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External Review Draft

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

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

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LIST OF ACRONYMS AND ABBREVIATIONS

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

LIST OF UNITS

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

PREFACE

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

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

AUTHORS AND REVIEWERS

AUTHORS

Laurie C. Alexander, PhD
U.S. Environmental Protection Agency
Office of Research and Development, National Center for Environmental Assessment
Washington, DC

Bradley Autrey, MS, JD
U.S. Environmental Protection Agency
Office of Research and Development, National Exposure Research Laboratory
Cincinnati, OH

Julie DeMeester, PhD
AAAS Fellow
U.S. Environmental Protection Agency
Office of Research and Development, National Center for Environmental Assessment
Washington, DC

Ken M. Fritz, PhD
U.S. Environmental Protection Agency
Office of Research and Development, National Exposure Research Laboratory
Cincinnati, OH

David C. Goodrich, PhD
U.S. Department of Agriculture
Agricultural Research Service
Tucson, AZ

William G. Kepner, MS, MPA
U.S. Environmental Protection Agency
Office of Research and Development, National Exposure Research Laboratory,
Environmental Sciences Division
Las Vegas, NV

Charles R. Lane, PhD
U.S. Environmental Protection Agency
Office of Research and Development, National Exposure Research Laboratory
Cincinnati, OH

Stephen D. LeDuc, PhD
U.S. Environmental Protection Agency
Office of Research and Development, National Center for Environmental Assessment
Washington, DC

This document is a draft for review purposes only and does not constitute Agency policy.

AUTHORS AND REVIEWERS (continued)

AUTHORS (continued)

Scott G. Leibowitz, PhD
U.S. Environmental Protection Agency
Office of Research and Development, National Health and Environmental Effects Research
Laboratory, Western Ecology Division
Corvallis, OR

Michael McManus, PhD
U.S. Environmental Protection Agency
Office of Research and Development, National Center for Environmental Assessment
Cincinnati, OH

Amina I. Pollard, PhD
U.S. Environmental Protection Agency
Office of Water, Office of Wetlands, Oceans, and Watersheds
Washington, DC

Hadas Raanan-Kiperwas, PhD
ORISE Fellow, U.S. Environmental Protection Agency
Office of Water, Office of Wetlands, Oceans, and Watersheds
Washington, DC

Caroline E. Ridley, PhD
U.S. Environmental Protection Agency
Office of Research and Development, National Center for Environmental Assessment
Washington, DC

Kate Schofield, PhD
U.S. Environmental Protection Agency
Office of Research and Development, National Center for Environmental Assessment
Washington, DC

Parker J. Wigington, PhD
U.S. Environmental Protection Agency
Office of Research and Development, National Health and Environmental Effects Research
Laboratory, Western Ecology Division,
Corvallis, OR

AUTHORS AND REVIEWERS (continued)

REVIEWERS

Peer consultation reviewers

Robert T. Brooks, PhD
U.S. Department of Agriculture Forest Service, Amherst, MA

William H. Eldridge, PhD
Stroud Water Research Center, Avondale, PA

Keith B. Gido, PhD
Kansas State University, Manhattan, KS

Arthur J. Gold, PhD
University of Rhode Island, Kingston, RI

Tracie-Lynn Nadeau, PhD
U.S. Environmental Protection Agency, Portland, OR

Denis Newbold, PhD
Stroud Water Research Center, Avondale, PA

Michael J. Paul, PhD
TetraTech Inc., Owings Mills, MD

Donald Rosenberry, PhD
U.S. Geological Survey, Lakewood, CO

Doug Samson, PhD
The Nature Conservancy, Bethesda, MD

Rebecca Sharitz, PhD
Savannah River Ecology Laboratory, Aiken, GA

Kirk O. Winemiller, PhD
Texas A&M University, College Station, TX

AUTHORS AND REVIEWERS (continued)

REVIEWERS (continued)

External Peer Review Panel

David J. Cooper, PhD
Colorado State University, Fort Collins, CO

William G. Crumpton, PhD
Iowa State University, Ames, IA

Kenneth W. Cummins, PhD
Humbolt State University, Arcata, CA

Walter K. Dodds, PhD (Chair)
Kansas State University, Manhattan, KS

James W. La Baugh, PhD
U.S. Geological Survey, Reston, VA

Mark C. Rains, PhD
University of South Florida, Tampa, FL

John S. Richardson, PhD
University of British Columbia, Vancouver, BC

Joel W. Snodgrass, PhD
Towson University, Towson, MD

Arnold van der Valk, PhD
Iowa State University, Ames, IA

Mark S. Wipfli, PhD
U.S. Geological Survey, Fairbanks, AK

William R. Wise, PhD
University of Florida, Gainesville, FL

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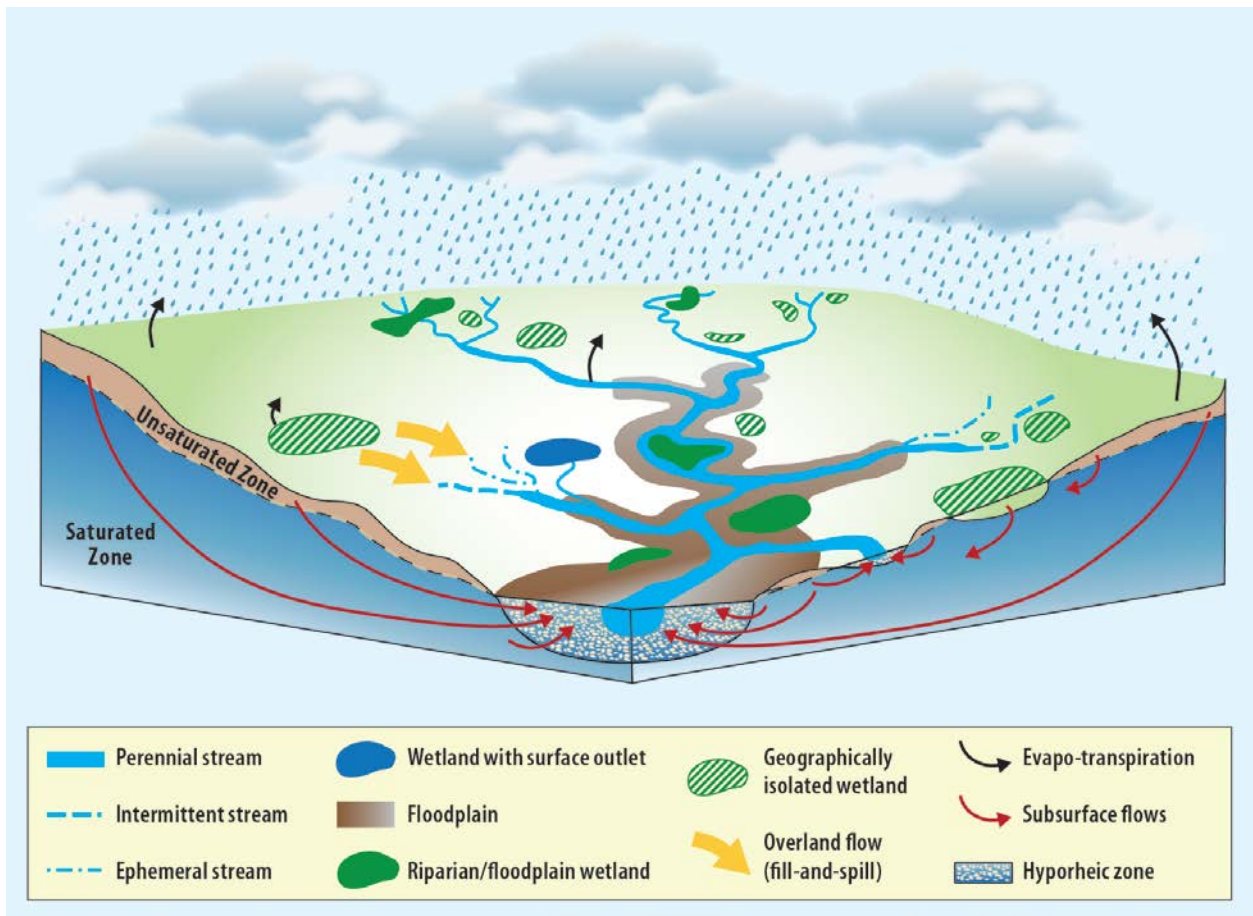
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1 **1. EXECUTIVE SUMMARY**

2 **1.1. BACKGROUND**

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

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



1
2
3 **Figure 1-1. Overview of watershed elements discussed in this review.** This is
4 a simplified overview of the watershed elements and connection pathways
5 discussed in this review. Blue lines represent stream and river channels, which
6 include ephemeral, intermittent, and perennial tributaries to a river mainstem,
7 shown at the center of the diagram. In addition to surface flows through stream
8 channels, water and materials can move into streams and rivers through overland
9 flow, shown here in yellow, and groundwater flows, shown here in red. Flowpath
10 details (e.g., bidirectional exchanges between channels and hyporheic zones,
11 confining layers, etc.) are omitted for clarity.

12
13
14 areas and floodplains; see Section 5.4). Directionality of hydrologic flow was selected as an
15 organizational principle for this section because hydrologic flow direction has a dominant role in
16 determining the types of connectivity and downstream effects (if any) of wetlands. Importantly,
17 our use of these landscape settings based on hydrologic directionality should not be construed as
18 suggesting directionality of geochemical or biological flows. In addition, the terms
19 “unidirectional” and “bidirectional” describe the landscape setting in which wetlands and open-
20 waters occur, and do not refer to wetland type or class. Four case studies from the literature,
21 representing different landscape settings and geographic regions, examine evidence pertaining to

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1 connectivity and downstream effects of oxbow lakes (see Section 5.6), Carolina and Delmarva
2 bays (see Section 5.7), prairie potholes (see Section 5.8), and vernal pools (see Section 5.9) in
3 greater detail. Chapter 6 discusses key findings and major conclusions of the review, which also
4 are included at the end of each review section and in the next section of this executive summary.
5

6 **1.2. SUMMARY OF MAJOR CONCLUSIONS**

7 Based on the review and synthesis of more than 1,000 publications from the
8 peer-reviewed scientific literature, the available evidence supports three major conclusions:
9

- 10
11 1. The scientific literature demonstrates that streams, individually or cumulatively, exert
12 a strong influence on the character and functioning of downstream waters. All
13 tributary streams, including perennial, intermittent, and ephemeral streams, are
14 physically, chemically, and biologically connected to downstream rivers via channels
15 and associated alluvial deposits where water and other materials are concentrated,
16 mixed, transformed, and transported. Headwater streams (headwaters) are the most
17 abundant stream type in most river networks and supply most of the water in rivers.
18 In addition to water, streams transport sediment, wood, organic matter, nutrients,
19 chemical contaminants, and many of the organisms found in rivers. Streams are
20 biologically connected to downstream waters by the dispersal and migration of
21 aquatic and semiaquatic organisms, including fish, amphibians, plants,
22 microorganisms, and invertebrates, that use both up- and downstream habitats during
23 one or more stages of their life cycles, or provide food resources to downstream
24 communities. Physical, chemical, and biological connections between streams and
25 downstream waters interact via processes such as nutrient spiraling, in which stream
26 communities assimilate and chemically transform large quantities of nitrogen (N) and
27 other nutrients that would otherwise increase nutrient loading downstream.
- 28 2. Wetlands and open-waters in landscape settings that have bidirectional hydrologic
29 exchanges with streams or rivers (e.g., wetlands and open-waters in riparian areas and
30 floodplains) are physically, chemically, and biologically connected with rivers via the
31 export of channel-forming sediment and woody debris, temporary storage of local
32 groundwater that supports baseflow in rivers, and transport of stored organic matter.
33 They remove and transform excess nutrients such as nitrogen and phosphorus (P).
34 They provide nursery habitat for breeding fish, colonization opportunities for stream
35 invertebrates, and maturation habitat for stream insects. Moreover, wetlands in this
36 landscape setting serve an important role in the integrity of downstream waters
37 because they also act as sinks by retaining floodwaters, sediment, nutrients, and
38 contaminants that could otherwise negatively impact the condition or function of
39 downstream waters.
- 40 3. Wetlands in landscape settings that lack bidirectional hydrologic exchanges with
41 downstream waters (e.g., many prairie potholes, vernal pools, and playa lakes)
42 provide numerous functions that can benefit downstream water quality and integrity.

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

21
22 We provide below an overview of the conceptual framework we used, with further
23 discussion of the key findings for streams, riparian and floodplain areas, and unidirectional
24 wetlands.

26 **1.3. CONCEPTUAL FRAMEWORK OVERVIEW**

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

39 We define connectivity as the degree to which components of a system are joined, or
40 connected, by various transport mechanisms. Connectivity is determined by the characteristics

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

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

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

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

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

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

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

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

1.4. DISCUSSION OF MAJOR CONCLUSIONS

1.4.1. Conclusion (1): Streams

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

1 provide food resources to downstream communities. Physical, chemical, and biological
2 connections between streams and downstream waters interact via processes such as nutrient
3 spiraling, in which stream communities assimilate and chemically transform large quantities of
4 nitrogen and other nutrients that would otherwise increase nutrient loading downstream.

