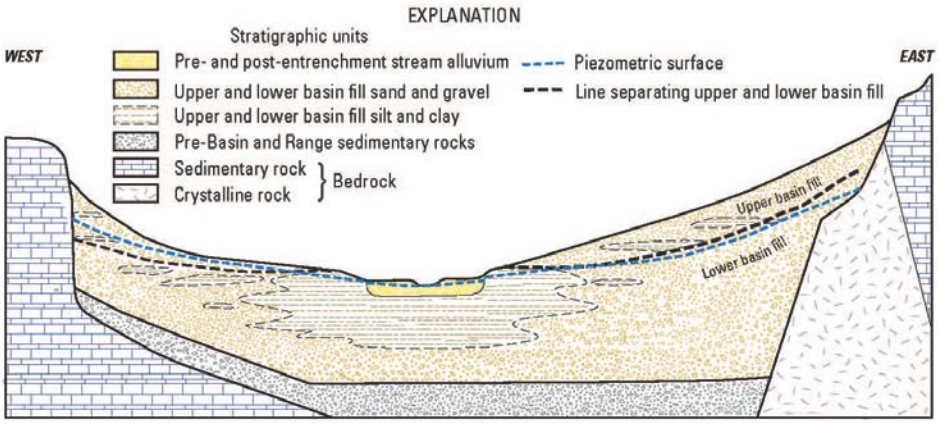
The wet-dry survey data is accessible at:
(http://azconservation.org/downloads/category/san_pedro_river).

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 southwestern semiarid landscapes (Goodrich et al., 1997) dominate the valley floor vegetation.

At the Walnut Gulch Experimental Watershed (WGEW—a subwatershed of the San Pedro watershed near Tombstone, Arizona), operated by U.S. Department of Agriculture, Agricultural Research Service (USDA-ARS), approximately two-thirds of the 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 elevations of the WGEW is generated almost exclusively from convective storms during the 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). Ground water 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 (Figure B-9). 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) supports 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 also are zones of extensive hyporheic exchange (Stanford and Ward, 1988; Fernald et al., 2001).

Figure B-9. Generalized east-west section and stratigraphic units in the middle San Pedro watershed. From Dickinson et al. (2010).



B.5.4.2 Ephemeral Stream Connections and Their Influence on the San Pedro River

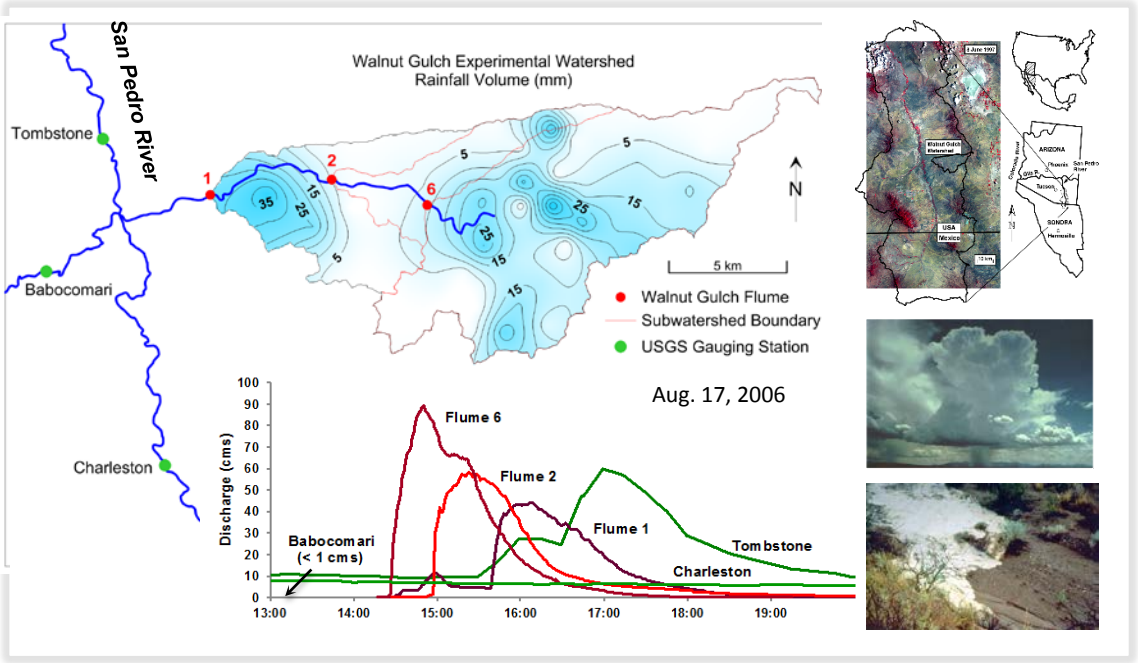
Overland runoff generation and associated ephemeral streamflow is common in San Pedro tributary streams. Goodrich et al. (1997) examined hundreds of hydrologic events in different-sized catchments at the USDA-ARS WGEW and found that the relationship between watershed area and runoff volume was