5 Key findings:

- 6
- 7 a. Streams are hydrologically connected to downstream waters via channels that convey
8 surface and subsurface water year-round (perennial flow), weekly to seasonally
9 (intermittent flow), or only in direct response to precipitation (ephemeral flow).
10 Streams are the dominant source of water in most rivers, and the great majority of
11 tributaries are perennial, intermittent, and ephemeral headwater streams. For
12 example, headwater streams, which are the smallest channels where stream flows
13 begin, are the source of approximately 60% of the total mean annual flow to all
14 northeastern U.S. streams and rivers.
- 15 b. Headwaters convey water into local storage compartments such as ponds, shallow
16 aquifers, or river banks and into regional and alluvial aquifers. These local storage
17 compartments are important sources of water for baseflow in rivers. The ability of
18 streams to keep flowing even during dry periods typically depends on the delayed
19 (lagged) release of local groundwater, also referred to as shallow groundwater,
20 originating from these water sources, especially in areas with shallow groundwater
21 tables and pervious subsurfaces. For example, in the southwestern United States,
22 short-term shallow groundwater storage in alluvial floodplain aquifers, with gradual
23 release into stream channels by intermittent and ephemeral streams, is a major source
24 of annual flow in rivers.
- 25 c. Even infrequent flows through ephemeral or intermittent channels influence
26 fundamental biogeochemical processes by connecting the channel and shallow
27 groundwater with other landscape elements. Infrequent, high-magnitude events are
28 especially important for transmitting materials from headwater streams in most river
29 networks. For example, headwater streams, including ephemeral and intermittent
30 streams, shape river channels by accumulating and gradually or episodically releasing
31 stored materials such as sediment and large woody debris. These materials slow the
32 flow of water through channels and provide substrate and habitat for aquatic
33 organisms.
- 34 d. Connectivity between streams and rivers provides opportunities for materials,
35 including nutrients and chemical contaminants, to be sequentially altered as they are
36 transported downstream. Although highly efficient at transport of water and other
37 physical materials, streams are not pipes: they are dynamic ecosystems with
38 permeable beds and banks that interact with other ecosystems above and below the
39 surface. The connections formed by surface and subsurface streamflows act as a
40 series of complex physical, chemical, and biological alterations that occur as
41 materials move through different parts of the river system. The amount and quality of
42 such materials that eventually reach a river are determined by the aggregate effect of

1 these sequential alterations that begin at the source waters, which can be at some
2 distance from the river. The greater the distance a material travels between a
3 particular stream reach and the river, the greater the opportunity for that material to
4 be altered in intervening stream reaches, which can allow for uptake, assimilation, or
5 beneficial transformation. One example of sequential alteration with significant
6 beneficial effects on downstream waters is the process of nutrient spiraling, in which
7 nutrients entering headwater streams are transformed by various aquatic organisms
8 and chemical reactions as they are transported downstream by streamflow. Nutrients
9 that enter the headwater stream (e.g., via overland flow) are first removed from the
10 water column by streambed algal and microbial populations. Fish or insects feeding
11 on algae and microbes take up some of those nutrients, which are subsequently
12 released back to the stream via excretion and decomposition, and the cycle is
13 repeated. In each phase of the cycling process—from dissolved inorganic nutrients in
14 the water column, through microbial uptake, subsequent transformations through the
15 food web, and back to dissolved nutrients in the water column—nutrients are subject
16 to downstream transport. Stream and wetland capacities for nutrient cycling have
17 important implications for the form and concentration of nutrients exported to
18 downstream waters.

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

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

43

1 **1.4.2. Conclusion (2): Riparian/Floodplain Waters**

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

13 Key Findings:

- 14
- 15 a. Riparian areas act as buffers that are among the most effective tools for mitigating
16 nonpoint source pollution. The wetland literature shows that collectively, riparian
17 wetlands improve water quality through assimilation, transformation, or sequestration
18 of nutrients, sediment, and other pollutants—such as pesticides and metals—that can
19 affect downstream water quality. These pollutants enter wetlands via various
20 pathways that include various sources such as dry and wet atmospheric deposition,
21 some runoff from upland agricultural and urban areas, spray drift, and subsurface
22 water flows, as well as point sources such as outfalls, pipes, and ditches.

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

 - 35 c. Riparian and floodplain areas can reduce flood peaks by storing and desynchronizing
36 floodwaters. They also can contribute to maintenance of flow by recharging alluvial
37 aquifers. Many studies have documented the ability of riparian and floodplain areas
38 to reduce flood pulses by storing excess water from streams and rivers. One review
39 of wetland studies reported that riparian wetlands reduced or delayed floods in 23 of
40 28 studies. For example, peak discharges between upstream and downstream gaging

1 stations on the Cache River in Arkansas were reduced 10–20% primarily due to
2 floodplain water storage.

- 3 d. Riparian and floodplain areas store large amounts of sediment and organic matter
4 from upland areas before those sediments enter the stream. For example, riparian
5 areas have been shown to filter 80–90% of sediments leaving agricultural fields in
6 North Carolina.
- 7 e. Ecosystem function within a river system is driven by interactions between the
8 physical environment and the diverse biological communities living within the river
9 system. Movements of organisms connect aquatic habitats and populations in
10 different locations—even across different watersheds—through several processes
11 important for the survival of individuals, populations, and species, and for the
12 functioning of the river ecosystem. For example, lateral expansion and contraction of
13 the river in its floodplain results in an exchange of matter and organisms, including
14 fish populations that are adapted to use floodplain habitat for feeding and spawning
15 during high water. Refuge populations of aquatic plants in floodplains can become
16 important seed sources for the river network, especially if catastrophic flooding
17 scours vegetation and seed banks in other parts of the channel. Many invertebrates
18 exploit temporary hydrologic connections between rivers and floodplain wetland
19 habitats, moving into these wetlands to feed, reproduce, or avoid harsh environmental
20 conditions and then returning to the river network. Amphibians and aquatic reptiles
21 in many parts of the country commonly use both streams and wetlands, including
22 wetlands in riparian and floodplain areas, to hunt, forage, overwinter, rest, or hide
23 from predators.

24 25 **1.4.3. Conclusion (3): Unidirectional Wetlands**

26 Wetlands in landscape settings that lack bidirectional hydrologic exchanges with
27 downstream waters (e.g., many prairie potholes, vernal pools, and playa lakes) provide numerous
28 functions that can benefit downstream water quality and integrity. These functions include
29 storage of floodwater; retention, and transformation of nutrients, metals, and pesticides; and
30 recharge of groundwater sources of river baseflow. The functions and effects of this diverse
31 group of wetlands, which we refer to as “unidirectional wetlands,” affect the condition of
32 downstream waters if a surface or shallow subsurface water connection to the river network is
33 present. In unidirectional wetlands that are not connected to the river network through surface or
34 shallow subsurface water, the type and degree of connectivity varies geographically within a
35 watershed and over time. Because such wetlands occur on a gradient of connectivity, it is
36 difficult to generalize about their effects on downstream waters from the currently available
37 literature. This evaluation is further complicated by the fact that, for certain functions (e.g.,
38 sediment removal and water storage), downstream effects arise from wetland isolation rather
39 than connectivity. The literature we reviewed does not provide sufficient information to evaluate

1 or generalize about the degree of connectivity (absolute or relative) or the downstream effects of
2 wetlands in unidirectional landscape settings. However, evaluations of individual wetlands or
3 groups of wetlands could be possible through case-by-case analysis. Further, while our review
4 did not specifically address other unidirectional water bodies, our conclusions apply to these
5 water bodies (e.g., ponds and lakes that lack surface water inlets) as well, since the same
6 principles govern hydrologic connectivity between these water bodies and downstream waters.

7 Key Findings:

- 8
- 9 a. Water storage by wetlands well outside of riparian or floodplain areas can affect
10 streamflow. Hydrologic models of prairie potholes in the Starkweather Coulee
11 subbasin (North Dakota) that drains to Devils Lake indicate that increasing the
12 volume of pothole storage across the subbasin by approximately 60% caused
13 simulated total annual streamflow to decrease 50% during a series of dry years and
14 20% during wet years. Similar simulation studies of watersheds that feed the Red
15 River of the North in North Dakota and Minnesota demonstrated qualitatively
16 comparable results, suggesting that the ability of potholes to modulate streamflow
17 may be widespread across portions of the prairie pothole region (PPR). This work
18 also indicates that reducing wetland water storage capacity by connecting formerly
19 isolated potholes through ditching or drainage to the Devils Lake and Red River
20 basins could enhance stormflow and contribute to downstream flooding. In many
21 agricultural areas already crisscrossed by extensive drainage systems, total
22 streamflow and baseflow are enhanced by directly connecting potholes to stream
23 networks. The impacts of changing streamflow are numerous, including altered flow
24 regime, stream geomorphology, habitat, and ecology. The presence or absence of an
25 effect of prairie pothole water storage on streamflow depends on many factors,
26 including patterns of precipitation, topography, and degree of human alteration. For
27 examples, in parts of the prairie pothole region with low precipitation, low stream
28 density, and little human alteration, hydrologic connectivity between prairie potholes
29 and streams or rivers is likely to be low.
- 30 b. Unidirectional wetlands act as sinks and transformers for various pollutants,
31 especially nutrients, which pose a serious pollution problem in the United States. In
32 one study, sewage wastewaters were applied to forested unidirectional wetlands in
33 Florida for a period of 4.5 years. More than 95% of the phosphorus, nitrate (NO₃),
34 ammonium, and total nitrogen were removed by the wetland during the study period,
35 and 66–86% of the nitrate removed was attributed to the process of denitrification. In
36 another study, sizeable phosphorus retention occurred in unidirectional marshes that
37 comprised only 7% of the lower Lake Okeechobee basin area in Florida. A
38 unidirectional bog in Massachusetts was reported to sequester nearly 80% of nitrogen
39 inputs from various sources, including atmospheric deposition, and prairie pothole
40 wetlands in the upper Midwest were found to remove >80% of the nitrate load via
41 denitrification. A large unidirectional prairie marsh was found to remove 86% of
42 nitrate, 78% of ammonium, and 20% of phosphate through assimilation and
43 sedimentation, sorption, and other mechanisms. Together, these and other studies

1 indicate that on-site removal of nutrients by unidirectional wetlands is significant and
2 geographically widespread. The effects of this removal on rivers are generally not
3 reported in the literature.

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

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

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

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

This document is a draft for review purposes only and does not constitute Agency policy.

1 downstream waters through stream channels even when the individual wetland
2 components are geographically isolated.

3 4 **1.5. CLOSING COMMENTS**

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

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

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

35 Unidirectional wetlands can reduce and attenuate floods through water storage, and can
36 recharge groundwater, thereby contributing to stream and river baseflow. These wetlands also

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

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

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

2. INTRODUCTION

2.1. PURPOSE AND SCOPE

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

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

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

2.2. APPROACH

We used two types of evidence from the peer-reviewed published literature to identify connections and effects of wetlands, streams, and other water bodies on downstream waters: (1) direct evidence demonstrating a connection or effect (e.g., observed transport of materials or movement of organisms from streams or wetlands to rivers) and (2) indirect evidence supporting

1 inference of a connection or effect (e.g., presence of environmental factors known to influence
2 connectivity, a gradient of impairment associated with cumulative loss of streams or wetlands).
3 In some cases, an individual line of evidence demonstrated connections along the entire river
4 network (e.g., from headwaters to large rivers). In most cases, multiple sources of evidence were
5 gathered and conclusions drawn via logical inference—for example, when one body of evidence
6 shows that headwaters are connected to downstream segments, another body of evidence shows
7 those downstream segments are linked to other segments farther downstream, and so on. This
8 approach, which borrows from weight-of-evidence approaches in causal analysis (Suter et al.,
9 2002), is an effective way to synthesize the diversity of evidence needed to address questions at
10 regional and national scales.

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

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

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

3 **3.1. INTRODUCTION**

4 A river is the time-integrated result of all waters contributing to it, and connectivity is the
5 property that spatially integrates individual components. In a discussion of connectivity, the
6 watershed scale is the appropriate context for interpreting technical evidence about individual
7 watershed components (Newbold et al., 1982b; Stanford and Ward, 1993; Bunn and Arthington,
8 2002; Power and Dietrich, 2002; Benda et al., 2004; Naiman et al., 2005; Nadeau and Rains,
9 2007a; Rodriguez-Iturbe et al., 2009). This requires that freshwater resources be viewed within a
10 landscape, or systems context (Baron et al., 2002). Addressing the questions asked in this report
11 (see Section 2.1), therefore, requires an integrated systems perspective that considers both the
12 components contributing to the river and the connections between those components and the
13 river. This chapter provides a conceptual framework that describes this integrated systems
14 perspective. Section 3.2 outlines the basic hydrologic foundation of river systems. Section 3.3
15 provides a general overview of how streams and wetlands affect downstream waters, focusing on
16 functions within streams and wetlands and how they are connected to downstream waters.
17 Finally, Section 3.4 examines key factors that affect connectivity between streams and wetlands
18 and rivers. Although we focus our discussion here on interactions between streams, wetlands,
19 and rivers, it should be noted that similar exchanges of water, influenced by many of the same
20 factors, also occur between rivers, lakes, estuaries, and marine waters.

21
22 **3.2. AN INTRODUCTION TO RIVER SYSTEMS**

23 **3.2.1. River System Components**

24 In this report, the term **river** refers to a relatively large volume of flowing water within a
25 visible channel, including subsurface water moving in the same direction as the surface water,
26 and lateral flows exchanged with associated floodplain and riparian areas (Naiman and Bilby,
27 1998). **Channels** are natural or constructed passageways or depressions of perceptible linear
28 extent that convey water and associated materials downgradient. They are defined by the
29 presence of continuous bed and bank structures, or uninterrupted (though not impermeable)
30 bottom and lateral boundaries. While bed and bank structures may in places be perceived as
31 being disrupted (e.g., bedrock outcrops, braided channels, flow-through wetlands), the
32 continuation of bed and banks down gradient from such disruptions is evidence of the surface
33 connection with the channel that is up gradient of the perceived disruption. Such disruptions are
34 associated with changes in the material and gradient over and through which water flows. If a

1 disruption in the bed and bank structure prevented connection, then the area down gradient
2 would lack a bed and banks, be colonized with terrestrial vegetation, and would not be
3 discernible from the adjacent land. The concentrated longitudinal movement of water and
4 sediment through these channels lowers local elevation, prevents soil development, selectively
5 transports and stores sediment, and hampers the colonization and persistence of terrestrial
6 vegetation. **Streams** are defined in a similar manner as rivers: a relatively small volume of
7 flowing water within a visible channel, including subsurface water moving in the same direction
8 as the surface water, and lateral flows exchanged with associated floodplain and riparian areas
9 (Naiman and Bilby, 1998).

10 A **river network** is a hierarchical, interconnected population of channels that drains
11 surface and subsurface water (see Sections 3.2.2 and 3.2.3) from a drainage basin to a river and
12 includes the river itself. Drainage basin boundaries are traditionally topographically defined,
13 such as by ridges, but groundwater sources and losses may occur outside of topographic
14 boundaries (Winter et al., 2003). These channels can convey water year-round, weekly to
15 seasonally, or only in direct response to rainfall and snowmelt (Frissell et al., 1986; Benda et al.,
16 2004). The smallest of these channels, where stream flows begin, are considered **headwater**
17 **streams**. Headwater streams are first to third-order streams (Vannote et al., 1980; Meyer and
18 Wallace, 2001; Gomi et al., 2002; Fritz et al., 2006; Nadeau and Rains, 2007b), where stream
19 order is a classification system based on the position of the stream in the river network (see
20 Figure 3-1; Strahler, 1957). The point at which stream or river channels intersect within a river
21 network is called a **confluence** (see Figure 3-1). The confluence of two streams with the same
22 order results in an increase of stream order (i.e., two first-order streams join to form a second-
23 order stream, two second-order streams join to form a third-order stream, and so on); when
24 streams of different order join, the order of the larger stream is retained.

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

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

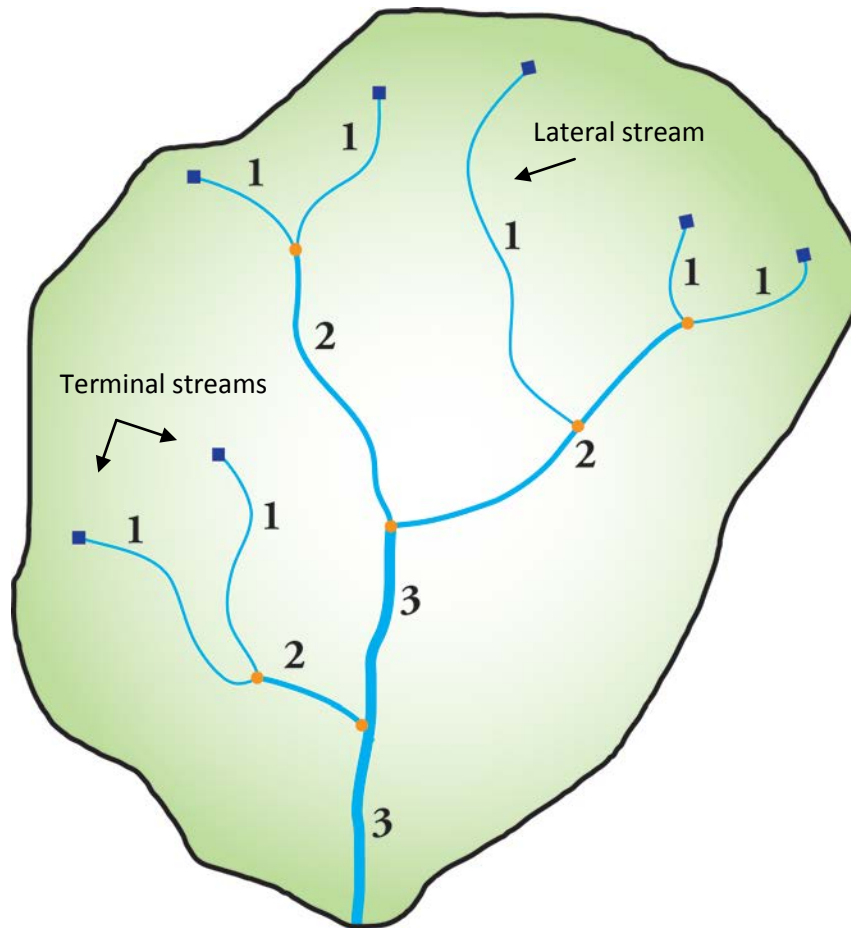


Figure 3-1. A generalized example of a river network within its drainage basin. Blue lines illustrate the river network, within the light green area of its drainage basin. Numbers represent Strahler stream order, with streams increasing in order when two streams of equal order join. Channel heads (blue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

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

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

When two streams join at a confluence, the smaller stream (i.e., that with the smaller drainage area, or lower mean annual discharge) is called a **tributary** of the larger stream, which is referred to as the **mainstem**. A basic way of classifying tributary contributions to a

1 mainstem is the **symmetry ratio**, which describes the size of a tributary relative to the mainstem
2 at their confluence, in terms of their respective discharges, drainage areas, or channel widths
3 (Roy and Woldenberg, 1986; Rhoads, 1987; Benda, 2008).

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

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

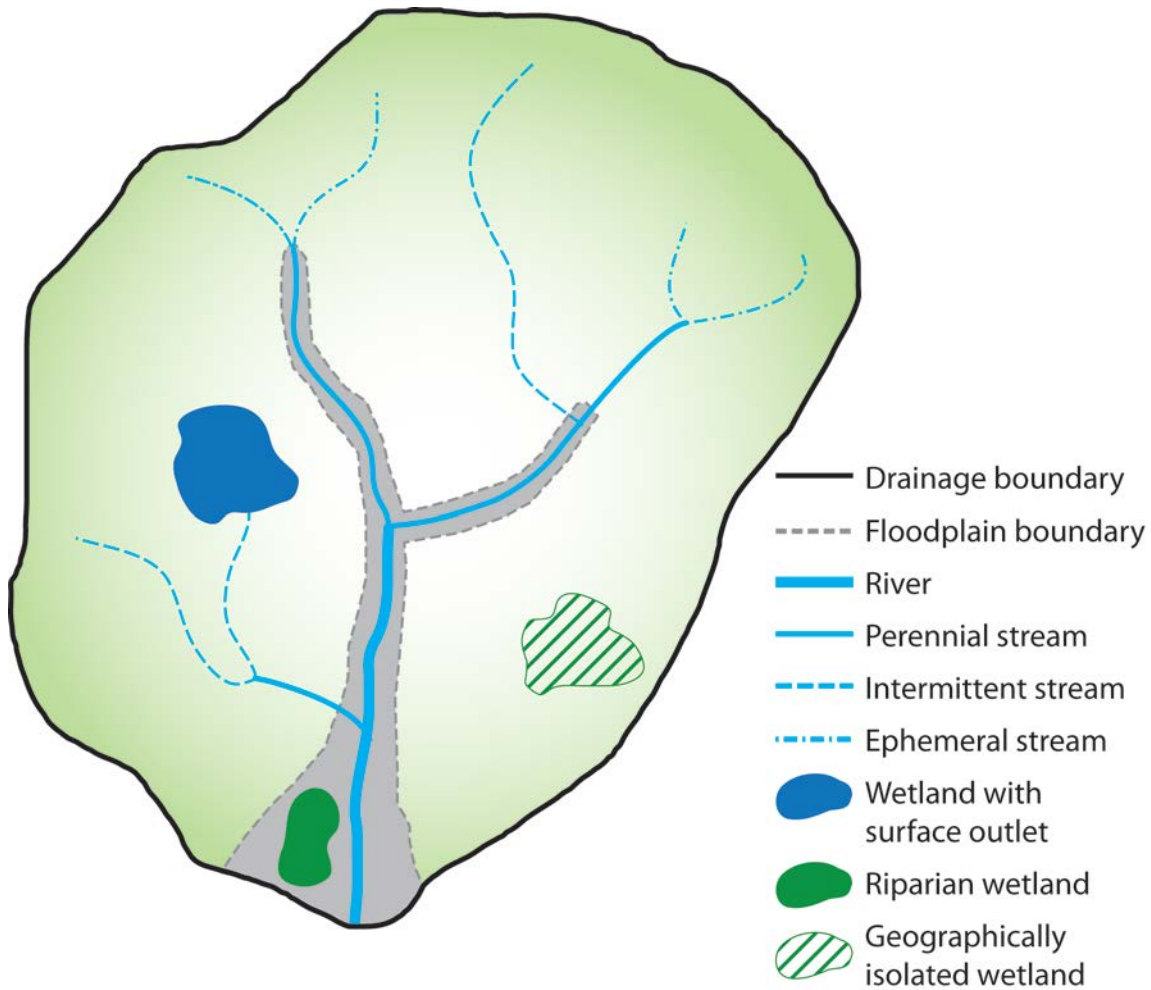
15 Riparian areas and floodplains are important components of river systems (see
16 Figure 3-3). **Riparian areas** are transition zones between terrestrial and aquatic ecosystems that
17 are distinguished by gradients in biophysical conditions, ecological processes, and biota. They
18 are areas through which surface and subsurface hydrology connect water bodies with their
19 adjacent uplands, and they include those portions of terrestrial ecosystems that significantly
20 influence exchanges of energy and matter with aquatic ecosystems (National Research Council,
21 2002). Riparian areas often are locations with high biodiversity (Naiman et al., 2005).

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

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

31 Floodplains are also considered riparian areas, but not all riparian areas have floodplains.
32 All rivers and streams within river networks have riparian areas, but small streams in constrained
33 valleys are less likely to have floodplains than larger streams and rivers in unconstrained valleys
34 (see Figures 3-2 and 3-3). The Federal Emergency Management Agency defines the area that
35 will be inundated by the flood event having a 1% chance of being equaled or exceeded in any

- 1 given year as the “Special Flood Hazard Area,” also referred to as the “100-year floodplain.”
- 2 The 100-year floodplain may or may not coincide with the geomorphic floodplain.



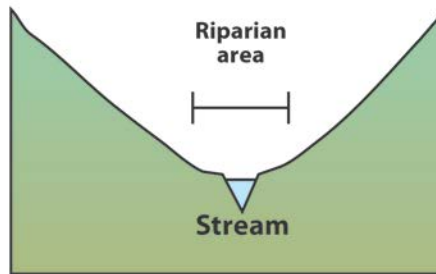
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Figure 3-2. Elements of a river system. These elements include: the drainage basin (light green area), river network (rivers and streams), and other water bodies (riparian and floodplain wetlands, lakes, and unidirectional wetlands). Note that the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

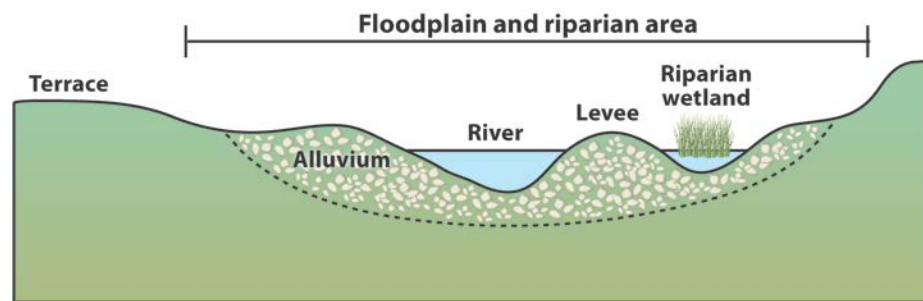
12 Like riparian areas, wetlands are transitional areas between terrestrial and aquatic
13 ecosystems. According to Cowardin et al. (1979), an area is classified as a wetland if it has one
14 or more of the following three attributes: (1) the area supports predominantly hydrophytes (i.e.,
15 water-loving plants) at least periodically; (2) the land has substrate that is predominantly
16 undrained hydric soil; or (3) the land has nonsoil substrate that is saturated with water or covered
17 by shallow water at some time during the growing season of each year. Note that the Cowardin

1 et al. (1979) definition requires only one of these characteristics, in contrast to the Federal
2 regulatory definition, which requires all three (33 CFR 328.3(b); see also USACE, 1987). Thus,
3

A. Headwater Stream with Riparian Area and Minimal or No Floodplain



B. River with Riparian Area and Floodplain



4
5 **Figure 3-3. Hypothetical cross-sections of (A) a headwater stream and (B) a**
6 **large river within a river network.** Each cross-section shows the width of the
7 riparian and floodplain area. The headwater stream (A) is a constrained reach
8 with a narrow riparian area but no floodplain; the river (B) has both a riparian
9 area and a floodplain with the same spatial extent. Examples of other common
10 natural floodplain features are shown in (B). The lateral extent of riparian areas
11 may vary depending on the criteria used for delineation.

12
13
14 as used in this report, a wetland need not meet the Federal regulatory definition. Wetlands
15 include areas such as swamps, bogs, fens, marshes, ponds, and pools (Mitsch et al., 2009).

16 Many different classification systems have been developed for wetlands (Mitsch and
17 Gosselink, 2007). These classifications can focus on vegetation, hydrology, hydrogeomorphic
18 characteristics, or other factors (Cowardin et al., 1979; Brinson, 1993; Tiner, 2003a; Comer et
19 al., 2005). Because the focus of this report is on downstream connectivity, here we consider two
20 landscape settings in which wetlands occur based on directionality of hydrologic flows.
21 Directionality of flow is also included as a component of hydrodynamic setting in the
22 hydrogeomorphic approach (Brinson, 1993; Smith et al., 1995), and as an element of water flow

1 path in an enhancement of National Wetlands Inventory data (Tiner, 2011). This emphasis on
2 directionality of flow is necessary because hydrologic connectivity plays a dominant role in
3 determining the types of effects wetlands have on downstream waters (see Section 3.3.2).

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

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

25 Our usage of landscape setting to define unidirectional and bidirectional wetlands is
26 similar to Tiner's (2011) use of landscape position to supplement the Cowardin et al. (1979)
27 classification. Our bidirectional setting is generally comprised of his estuarine, lotic, and lentic
28 landscape positions, while our unidirectional setting is similar to his terrene category (Tiner,
29 2011). One important difference is that Tiner (2011) would consider a wetland terrene if it were
30 located along a river but not subject to frequent overflow. Given that even infrequent flooding
31 can have profound effects on wetland development and function, we would consider such a
32 wetland bidirectional.

33 The terms unidirectional and bidirectional are meant to describe the landscape setting in
34 which wetlands occur, and do not refer to wetland type or class. Many wetland types occur in
35 both unidirectional and bidirectional settings. For example, a palustrine emergent wetland
36 (Cowardin et al., 1979) could be located outside of a floodplain, in which case it would be

1 considered unidirectional, or it could be located within a floodplain and subject to bidirectional
2 flows. A wetland that is classified as depressional in the hydrogeomorphic approach could have
3 any combination of inlets and outlets or none at all (Smith et al., 1995). The setting for such a
4 wetland would be bidirectional if it had both an input and output channel, since water from the
5 stream flows into and affects the wetland. However, a depressional wetland with a surface outlet
6 and no inlet, or with no outlets and inlets, would be considered unidirectional, since water could
7 only flow downgradient from the wetland to the river network, and not from a stream to the
8 wetland. Similarly, a riverine wetland (Smith et al., 1995) that serves as the origin for a stream
9 would be considered unidirectional if it had no input channel, even though it occurs in a riparian
10 area. In most cases, however, riverine wetlands would be considered bidirectional. Thus,
11 directionality of hydrologic flow is a function of landscape setting and cannot necessarily be
12 determined from wetland class.