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 generally is proportional to watershed area (Section 3.3.1). Two reasons for this variability in runoff produced per unit watershed area are: (1) the spatial variability and limited spatial extent of runoff producing precipitation, and (2) the loss of runoff by infiltration into the bed of ephemeral channels (transmission losses). Figure B-10 illustrates this process. During a major rainstorm on 17 August 2006, most of the precipitation from multiple air-mass thunderstorm cells occurred over relatively localized areas in the upper and lower portions of the USDA WGEW. 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. However, a substantial amount of runoff from this storm traversed the ephemeral Walnut Gulch tributary and reached the mainstem of the San Pedro River, augmenting the flow as measured at the USGS Tombstone stream gage. Runoff in Walnut Gulch (149 km^2 drainage area) and many arid and semiarid streams is characterized by short duration, highly episodic flows. The longitudinal extent of the effects of these flows on downstream waters is a function of the flow magnitude, its duration, the depth, conductivity and antecedent moisture conditions of the ephemeral channel substrate that the runoff flows across, and the depth to ground water. For example, in 2006 there were 23 runoff flows measured at Walnut Gulch flume 1 (the outlet of the WGEW). The average volume, peak runoff rate, and duration of these runoff events was 31,460 m^3, 7.23 m^3/s, and 239 minutes, respectively. Four (4) of the 23 runoff events recorded at Flume 1 were estimated to have measureable impacts on flows measured at the downstream USGS Tombstone stream gage (4510 km^2) on the San Pedro River (including the event shown in Figure B-10).

Evidence is strong 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 ground-water 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 ground-water recharge from ephemeral streams ranged from approximately 15 to 40% of total average annual recharge as estimated from a calibrated regional ground-water 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 main sources of water in the alluvial aquifer for the upper San Pedro River: (1) regional ground water

Figure B-10. Storm rainfall and downstream hydrographs with decreasing runoff volume and peak rate due to channel transmission losses as measured by in the USDA-ARS Walnut Gulch Experimental Watershed (WGEW) and the impact of this storm runoff on the San Pedro River in SE Arizona. Inset photos show a typical air-mass thunderstorm and the front of surface flow progressing down an ephemeral channel. Photo of ephemeral stream from Levick et al. (2008).



recharged along the Huachuca Mountains (mountain block, mountain front) to the west, and (2) local recharge from monsoon floodwaters. Alluvial ground-water composition varied between gaining and losing reaches. Locally recharged floodwater comprised 60 to 85% of the alluvial ground water 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.

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, a reach-scale study in the WGEW estimated sand transport distances of only 401 and 734 m in nine floods over two consecutive years (Powell et al., 2007). In another study, Lekach et al. (1992) found that more than 90% of the bedload yield originated from the mid-watershed channels during larger runoff events from an arid watershed in Israel. 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).

Ephemeral tributary stormflow inputs heavily influence the nutrient and biogeochemical status of the San Pedro River. 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 values of both chloride and oxygen isotope tracers indicated that stream water and alluvial ground water 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 ground water-soil water end-member and a precipitation end-member (indicative of overland flow) contributed to the floods. The highest percentage of ground water-soil water in the flood flow (46%) occurred during an early 2001 flood and the lowest during large monsoonal floods of 2002. They noted that ground water probably made lower contributions than soil water to streamflow, because high river stage during flood events created hydraulic gradients from the river to alluvial ground water in the riparian area (water moved from the river to alluvial ground water via bank storage, Figure 2-13B). 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.

B.5.5 Other Southwestern Rivers

B.5.5.1 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 ground water: (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 ground-water recharge processes in the Rio Puerco, a tributary river to the Rio Grande, and in the Rio Grande itself. They note that a summer monsoonal 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 (Figure 3-2). 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.