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

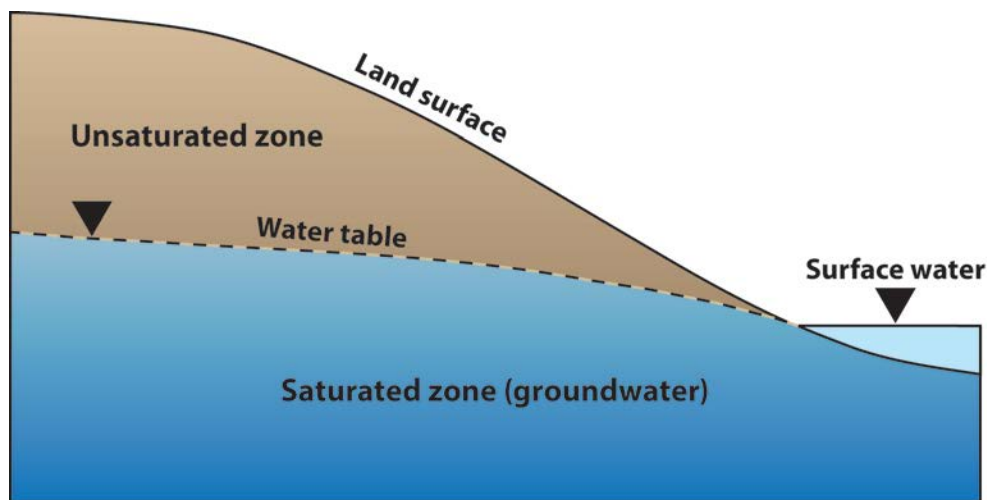
27 Both unidirectional and bidirectional wetlands can include **geographically isolated**
28 **wetlands**, or wetlands completely surrounded by uplands (Tiner, 2003b). Here, we define an
29 **upland** as any area not meeting the Cowardin et al. (1979) three-attribute wetland criteria,
30 meaning that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

1 additional information and analyses would be necessary to determine whether connections
2 through spillage or groundwater occur (see also Section 5.4.5).

3.2.2. River System Hydrology

5 Water moves from drainage basins to river networks, within river networks, and from
6 river networks to drainage basins via numerous hydrologic flowpaths, both above and below
7 ground. Similar flowpaths also occur between riparian/floodplain wetlands, unidirectional
8 wetlands, and other components of river systems. This water movement shapes the development
9 and function of river systems and is critical to maintaining their long-term health (Montgomery,
10 1999; Church, 2002).

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



21
22
23 **Figure 3-4. Water below the land surface occurs in either the unsaturated or**
24 **the saturated zone.** The upper surface of the saturated zone is the water table.
25 Groundwater and groundwater flow occur in the saturated zone. If a surface
26 water body is connected to the groundwater system, the water table intersects the
27 water body at or near the surface of its shoreline.

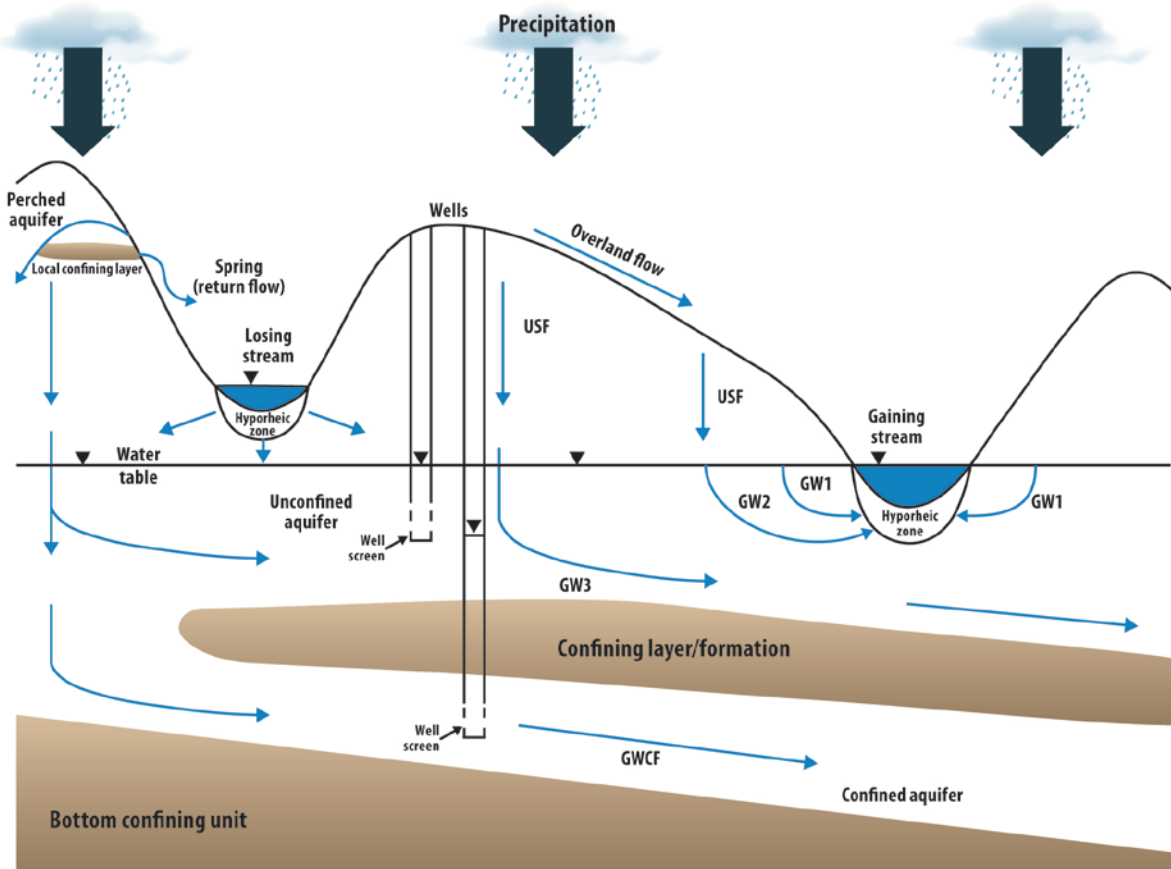
28
29 Modified from Winter et al. (1998).

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

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

28 Traditionally, identification of aquifers was based solely on their ability to support water
29 production wells, but in recent years hydrologists studying groundwater-surface water
30 interactions have recognized the need for a broader definition that recognized the importance of
31 low-flow geologic formations to aquatic ecosystems. Payne and Woessner (2010) recognized
32 the importance of aquifers with varying flow rates on streams and proposed a classification of
33 aquifer flow systems that ranged from high flow to low flow, with low flow aquifers having
34 limited groundwater discharge potential except for small streams and wetlands. Winter et al.
35 (1998) simply defined aquifers as the permeable materials (e.g., soil, rock) through which
36 groundwater flows. In this report, we have adopted the Winter et al. (1998) aquifer definition.

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



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

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13 Groundwater **recharge area** occurs where water from land surfaces or surface water
14 bodies infiltrates and moves into the saturated zone. A **discharge area** occurs where water flows
15 from the saturated zone into a river network or other water body, or onto the land surface. River
16 networks and other surface water bodies can gain water from or lose water to groundwater
17 sources with great spatial and temporal variability (Harrington et al., 2002; Wilson and Guan,
18 2004; Scanlon et al., 2006; Vivoni et al., 2006; Larned et al., 2008).

19 A **gaining stream** within a river network receives inflow of groundwater. In this
20 situation, the elevation of the water table in the vicinity of the stream must be greater than the
21 elevation of the stream water surface. In a **losing stream** water flows from the stream to

1 groundwater. In this situation, the water table elevation in the vicinity of the stream or wetland
2 is lower than the stream or wetland water surface. Conditions conducive to losing or gaining
3 streams and wetlands can change over short distances within river networks and river basins
4 (Winter et al., 1998). Overall, the volume and sustainability of streamflow within river
5 networks, however, typically depend on contributions from groundwater (Winter, 2007),
6 especially in areas with shallow groundwater tables and pervious subsurfaces (de Vries, 1995;
7 Kish et al., 2010).

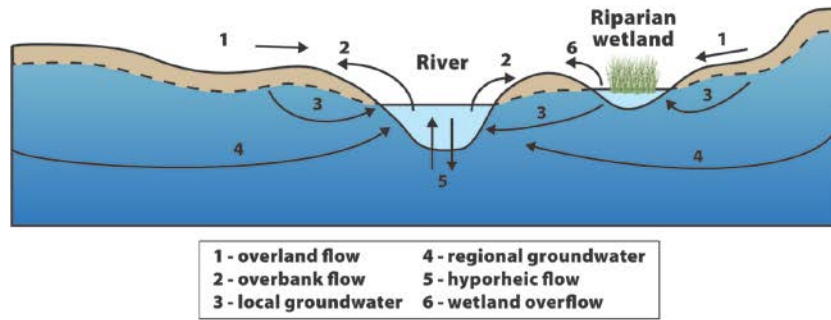
8 Groundwater flow systems within river basins can be complex with varying sizes and
9 depths that overlie one another (Toth, 1963; Winter et al., 1998; Haitjema and Mitchell-Bruker,
10 2005). Although in reality there is a continuum of flowpath lengths that occur within river
11 basins (Bencala et al., 2011), they are commonly grouped into three categories (see Figure 3-5).

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

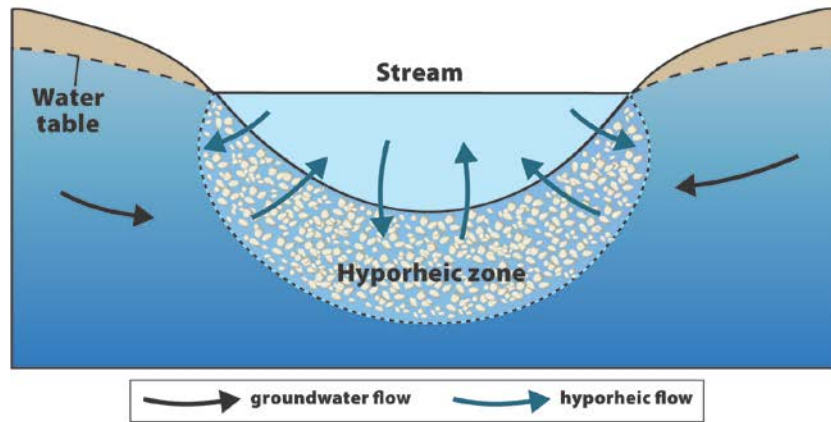
27 Other hydrologic flowpaths are also important to river systems. The most obvious
28 flowpath is the downstream water movement within stream or river channels, or **open channel**
29 **flow**. Water can reach riparian areas and floodplains via **overbank flow** (see Figure 3-6A),
30 which occurs when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

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

A. Common River-Floodplain Hydrologic Flowpaths



B. Hyporheic Zone Cross-Section



C. Hyporheic Zone Longitudinal Profile

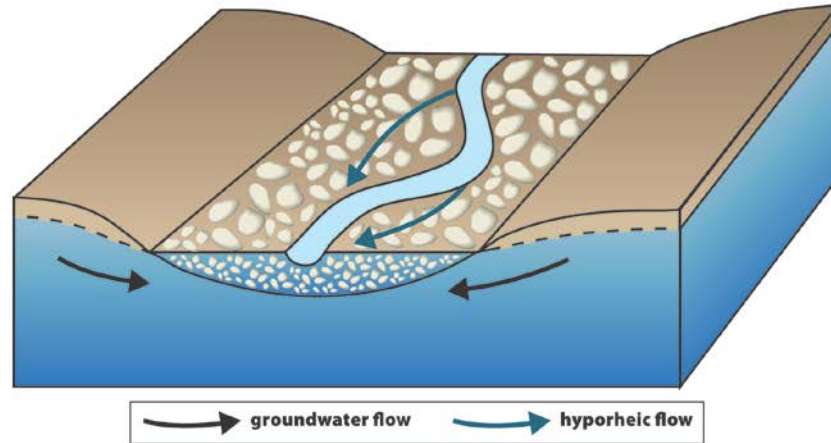


Figure 3-6. Hyporheic zone flows. (A) Common hydrologic flowpaths by which water flows between drainage basins and river networks. (B) and (C) The three-dimensional process of hyporheic flow, or the movement of water from a river or stream to adjacent alluvium and then back to the river or stream.

Modified from Winter et al. (1998).