Another important drainage basin type in the western and southwestern United States is endorheic or closed drainage basins draining to lakes and playas having no outlet to the ocean. The largest of these western basins is the Great Basin, which is approximately 490,000 km^2 (~5% of the area of the United States) and covers most of Nevada and parts of Oregon, Utah, and California (Atwood, 1994). Closed basins can contain ephemeral, intermittent, and perennial stream reaches. Although endorheic streams do not drain into oceans, many support downstream waters and habitat and numerous large perennial lakes such as Lake Tahoe in California and Nevada and the Great Salt Lake in Utah.

The Pecos River basin in eastern New Mexico and western Texas comprises part of southern Rocky Mountains in the north and 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 northeastern Arizona. As derived from the USGS National Hydrography Dataset, this basin contains a lower percentage of ephemeral and intermittent stream reaches (70%) as compared to the ~93% 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 and a decrease in the variability of alluvial ground water 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. Having 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 ground-

water 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.

B.5.5.2 Human Alterations

Anthropogenic uses and activities on arid and semiarid landscapes can have significant effects—both good and bad—on downstream waters and overall health of watersheds. Human alteration to arid and semiarid watersheds occurs in many forms and includes livestock grazing, land clearing, mining, timber harvesting, ground-water withdrawal, streamflow diversion for water supply and irrigation, channelization, urbanization, agriculture, roads and road construction, off-road vehicle use, camping, hiking, and vegetation conversion (Levick et al., 2008). Climate change likely will have increasing influence on streams and their connectivity in the Southwest. Most climate models predict important changes for the southwestern United States, including increased warming and drying, intensification of droughts, and increased variability of precipitation (Seager et al., 2007). These changes will result in less runoff, reduced snowpack, and changes in streamflow patterns. Reduced snowpack will result in shorter periods of longitudinal stream connectivity in intermittent streams, as snowmelt will occur more rapidly in a warmer climate.

Streamflow augmentation can occur in human-dominated watersheds in the form of treated municipal and industrial wastewater effluent discharges. Streams that would dry without these discharges are effluent-dependent streams, whereas those that receive most, but not all, of their flow from effluent are effluent-dominated streams (Brooks et al., 2006). Streams draining human-dominated areas also can acquire baseflow from ground water recharged by over-irrigation and leaky infrastructure (Lerner, 1986; Roach et al., 2008; Townsend-Small et al., 2013).

Riparian areas near mainly perennial streams, but also in many cases intermittent streams, historically have been attractive for human development, leading to their alteration on a scale similar to that of wetlands degradation nationally (National Research Council, 2002). This situation is especially true in arid and semiarid regions because riparian areas typically are indicative of water availability either as surface water or as shallow ground water. Riparian areas in arid and semiarid regions are also greener and cooler than most upland areas. Riparian areas are more sensitive to development impacts than wetter areas, however, because of their limited geographical extent, drier hydrologic characteristics, and fragile nature (e.g., erodible soils). Historically, riparian habitats represented about 1% of the landscape in the West, and within the past 100 years, an estimated 95% of this habitat has been lost due to a wide variety of land-use practices such as river channelization, unmanaged livestock grazing, agricultural clearing, water impoundments, and urbanization. The following subsections present some of the types of human-caused impacts on ephemeral and intermittent streams and their associated riparian areas.

B.5.5.2.1 Land development

Land development includes urban, suburban, and exurban development but is referred to here collectively as urban development. Before the 2008 recession, the Southwest was one of the fastest growing regions of the United States, having an increase in population of approximately 1,500% over the previous 90 years. In contrast, the population of the country as a whole grew by just 225% over that time. Arizona and Nevada have grown the most, with population increases of 2,880% and 2,840%, respectively. Typical urban development significantly changes the hydrologic characteristics of a watershed by covering uplands with impervious surfaces, and removal, channelization, or armoring of headwater streams (Box 3-1; Kennedy et al., 2013). Alteration of the natural stream network disrupts natural flow patterns and sediment transport and storage, resulting in downstream flooding and changes to the clarity and quality of the downstream flows and receiving waters. These effects can damage downstream water supplies and habitat. The aerial photograph presented in Figure B-11 shows a network of ephemeral streams that flows through a small community southeast of Tucson, AZ, to Cienega Creek, a protected perennial stream.