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

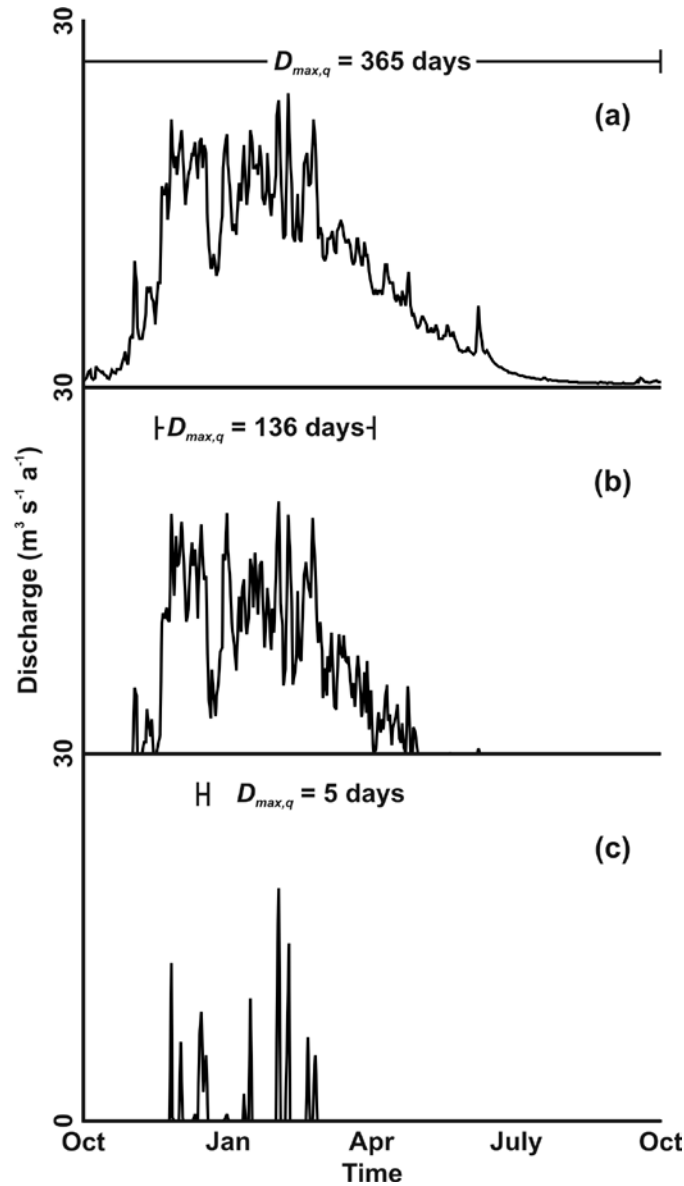
9 Both bidirectional wetlands and unidirectional wetlands can be connected directly to river
10 networks through channelized flow. Geographically isolated wetlands (bidirectional or
11 unidirectional) also can be hydrologically connected to the river network via nonchannelized
12 surface flow (e.g.,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

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

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

31 The relative importance of these different hydrologic flowpaths among river systems
32 varies, creating streams and rivers with different flow duration (or hydrologic permanence)
33 classes (see Figure 3-7). **Perennial streams** or stream reaches (see Figure 3-7a) typically flow
34 year-round, and are maintained by local or regional groundwater discharge or streamflow from
35 higher in the stream or river network. **Intermittent streams** or stream reaches (see Figure 3-7b)
36 flow continuously, but only at certain times of the year (e.g., during certain seasons such as

1 spring snowmelt); drying occurs when the water table drops lower than the channel bed
2 elevation. **Ephemeral streams** or stream reaches (see Figure 3-7c) flow briefly (typically hours
3 to days) during and immediately following precipitation; these channels are above the
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8 **Figure 3-7. Hypothetical hydrographs illustrating maximum duration of**
9 **flow ($D_{max,q}$) for (a) perennial, (b) intermittent, and (c) ephemeral streams.**
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11 From Leibowitz et al. (2008).
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13

1 water table at all times. Streams in these flow duration classes often transition longitudinally,
2 from ephemeral to intermittent to perennial, as drainage area increases and elevation decreases
3 along river networks. Many headwater streams, however, originate from permanent springs and
4 flow into intermittent downstream reaches, and at low flows, intermittent streams can contain dry
5 segments alternating with flowing segments. Transitions between flow duration classes can
6 coincide with confluences or with geomorphic discontinuities within the network (May and Lee,
7 2004; Hunter et al., 2005).

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

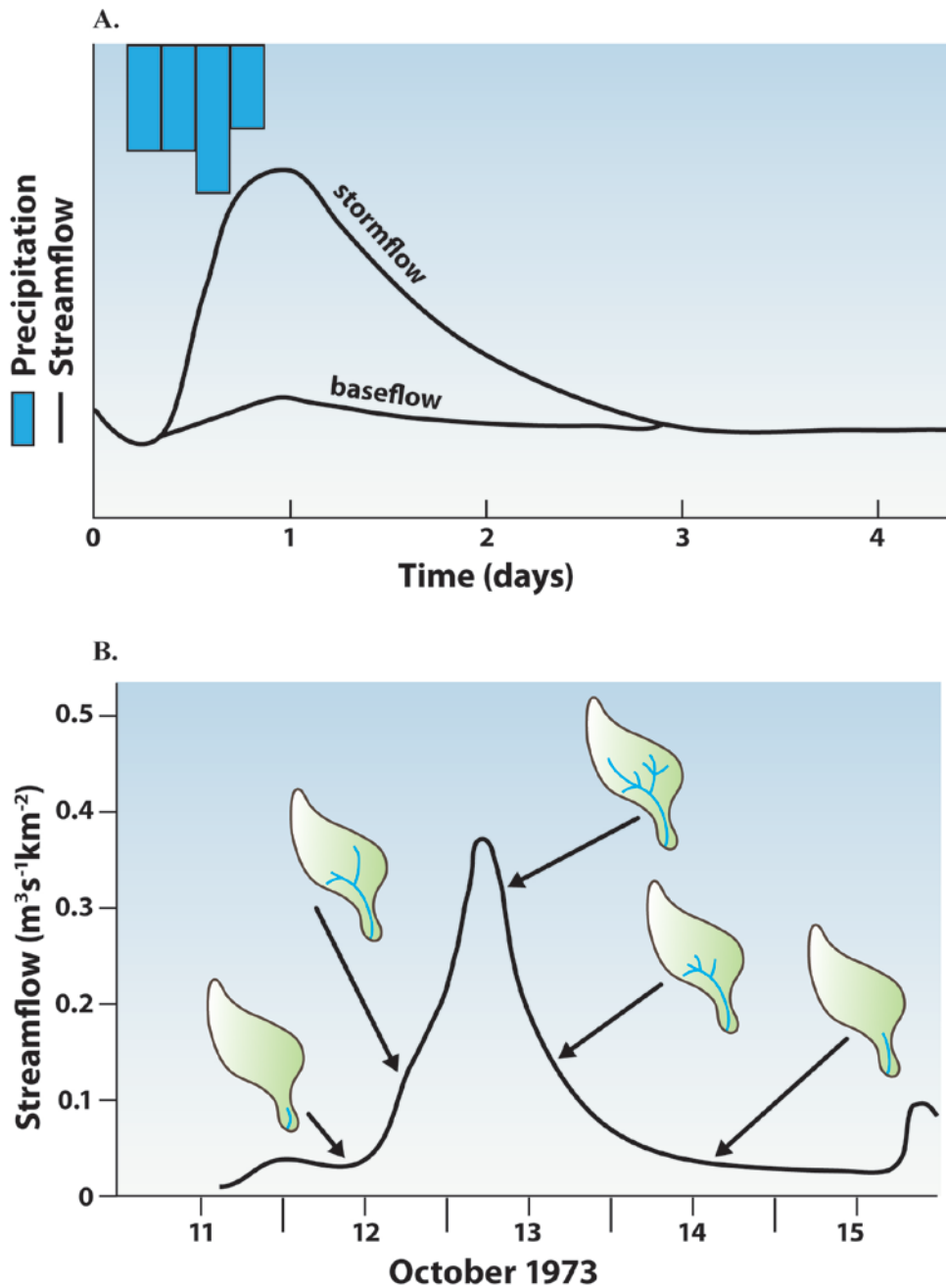
14 Variation of streamflow within river systems occurs in response to **hydrologic events**
15 resulting from rainfall or snowmelt. **Stormflow** is streamflow that occurs in direct response to
16 rainfall or snowmelt (see Figure 3-8A), which might stem from multiple groundwater and
17 surface water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

27 **3.2.3. River Network Expansion and Contraction**

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

1 discontinuous (Stanley et al., 1997; Hunter et al., 2005; Larned et al., 2010) or interspersed with
2 intermittently flowing stream reaches.

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

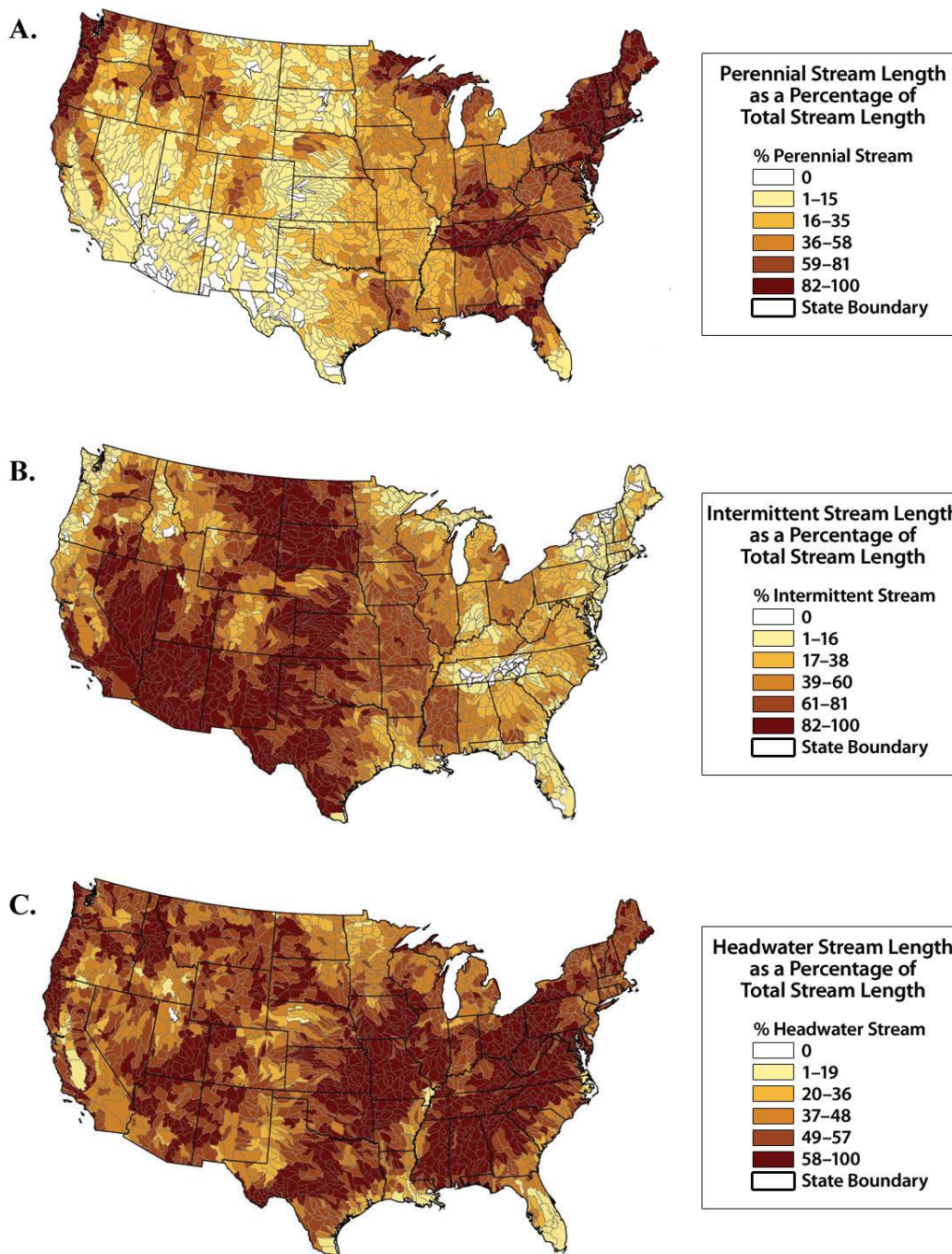
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Modified from NRCS (2007) (A) and Cheng et al. (1988) (B).

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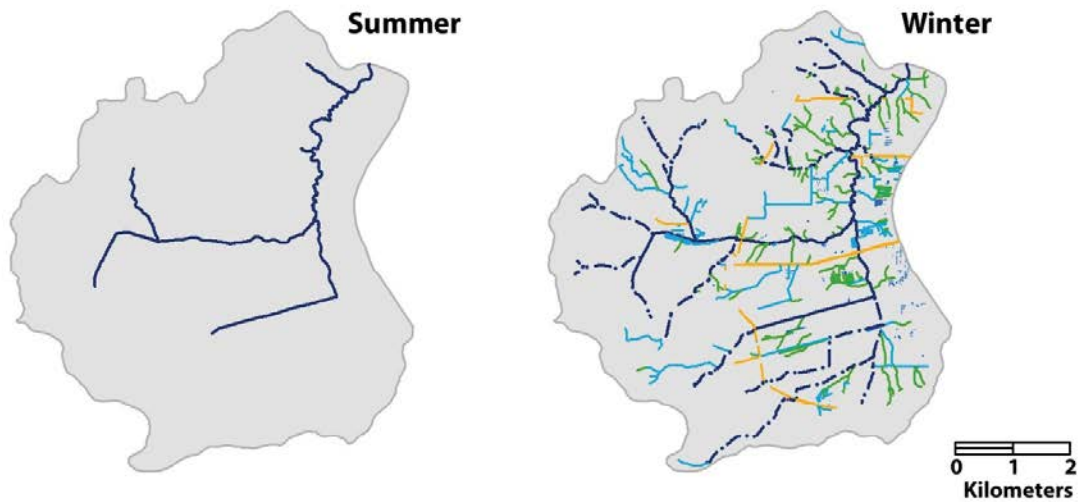
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Figure 3-9. Characteristics of U.S. streams by watershed, in terms of percent of total stream length as (A) perennial, (B) intermittent, and (C) headwater streams. Data from the National Hydrographic Dataset (NHD) Reach Address Database (RAD) v2.0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

A. Spring Valley Creek



B. Spoon Creek

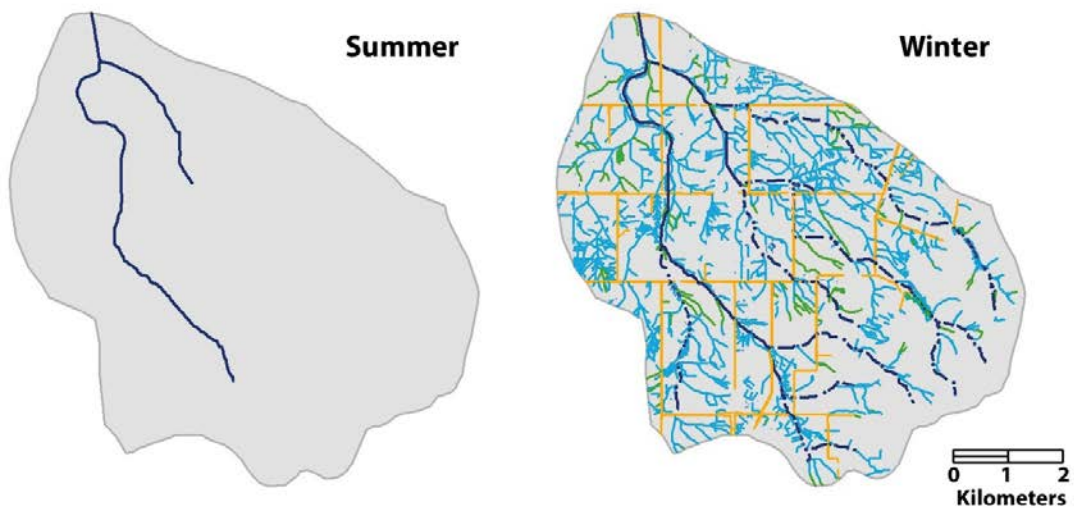


Figure 3-10. Extent and connectivity of streams with flowing water, wetlands, and other water bodies in (A) Spring Valley Creek, OR, and (B) Spoon Creek, OR during dry summer (left) and wet winter (right) conditions.