Figure B-11. Aerial photograph showing ephemeral tributaries to Cienega Creek, a perennial stream, flowing through the small community of Vail, southeast of Tucson, AZ. Photograph: Lainie Levick/Aerial flight courtesy of Lighthawk, www.lighthawk.org.



The impact of urbanization increases as the percentage of impermeable surface increases. Various studies have shown that semiarid stream systems become irreparably impaired once the impervious surfaces within the watershed exceed about 10% and experience dramatic morphological changes once those surfaces exceed about 20% (Schueler, 1994; Miltner et al., 2004).

As the amount of impervious surface increases, runoff increases and infiltration decreases (Kennedy et al., 2013), starting a chain of events that includes flooding, erosion, stream-channel alteration, increases in human-caused pollutants, and ecological damage. Floods become more severe and more frequent, and

peak flows and runoff volumes will be many times greater than in natural basins. The greater volume and intensity of flooding causes increased erosion and sediment transport downstream. To accommodate the increased flow and sediment load, streams in urbanized areas tend to become deeper and straighter over time. The resulting bank erosion can destroy established streamside habitat and tree cover, leading to higher temperatures, sedimentation, and disruption of wildlife corridors.

Storm sewers and lined drainages increase the rate of water delivery to the downstream channel network. Erosion and sedimentation increases during construction and road building for new urban areas. Improperly constructed and maintained roads, especially unpaved roads, can alter hillslope drainage, and change baseflow and precipitation-runoff relationships, causing erosion and sedimentation in streams (USDA, 2002). The primary geomorphic consequence of these hydrologic changes is the erosional entrenchment of nearby channels and associated transportation of the excavated sediment downstream, causing a significant increase in sediment load. Sediment is of particular concern in arid and semiarid regions because many other pollutants tend to adhere to eroded soil particles. Additional pollutants from urban runoff can include pathogens, nutrients, toxic contaminants, sediment, and debris. Consequently, urban areas require stormwater management plans both during and after construction to control runoff and offsite pollution.

Streams are channelized in urbanizing areas to protect private property and control streambank erosion. Channelization typically straightens and steepens the stream, however, resulting in increased flow velocity and sediment movement. These changes transfer flooding and bank erosion downstream of the protected area. In the channelized reaches, the greatly reduced out-of-bank flow disrupts water, sediment, organic matter, and nutrient enrichment of the flood plain (National Research Council, 2002). In addition, removal of vegetation as part of the channelization process degrades wildlife habitat.

Habitat fragmentation is a common consequence of urbanization (Hilty et al., 2006). New developments can alter large areas of land, removing natural drainage systems and wildlife habitat, and replacing them with houses and roads. Altering, bisecting, or channelizing streams effectively can eliminate the main biological functions of the stream channel by disrupting vegetation communities and hydrologic function. Habitat fragmentation reduces wildlife diversity and abundance and might cause sensitive species to disappear (England and Laudenslayer, 1995).

B.5.5.2.2 Land use

In addition to urbanization, agriculture (livestock and crops) and mining, including sand and gravel operations, are major land uses in the desert Southwest. Livestock grazing is one of the more common uses of rural land in the Southwest. Late 1800s estimates of cattle numbers in Arizona and New Mexico exceeded 1.5 million and 2 million, respectively. During this period, the region experienced both significant droughts and floods. During drought, the resulting desiccation of the uplands drove cattle to the riparian areas, which were heavily damaged as a result. When the rains returned to the denuded landscape, erosive processes were greatly enhanced. The overgrazing that occurred during this time is one of the factors attributed to a relatively widespread period of channel downcutting, forming deep arroyos and lowering ground-water levels (Schumm and Hadley, 1957; Hastings, 1959; Graf, 1988).

In modern grazing-land management, livestock are provided with watering sources away from streams when possible, but frequently they must depend on the streams for water. Livestock management efforts attempt to avoid overuse of an area, but because water is scarce in arid environments, cattle and wildlife tend to linger near water sources. Where not properly managed, cattle can remain too long in a riparian area and trample streambanks, eat the riparian vegetation to the ground, contaminate the water with wastes, and compact the soil (Levick et al., 2008). Several literature sources have stressed that the cumulative impacts of unmanaged livestock in southwestern riparian ecosystems for the past several hundred years probably have been the single most important factor in riparian ecosystem degradation (Wagner, 1978; Ohmart, 1995).

Mining is another activity that historically has played a large role in the economy and land use in the Southwest. Some of the largest copper and gold mines in the world are found in this region, and some cover many thousands of hectares. Mining can cause major impacts on riparian areas along tributaries and downstream waters by altering the local hydrology. Mining not only dewaters the area, it removes vegetation and soil and changes the topography, severely affecting the watershed. Instream and floodplain gravel mining can alter channel dimensions, increase sediment yield, and increase fine sediment loading and deposition that can reduce infiltration into ephemeral channels (Bull and Scott, 1974).

Cultivated agriculture has had a long history in the southwestern deserts, and areas such as the Central Valley in California provide much of the country's food supply. Most crops, however, must be irrigated due to the low annual rainfall. Impacts to local hydrology from agricultural activities include (Levick et al., 2008):

- Increased salinity caused by clearing of native vegetation that raises the ground-water reservoir;
- Reduced flows from ground-water pumping or stream diversions for irrigation;
- Increased nutrients and turbidity from the use of fertilizers that run off into the streams across the land surface or through the soil, causing excessive algal growth; and
- Fish, aquatic invertebrate, and bird kills from pesticides that run off into the streams or leach into the ground water.

Due to the abundant solar resources in the arid and semiarid Southwest, numerous, large-scale solar energy projects are envisioned or already under development. O'Connor et al. (2014) note that development of solar energy zones will significantly affect ephemeral channel systems; the authors have developed a scoring system to conduct ephemeral stream assessments using publicly available geospatial data and high-resolution aerial imagery.

B.5.5.2.3 Water resources impacts

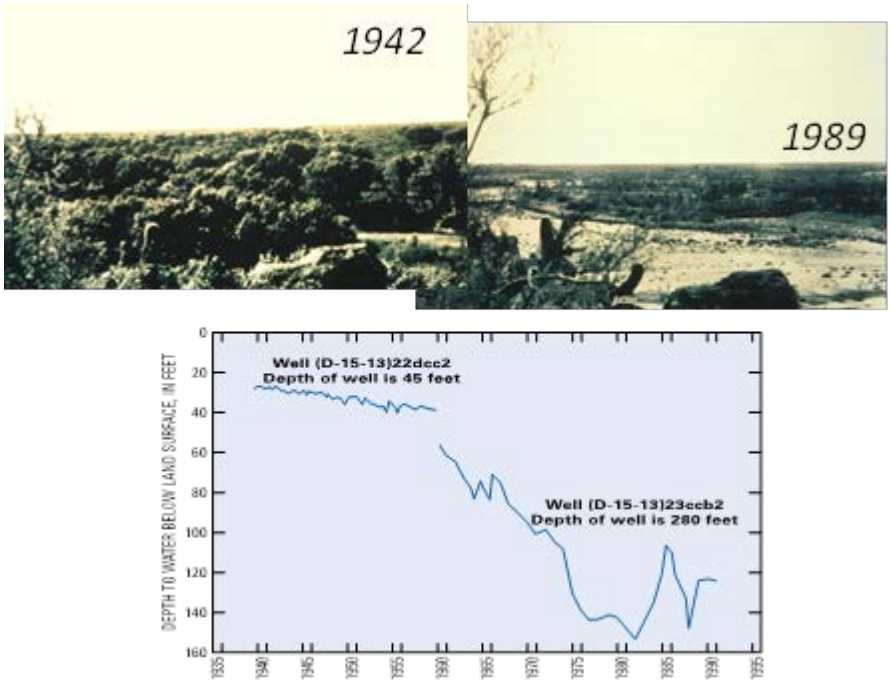
The Southwest has experienced rapid growth over the past several decades. This growth can be sustained only with reliable water supplies. Lack of surface-water flows has placed increased reliance on

ground water for human and agricultural uses. The percentage of population dependent on ground water for domestic water needs in New Mexico, Arizona, and California is 90%, 60%, and 45% respectively (Anderson and Woosley, 2005). When ground-water pumping is sufficiently large or prolonged, it can result in lower water-table levels in regional and alluvial aquifers. If these aquifers are a primary source of water for sustaining surface-water flow in perennial or intermittent streams and if the drop in aquifer water levels is large enough, the pumping can effectively dewater these stream reaches, severing longitudinal and vertical connectivity (Winter et al., 1998; Scanlon et al., 2012). The perennial and intermittent streams effectively become ephemeral streams, and the habitat supported by reliable surface flow or shallow ground water is lost (Stromberg et al., 1996).