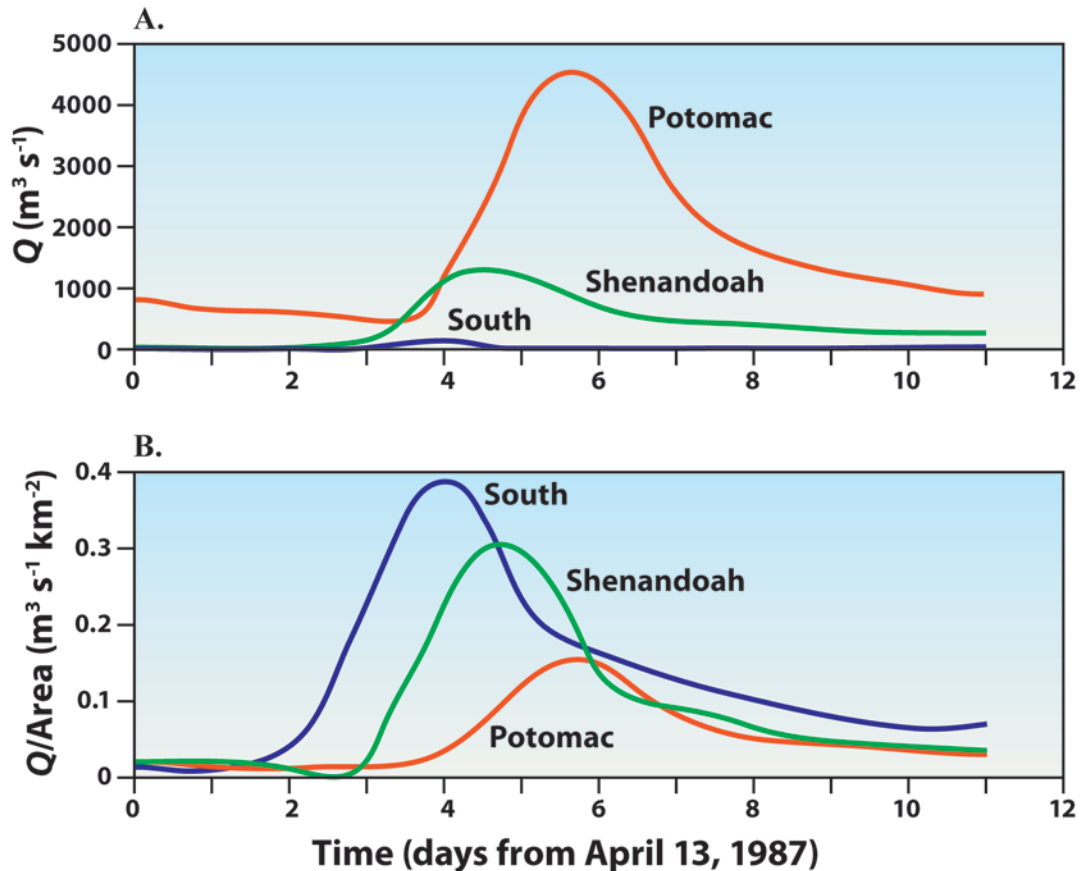
Modified from Wigington et al. (2005).

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

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

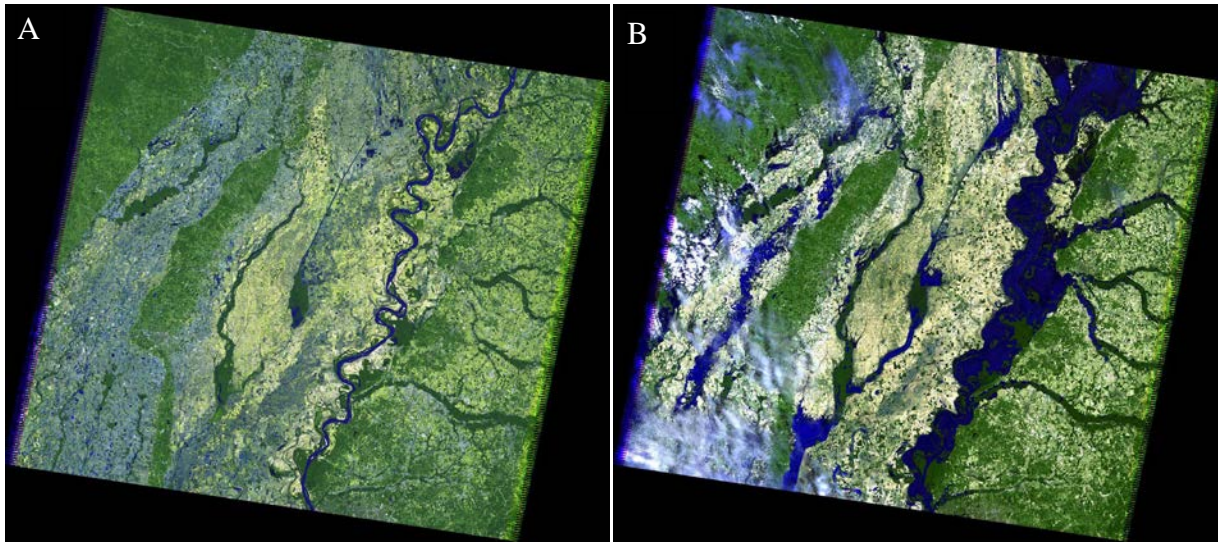
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3 **Figure 3-11. Stormflow moves downstream through the river network and**
4 **interacts with lower stream reaches, floodplains, and alluvial aquifers.** (A)
5 Hydrographs for three nested rivers in the Potomac River drainage (drainage area
6 Potomac > Shenandoah > South). (B) Hydrographs for the same three rivers with
7 streamflow normalized by drainage area.
8

9 Modified from Hornberger et al. (1998).

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



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4 **Figure 3-12. Landsat 5 satellite images of the Mississippi River along the**
5 **borders of Tennessee, Kentucky, Missouri, and Arkansas on (A) May 12,**
6 **2006 and (B) May 10, 2011.**

7
8 Images courtesy of USGS/NASA.
9

10
11 unidirectional wetlands and the river network varies with lateral expansion and subsequent
12 contraction.

13 One factor affecting the lateral distance that overbank flow spreads is preexisting
14 moisture conditions on the floodplain (Mertes, 1997; Naiman et al., 2005). River overbank flow
15 that enters a dry floodplain will spread and then infiltrate the soil (Naiman et al., 2005). If
16 inflows from streams, rainfall, or groundwater have water tables elevated to the floodplain
17 surface, water entering the riparian area from overbank flow cannot infiltrate soils. The result is
18 standing water on the floodplain and subsequent movement of water to lower elevations of the
19 floodplain. This water can alter the geomorphology of the floodplain (Hupp and Osterkamp,
20 1996), be biogeochemically transformed (see Section 5.3.2; Naiman et al., 2005), be lost by
21 evaporation, or be transpired by vegetation (Meyboom, 1964). As the river and floodplain water
22 table elevations decrease, surface water on the floodplain can flow back into the river or infiltrate
23 floodplain soils.

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

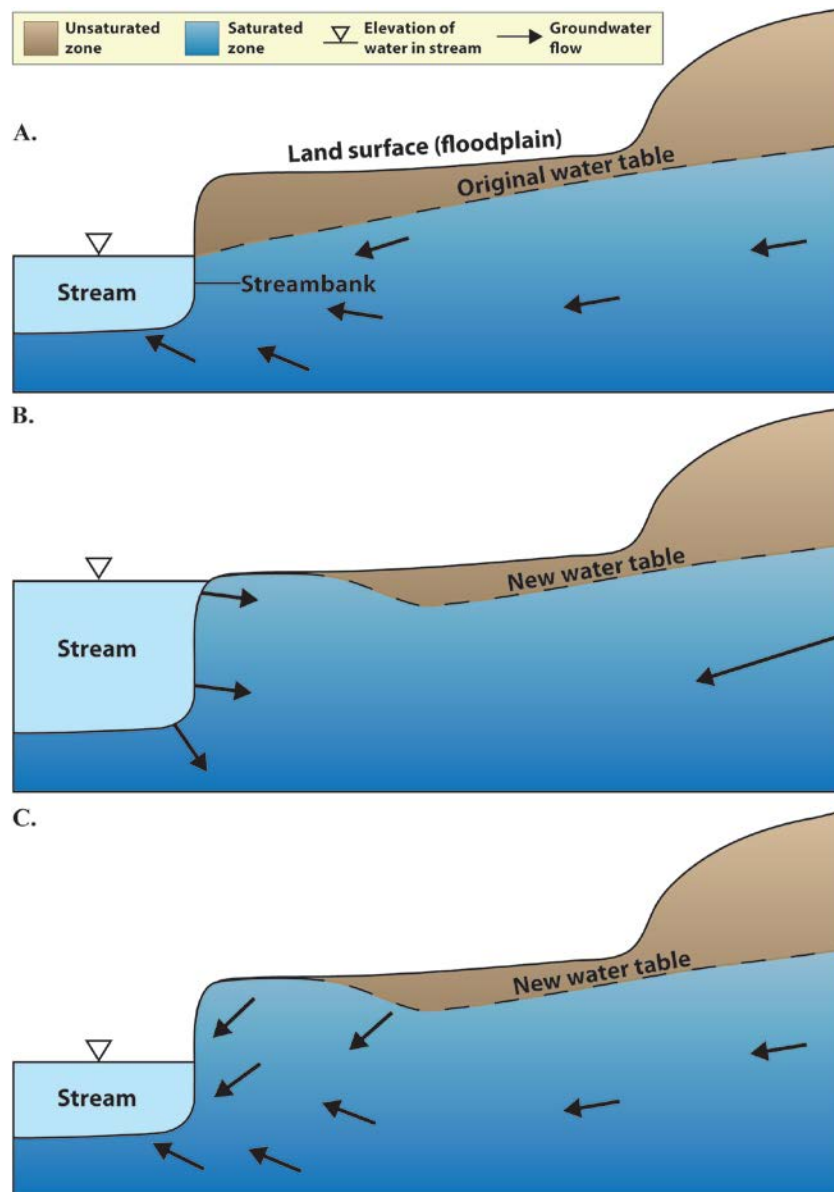
1 primarily due to floodplain water storage. Locations within floodplains and riparian areas with
2 higher elevations likely provide flood storage on a less frequent basis than lower elevation areas.

3 The interaction of high flows with floodplains and associated alluvial aquifers of river
4 networks are important determinants of hydrologic and biogeochemical conditions of rivers
5 (Ward, 1989; Stanford and Ward, 1993; Boulton et al., 1998; Burkart et al., 1999; Malard et al.,
6 1999; Amoros and Bornette, 2002; Malard et al., 2006; Poole, 2010). Bencala (1993; 2011)
7 noted that streams and rivers are not pipes: they interact with the alluvium and geologic materials
8 adjacent to and under channels. In stream or river reaches constrained by topography, significant
9 floodplain and near-channel alluvial aquifer interactions are limited (see Figure 3-3A). In
10 reaches with floodplains, however, stormflow commonly supplies water to alluvial aquifers
11 during high flow periods through the process of **bank storage** (see Figure 3-13; Whiting and
12 Pomeranets, 1997; Winter et al., 1998; Chen and Chen, 2003). As streamflow decreases after
13 hydrologic events, the water stored in these alluvial aquifers can serve as another source of
14 baseflow in rivers (see Figure 3-13C).

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

28 29 **3.3. INFLUENCE OF STREAMS AND WETLANDS ON DOWNSTREAM WATERS**

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



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

Modified from Winter et al. (1998).