The impact of aquifer water-level declines is illustrated in Figure B-12 with repeat photography of the Santa Cruz River south of Tucson from 1942 and 1989 showing changes in riparian vegetation. Tucson's population in 1940 was roughly 36,000 and increased to approximately 405,000 by 1990. Until the Central Arizona Project brought Colorado River water to Tucson in the early 1990s, Tucson's domestic water supply was solely provided by ground water. As ground-water pumping increased to supply the growing population, the aquifer water level dropped by more than 25 meters and the riparian habitat was completely altered, as all phreatophytic vegetation died out. The growing population of Tucson also resulted in proportional increases in discharge of treated effluent. Portions of the Santa Cruz River downstream of the reach photographed in Figure B-12 near treatment plant outfalls are now effluent-dependent perennial stream reaches. Depending on the level of treatment, effluent can have various effects on the stream ecosystem (Brooks et al., 2006). Without careful water management and reuse (Bischel et al., 2013), the benefits of baseflow augmentation can be overshadowed by potential risks, such as increased contaminant and pathogen exposures (Jackson and Pringle, 2010).

Dams and retention or detention basins frequently are used to store water or as flood-control devices in the Southwest. They disrupt natural surface flow and sediment transport, interfere with natural geomorphic processes, alter water temperatures, and fragment the natural stream systems both upstream and downstream of the structure (Williams and Wolman, 1984). Upstream locations can experience flooding, whereas downstream locations can be dewatered and become starved of sediment (Sections 2.4.4 and 3.3.2).

Figure B-12. Change in riparian vegetation along the Santa Cruz River, Tucson, AZ, as the result of water-level declines in the regional aquifer. Photographs of the Santa Cruz River looking south from Tucson, AZ, provided by Robert H. Webb, U.S. Geological Survey Anderson and Woosley (2005).



B.5.5.3 Biological Connections

Much of the material in this section, as in Section B.5.5.2, is derived from the material presented in Levick et al. (2008). As noted in Chapter 3, ephemeral and intermittent streams perform many of the same functions in a watershed as perennial streams. In particular, in arid and semiarid regions, riparian areas, including those near ephemeral and intermittent streams, support the vast majority of wildlife species, are the predominant sites of woody vegetation including trees, and surround what are often the only available surface-water sources, even if they are available only for limited periods. Desert washes are easily recognizable by their dense corridors of vegetation that strongly contrast with the more sparsely vegetated uplands (Figure B-13). In contrast to the nearby uplands, these stream corridors and their associated vegetation communities provide structural elements of food, cover, nesting, and breeding habitat, and movement/migration corridors for organisms. These corridor vegetation communities moderate soil and air temperatures, stabilize channel banks, provide seed banking and trap silt and fine sediment that favor the establishment of diverse floral and faunal species, and dissipate stream energy (Levick et al., 2008). The resulting microclimates in and around ephemeral and intermittent stream vegetation corridors are used extensively by fauna. In arid climates, such conditions often benefit less mobile species that cannot avoid the harsh desert environment by moving to microclimates that are more favorable. These stream corridors provide primary habitat, predator protection, breeding and nesting sites, shade, travel corridors, migration stopover sites, and food sources.

Figure B-13. Aerial photograph showing dense corridor of vegetation lining ephemeral washes in southeastern Arizona. Image accessed from Google Earth from May 2005 imagery date.



Both passive and active biological connections exist in the intermittent and ephemeral streams network. Passive connections involve the transport of organisms and organic matter driven by water flow; these connections thus depend on hydrologic connectivity. Active connections do not depend on flowing water; instead, dispersal of organisms and organic matter occurs throughout the stream network through walking, flying, or hitchhiking on mobile organisms. All these organism-mediated connections form the basis of biological connectivity between headwater streams and downstream waters. Movement can be both longitudinal along the stream network and lateral, and can occur over the life cycles of numerous organisms (Schlosser, 1991; Fausch et al., 2002).

Meyer et al. (2007) noted the importance of headwater streams, including ephemeral and intermittent streams, as vital parts of the biological integrity of U.S. waterways. Ephemeral and intermittent stream channels are bordered by a zone of continuous or near-continuous vegetation, and thus they provide important wildlife movement corridors as they afford both cover and food. Summer monsoons in the Southwest coincide with periods when herptofauna such as snakes and amphibians are most active; the episodic flows provide a generally continuous aquatic corridor for their dispersal. The translocation and dispersal of species enables genetic interchange between subpopulations that are often isolated for most of the year. In addition, recolonization of sites can occur when subpopulations are lost due to drought or disturbance. Degradation of these habitats and loss of their connections to larger streams can have negative consequences for the diversity of downstream and riparian ecosystems and for the biological integrity of the entire river network. Nearly 81% of all streams are ephemeral or intermittent in the six Southwestern states (USGS, 2006). From a strictly numerical viewpoint, therefore, degradation of these ephemeral streams diminishes ecosystem functions in most southwestern watersheds.

B.5.5.3.1 Physical features important to biological connectivity and integrity

Ephemeral and intermittent riverbanks in the arid Southwest provide shelter for numerous species of wildlife, including reptiles, amphibians, birds, mammals, and invertebrates. These shelters typically are independent of whether the streams contain water year-round. Shelters are created through the action of water, wind, and gravity. Ephemeral dry-wash embankments notoriously are full of small caves and crevices critical in the life of desert animals such as the desert tortoise (*Gopherus agassizii*) (Van Devender, 2002). The alluvium in ephemeral and intermittent streams is often looser than the soils or colluvium of surrounding uplands. These conditions provide enhanced habitat by specialized sand-burrowing species of wildlife. High-value shelters also are created when woody debris is swept in from the watershed and collects in the floodplain and stream channel. In cases of deep ephemeral stream incision, cooler canyon-type environments might be created in which moisture loss is retarded.

B.5.5.3.2 Vegetation habitat features important to biological connectivity and integrity

Large ephemeral washes with shallow ground-water zones often are colonized with a variety of phreatophytic trees, such as Fremont cottonwood (*Populus fremontii*), Arizona sycamore (*Platanus wrightii*), and Arizona ash (*Fraxinus velutina*). These washes also include distinctive shrubs, such as willow (*Salix* spp.), seepwillow (*Baccharis* spp.), burrobrush (*Ambrosia monogyra*), and saltcedar (*Tamarix ramosissima*), and dense grass stands of sacaton (*Sporobolus* spp.). Those washes that lack a shallow ground-water system or water augmentation by effluent discharge nonetheless give rise to a distinctive vegetative habitat from the surrounding uplands. These environments often are referred to as xeroriparian habitat.

The floral species in these habitats is moderated by the frequency and magnitude of runoff events. Common tree species in xeroriparian habitat include subtropical legumes such as mesquite (*Prosopis* spp.), catclaw acacia (*Acacia greggii*), ironwood (*Olneya tesota*), and blue palo verde (*Cercidium floridum*). Mesquite has been identified as the key provider of food for numerous migrating birds (Van Riper and Cole, 2004). Netleaf hackberry (*Celtis reticulatata*) and Arizona sycamore (*Platanus wrightii*) have been identified as providing exceptional cover for nesting birds on intermittent streams (Powell and Steidl, 2002).

B.5.5.3.3 Hydrologic habitat features important to biological connectivity and integrity

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).

Episodic stream flow might be the most visually prominent hydrologic aspect of a stream but is seldom the only hydrologic habitat feature of biological significance. An arid stream wash with a shallow ground-water system also might have moist banks fed by capillary flow that provide sites for turtle or

insect reproduction. Distinct invertebrate fauna can inhabit the hyporheic (subsurface) zone of flow beneath a dry streambed. Episodic flooding, human excavations, and channel scour can produce in-channel or off-channel pools where amphibians breed. Within-channel or floodplain springs can provide distinct chemical compositions or thermal refuges from the main ephemeral or intermittent stream.

The natural episodic and intermittent flow regime in the arid Southwest is a competitive factor of native species over exotics adapted to lake and pond conditions (Minckley and Meffre, 1987; Poff et al., 1997). Louw and Seely (1982) and Williams (2005) concluded most desert species have developed adaptations to the water-limited conditions of these regions that enable them to survive under harsh environmental conditions. Fauna using ephemeral or intermittent waters include fish, mammals, amphibians, reptiles, birds, and invertebrates. The variability of climate and flow regime, which influences species abundance and diversity, however, makes evaluation difficult unless surveys are conducted over years in different community types (Boulton and Lake, 1992).