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

12

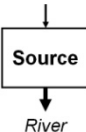
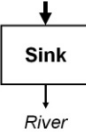
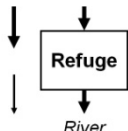
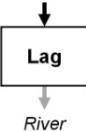
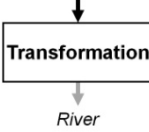
13 **3.3.1. Effects of Streams and Wetlands on Material Fluxes**

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

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

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

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

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

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

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

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

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

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

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1 3.3.2. Connectivity and Transport of Materials to and from Streams and Wetlands

2 3.3.2.1. *Connectivity and Isolation*

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

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

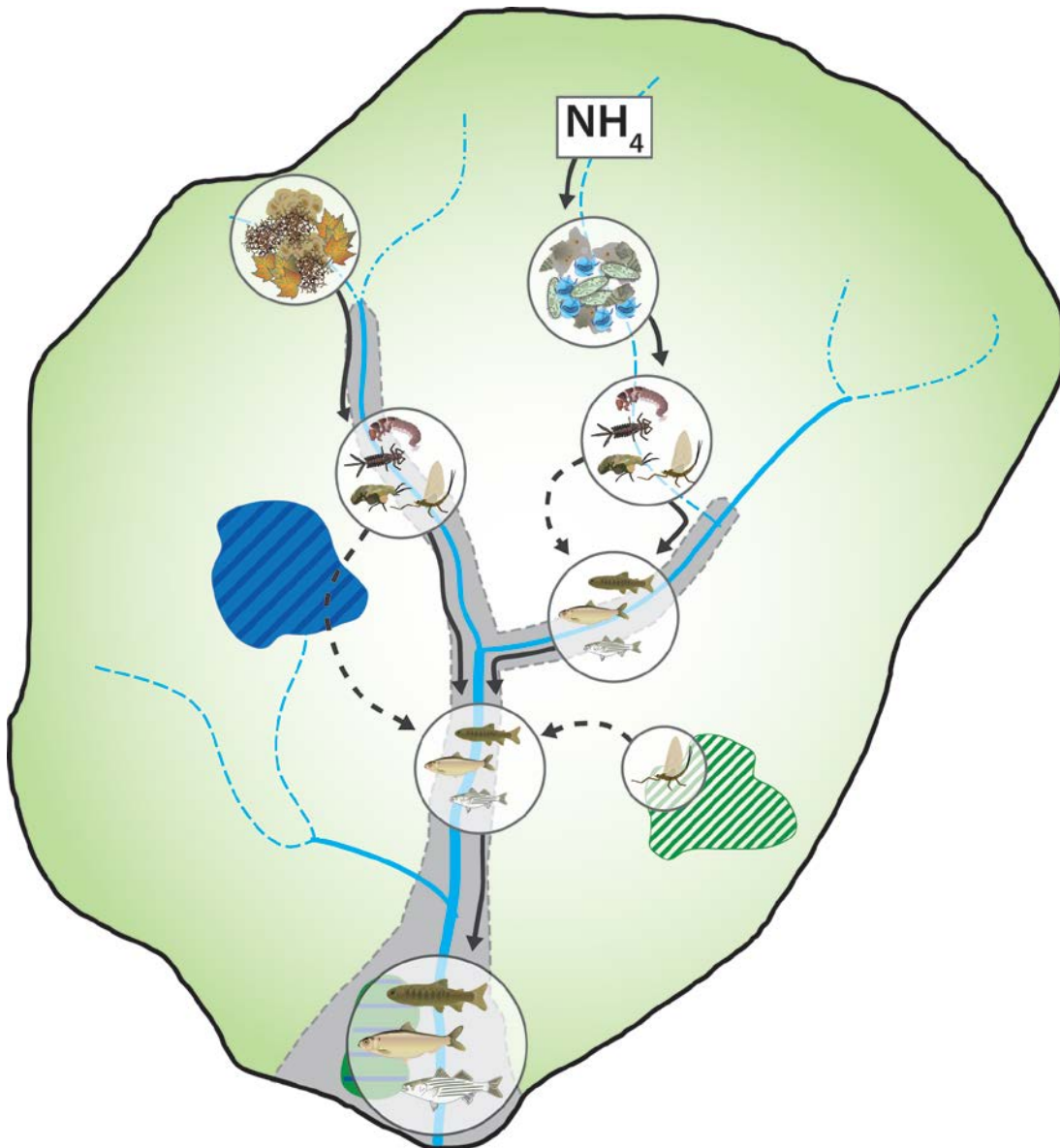
23 Ecosystem function within a river system is driven by interactions between its physical
24 environment and the diverse biological communities living within it (Wiens, 2002; Schroder,
25 2006). Thus, river system structure and function also depend on biological connectivity among
26 the system’s populations of aquatic and semiaquatic organisms. Biological connectivity refers to
27 the movement of biota, either in terms of entire organisms or reproductive materials (e.g., seeds,
28 eggs, genes), through river systems. These movements link aquatic habitats and populations in
29 different locations through several processes important for the survival of individuals,
30 populations, and species (see Sections 4.5, 5.3.3, and 5.4.4). Movements include dispersal, or
31 movement away from an existing population or parent organism; migration, or long-distance
32 movements undertaken on a seasonal basis; localized movement over an organism’s home range
33 to find food, mates, or refuge from predators or adverse conditions; and movement to different
34 habitats to complete life-cycle requirements. At the population and species levels, dispersal and
35 migration contribute to persistence at local and regional scales via colonization of new habitats

1 (e.g., Hecnar and McLoskey, 1996; Tronstad et al., 2007), location of mates and breeding
2 habitats (Semlitsch, 2008), rescue of small populations threatened with local extinction (Brown
3 and Kodric-Brown, 1977), and maintenance of genetic diversity (e.g., Waples, 2010). These
4 movements can result from passive transport by water, wind, or other organisms (e.g., birds,
5 terrestrial mammals), from active movement with or against water flow (e.g., upstream fish
6 migration), or from active movement over land (for biota capable of terrestrial dispersal) or
7 through the air (for birds or insects capable of flight). Thus, biological connectivity can occur
8 within aquatic ecosystems or across ecosystem or watershed boundaries, and it can be
9 multidirectional. For example, biota can move downstream from perennial, intermittent, and
10 ephemeral headwaters to rivers, upstream from estuaries to rivers to headwaters, or laterally
11 between floodplain wetlands, geographically isolated wetlands, rivers, lakes, or other water
12 bodies. Significant biological connectivity can also exist between aquatic and terrestrial habitats
13 (Nakano et al., 1999; Gibbons, 2003; Baxter et al., 2004), but here we focus on connections
14 among components of aquatic systems.

15 As noted in Section 3.2.3, streams and rivers are not pipes (Bencala, 1993; Bencala et al.,
16 2011); they provide opportunities for water to interact with internal components (e.g., alluvium,
17 organisms) through the five functions by which streams and wetlands alter material fluxes (see
18 Table 3-1). Connectivity between streams and wetlands provides opportunities for material
19 fluxes to be sequentially altered by multiple streams and wetlands as the materials are
20 transported downstream. The proportion of a material that ultimately reaches the river is
21 determined by the aggregate effect of these sequential fluxes. The form of the exported material
22 can change as it moves down the river network (see Figure 3-14), however, making quantitative
23 assessments of the importance of individual stream and wetland resources within the entire river
24 system difficult. For example, organic matter can be exported from headwater streams and
25 consumed by downstream macroinvertebrates (see Figure 3-14). Those invertebrates can drift
26 farther downstream and be eaten by juvenile fish that eventually move into the mainstem of the
27 river, where they feed further and grow.

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

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



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

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

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

26 27 **3.3.2.2. *Spatial and Temporal Variability of Connectivity***

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

33 The expansion and contraction of river networks affects the extent, magnitude, timing,
34 and type of hydrologic connectivity. For example, intermittent and ephemeral streams (see
35 Figure 3-7) only flow during wetter seasons (see Section 3.4) or during and immediately
36 following precipitation events. Thus, the spatial extent of connectivity between streams and

1 wetlands and rivers increases greatly during these high flow events because intermittent and
2 ephemeral streams are estimated to account for 59% of the total length of streams in the
3 contiguous United States (Nadeau and Rains, 2007b). Changes in the spatial extent of
4 connectivity due to expansion and contraction are even more pronounced in the arid and semiarid
5 Southwest, where more than 80% of all streams are intermittent or ephemeral (see Figure 3-9B;
6 Levick et al., 2008). Expansion and contraction also affect the magnitude of connectivity
7 because larger flows provide greater potential for material transport (e.g., see Section 4.3.2).

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

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

21 When dispersal, migration, and other forms of biotic movement are mediated by the flow
22 of water, biological and hydrologic connectivity can be tightly coupled. For example, seasonal
23 flooding of riparian/floodplain wetlands creates temporary habitat that fish, aquatic insects, and
24 other organisms use (Smock, 1994; Robinson et al., 2002; Tronstad et al., 2007). Factors other
25 than hydrologic dynamics can also affect the temporal and spatial dynamics of biological
26 connectivity. Such factors include movement associated with seasonal habitat use (Moll, 1990;
27 Lamoureux and Madison, 1999) and shifts in habitat use due to life history changes (Huryn and
28 Gibbs, 1999; Gibbons et al., 2006; Subalusky et al., 2009a), quality or quantity of food resources
29 (Smock, 1994), presence or absence of favorable dispersal conditions (Schalk and Luhring,
30 2010), physical differences in aquatic habitat structure (Grant et al., 2007), or the number and
31 size of nearby populations (Gamble et al., 2007). For a specific river system with a given spatial
32 configuration, variability in biological connectivity also occurs due to variation in the dispersal
33 distance of organisms and reproductive propagules (see Section 3.4.4; Semlitsch and Bodie,
34 2003).

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

1 Riverbeds or streambeds that temporarily go dry are utilized by aquatic biota having special
2 adaptations to wet and dry conditions, and can serve as egg and seed banks for a number of
3 organisms, including aquatic invertebrates and plants (Steward et al., 2012). These temporary
4 dry areas can also affect nutrient dynamics due to reduced microbial activity, increased oxygen
5 availability, and inputs of terrestrial sources of organic matter and nutrients (Steward et al.,
6 2012).

8 **3.4. FACTORS INFLUENCING CONNECTIVITY**

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

19 **3.4.1. Climate-Watershed Characteristics**

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

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

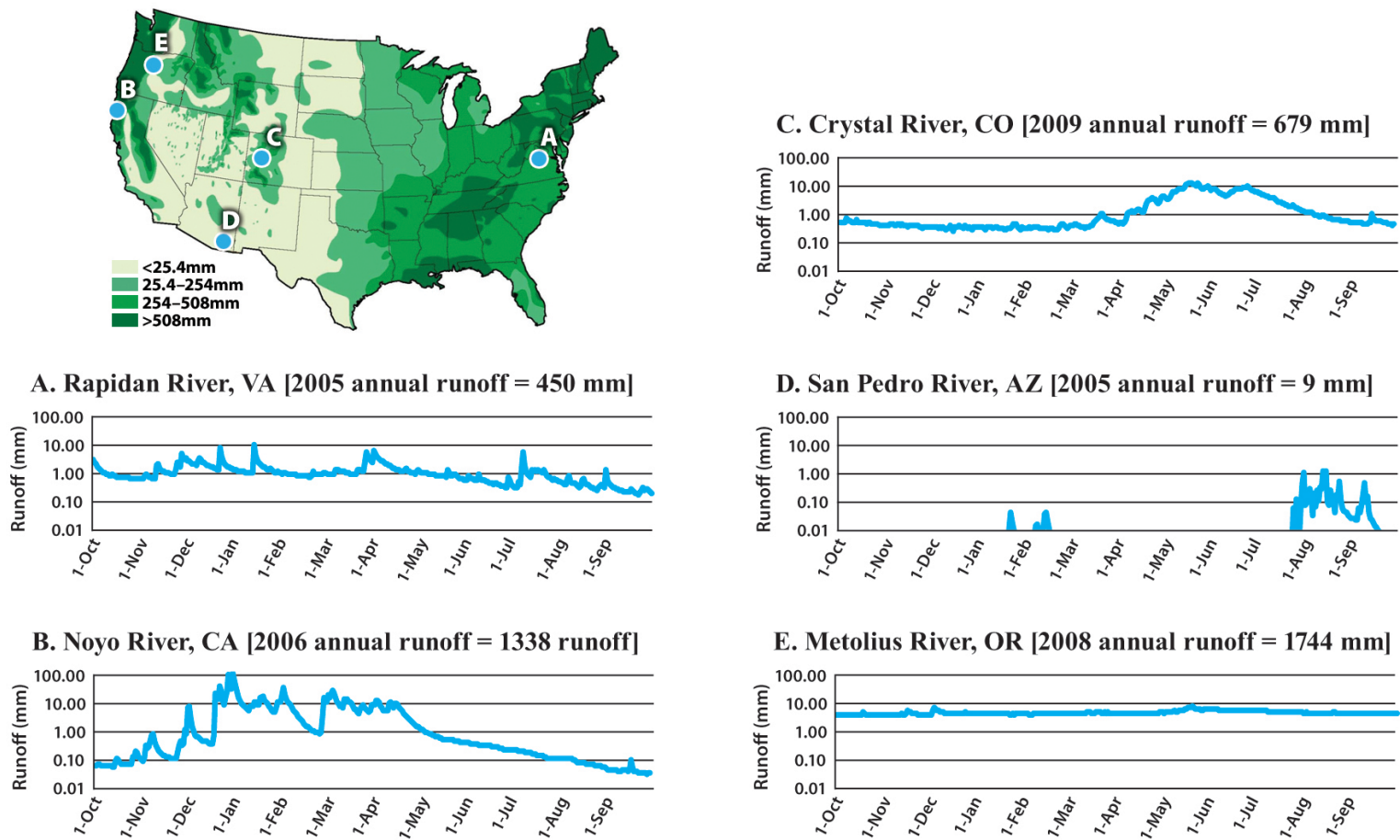


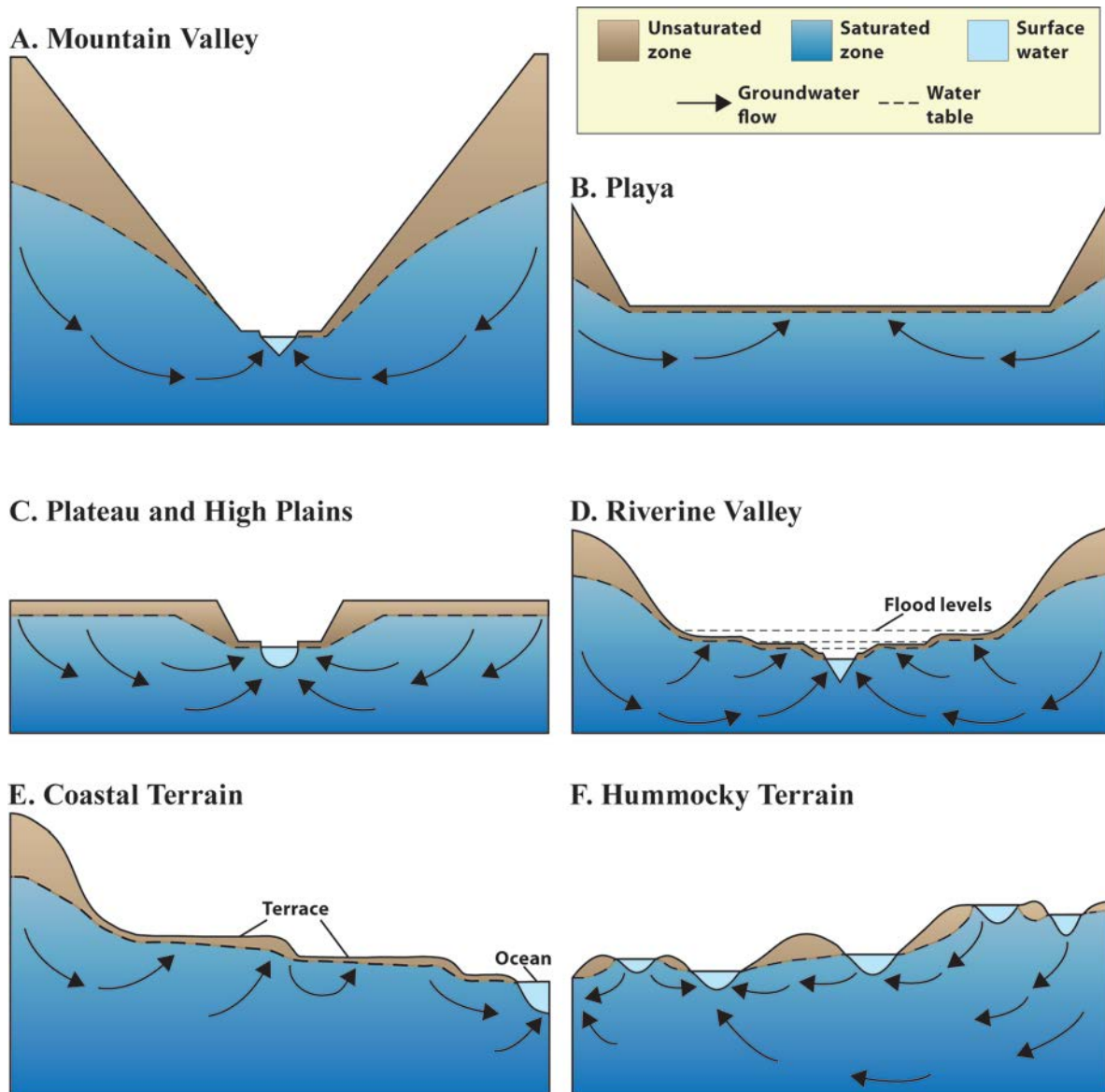
Figure 3-15. Map of annual runoff in contiguous United States showing locations of five example streams that illustrate daily runoff patterns and total annual runoff depths. (A) Rapidan River, VA; (B) Noyo River, CA; (C) Crystal River, CO; (D) San Pedro River, AZ; and (E) Metolius River, OR. All data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