B.5.5.3.4 Fish and aquatic insects

As discussed in the previous section, the interplay between stormflow from ephemeral tributary streams, water from alluvial aquifers, and water from regional ground water 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 were observed in the lower reaches of Aravaipa Creek, a tributary of the San Pedro River, which historically was only 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 could 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."

B.5.6 Southwestern Intermittent and Ephemeral Streams: Synthesis and Implications

Rivers of the arid and semiarid Southwest are products of a highly variable and dynamic environment. Ephemeral and intermittent streams and their tributaries in the American Southwest provide a wide range of functions that are critical to the health and stability of arid and semiarid watersheds and ecosystems. Most importantly, they provide hydrologic connectivity within a basin, linking ephemeral, intermittent, and perennial stream segments. This linkage and the corridor of connectivity facilitates the movement of water, sediment, nutrients, debris, fish, wildlife, and plant propagules throughout the watershed. The relatively more vegetated streams corridors connected to downstream perennial reaches provide wildlife habitat and more humid environment than do the surrounding uplands. During ephemeral and intermittent streamflow, energy dissipates as part of natural fluvial adjustment, and sediment, organic matter, and debris are transported. The variability of the hydrologic regime in these streams is the key determinant of spatial and temporal distribution of plant community structure and the types of plants and wildlife present. 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.
- Fishes and invertebrates native to mainstem rivers 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 help sustain 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 mainstream rivers during hydrologic flow events; nutrients occur in many forms and contribute to river productivity.
- Ephemeral and intermittent streams and their associated vegetation communities provide structural elements of food, cover, nesting and breeding habitat, and movement/migration corridors for organisms.
- Water, sediment, and nutrients exported to the river from ephemeral tributaries support riparian communities of mainstem rivers; the riparian communities profoundly influence river attributes through shading and allochthonous inputs of organic matter, detritus, wood, and invertebrates to the river.

- Regional ground-water 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.

B.6 Case Study: Vernal Pools

B.6.1 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.

B.6.2 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).

B.6.2.1 Geography and Geology

B.6.2.1.1 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 be known 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 ground-water 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 geologic 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).

B.6.2.1.2 Northern vernal pools

The geologic 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 ground water.

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.

B.6.2.2 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 varies, 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."

B.6.2.3 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).

B.6.3 Evidence

B.6.3.1 Physical Connections

Vernal pools are primarily precipitation fed and typically lack permanent inflows from or outflows to streams or other water bodies. They can be connected temporarily, however, to permanent waters by surface or shallow subsurface flow (flow through) or ground-water 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; ground-water exchange can occur in vernal pool systems without perching layers (Brooks, 2005).

B.6.3.1.1 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 (Table B-1). 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 (Table B-1; 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 ground water 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 ground-water system connected to the river network when precipitation exceeds storage capacity of the system (Rains et al., 2006; Rains et al., 2008). 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 showed 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 rare phenomena. Filling and spilling also can occur in other vernal pool types because all vernal pools are underlain by aquitards (Rains et al., 2008).

B.6.3.1.2 Northern vernal pools

Northern vernal pools include both perched and ground water-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

Table B-1. 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-elevation pools[b]	Surface flows between lowest elevation pool and stream network[b]
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 ground water	150–154	surface and horizontal subsurface	15 (10%)	90–92 (60%)

[a]October 1 2002–September 30, 2003.

[b] Units = days/water year[a], % of inundation period.

runoff or subsurface flows into shallow, nearby ground water (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 nearby vegetation during the spring growth period, and increase nutrient availability (Hobson and Dahlgren, 1998).

B.6.3.2 Biological Connections

Dispersal of vernal pool organisms can be active or passive and occurs at multiple scales: local scale (among nearby 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 enables plants and low-vagility animals such as microcrustaceans to move long distances. Examples of passive transport to and from unidirectional wetlands and pools include water-mediated dispersal of larvae (Hulsmans et al., 2007); transport of diapausing (dormant) eggs by waterbirds (Figuerola et al., 2005; Frisch et al., 2007) or flying insects (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 geologic 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 have become locally adapted to, different vernal pool landscapes, creating new endemic species from the rootstock 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 (Table 4-2).

B.6.4 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 ground water and thus to nearby streams.
- Many insects and amphibians that can live in streams or pools that are more permanent 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 organisms.

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