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

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

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

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



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

Modified from Winter (2001).

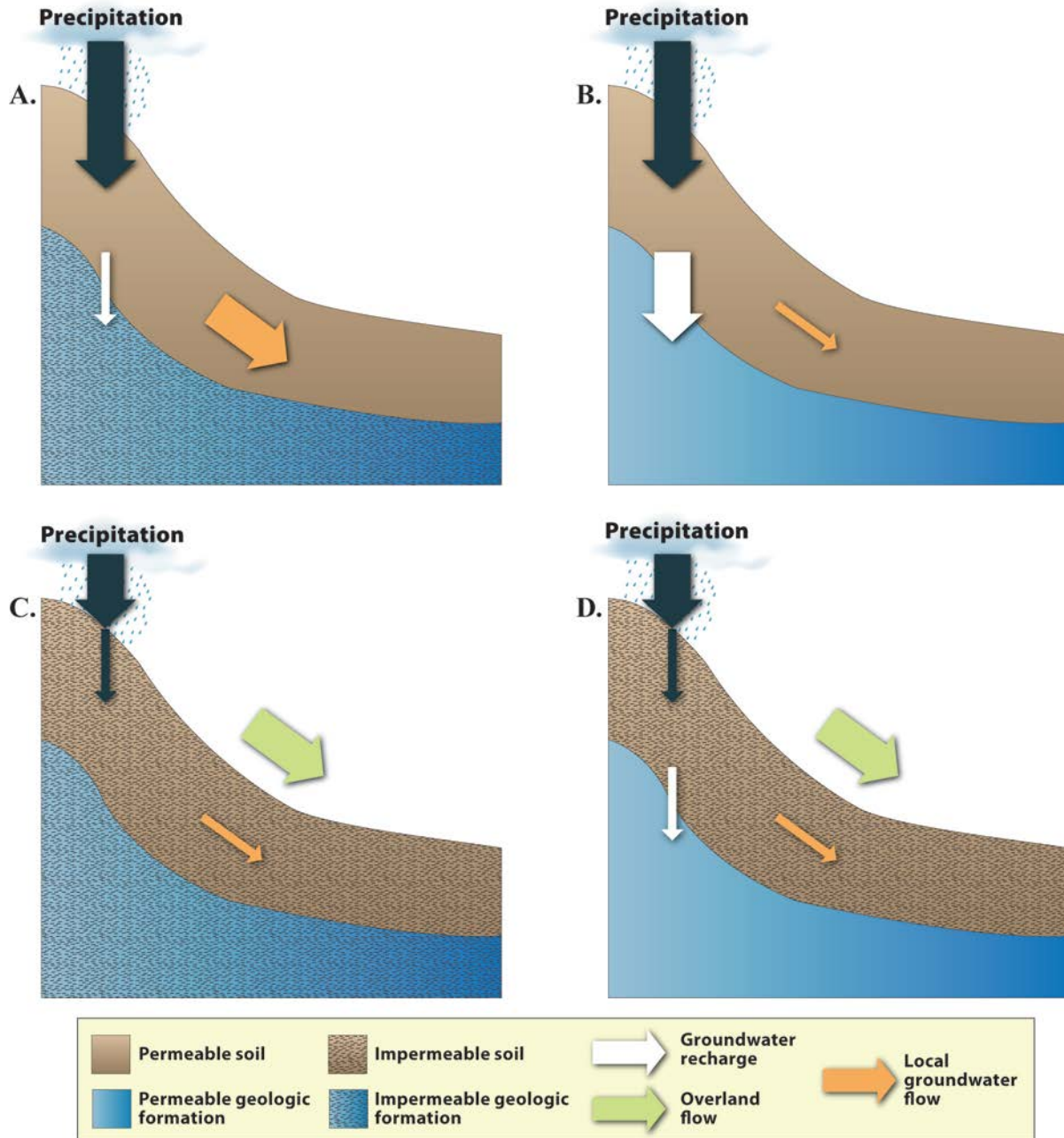


Figure 3-17. Major hydrologic flowpaths for hillslopes with combinations of permeable and impermeable soils and geologic formations. (A) Permeable soil and impermeable underlying geologic formation; (B) permeable soil and permeable underlying geologic formation; (C) impermeable soil and impermeable underlying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

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

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

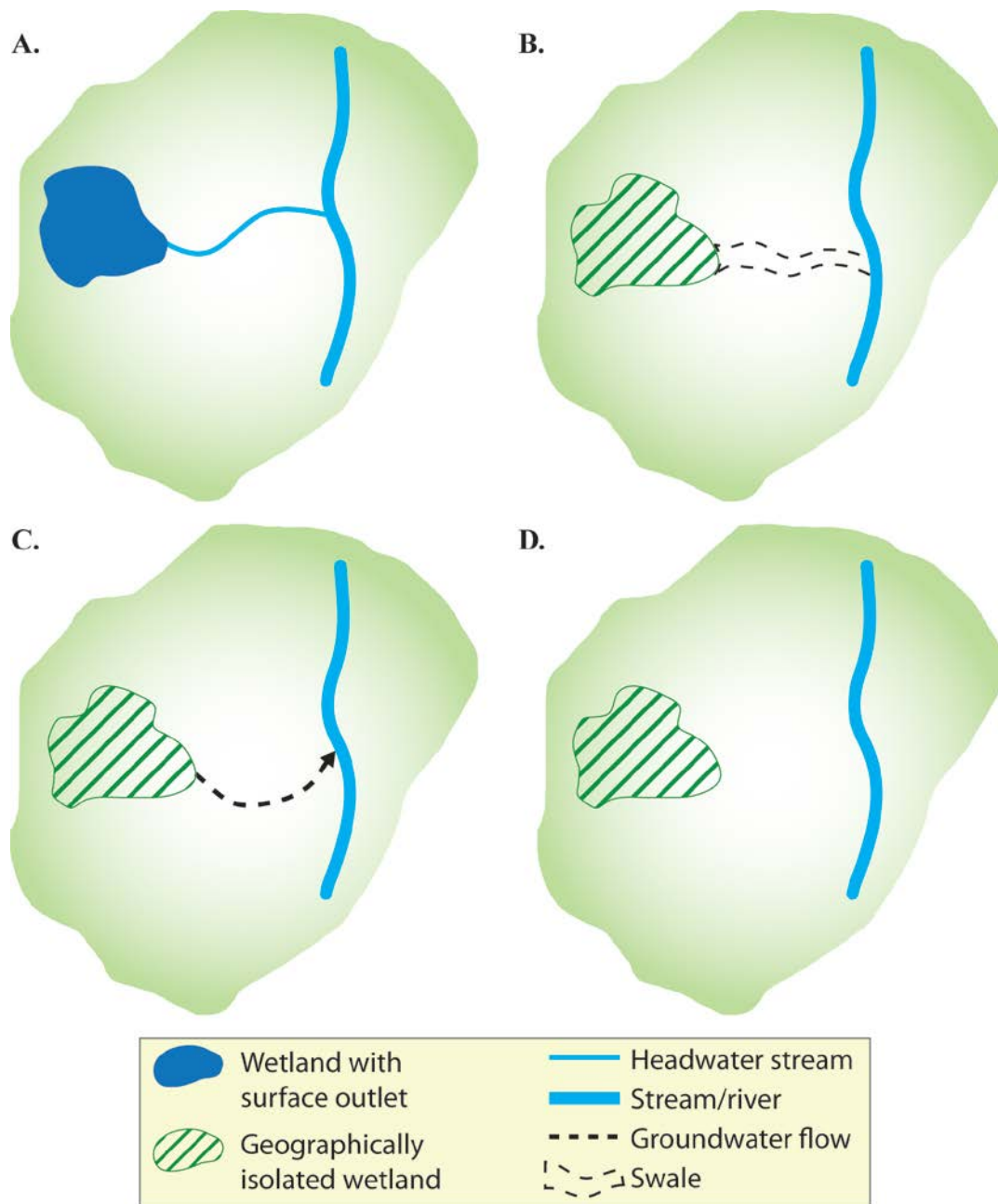


Figure 3-18. Types of hydrologic connections between unidirectional wetlands and streams or rivers. (A) Wetland connected to a river by surface flow through a headwater stream channel. (B) A wetland connected to a river by surface flow through a nonchannelized swale. Such a wetland would be considered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

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

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

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

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

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

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

34 Like the Crystal River, the Metolius River in Oregon (see Figure 3-15E) also has
35 snowpack in its higher elevations, but geologic conditions in the watershed alter the climate
36 signal. Meltwaters in the Metolius River flow through long flowpaths in porous bedrock to

1 springs in or adjacent to the river (James et al., 2000; Gannett et al., 2001). Although
2 intermittent and ephemeral streams occur in the Metolius basin, most streams are spring-fed and
3 are perennial.
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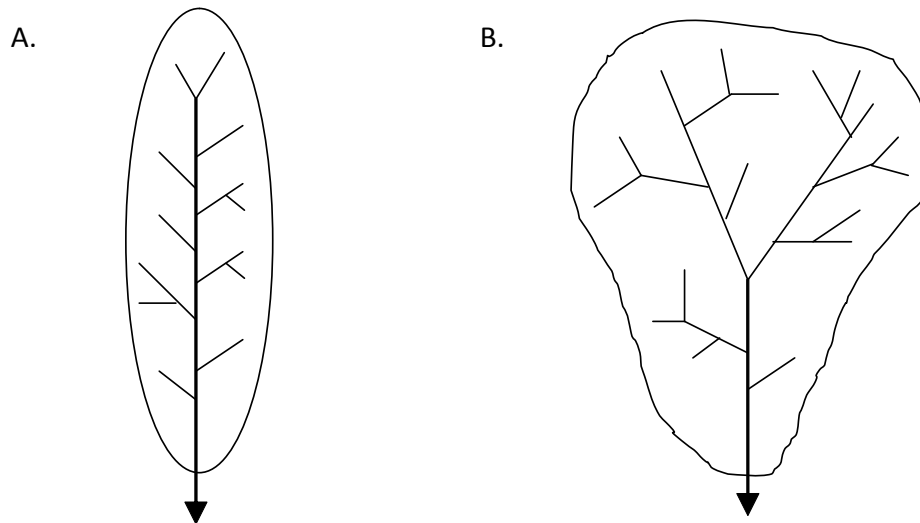
5 **3.4.2. Spatial Distribution Patterns**

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

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

30 The relationship between streams and the river network is a function of basin shape and
31 network configuration. Elongated basins tend to have trellis networks where relatively small
32 streams join a larger mainstem (see Figure 3-19A); compact basins tend to have dendritic
33 networks with tree-like branching, where streams gradually increase in size before joining the
34 mainstem (see Figure 3-19B). This network configuration describes the incremental
35 accumulation of drainage area along rivers, and therefore informs questions about the relative
36 contributions of streams to downstream waters. Streams in a trellis network are more likely to

1 connect directly to a mainstem, compared with a dendritic network. The relationship between
2 basin shape, network configuration, and connectivity, however, is complex. A mainstem in a
3 trellis network is also more likely to have a lower stream order than one in a dendritic network.
4 For example, the lower-most reach in the trellis network in Figure 3-19A is a third-order stream,
5 while that of the dendritic network (see Figure 3-19B) is a fourth-order stream.
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10 **Figure 3-19. Major types of basin shapes and network configurations.** (A) A
11 rectangular basin with trellis network, and (B) a compact basin with dendritic
12 network.
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15 Distance also affects connectivity between unidirectional and riparian/floodplain
16 wetlands and downstream waters. Riverine wetlands that serve as origins for lateral source
17 streams that connect directly to a mainstem river have a more direct connection to that river than
18 wetlands that serve as origins for terminal source streams high in a drainage network. This also
19 applies to riparian/floodplain wetlands that have direct surface water connections to streams or
20 rivers. If geographically isolated unidirectional wetlands have surface water outputs (e.g.,
21 depressions that experience surface water spillage or groundwater seeps; see Figure 3-18B), the
22 probability that surface water will infiltrate or be lost through evapotranspiration increases with
23 distance. For unidirectional wetlands connected through groundwater flows, less distant areas
24 are generally connected through shallower flowpaths (see Figure 3-5), assuming similar soil and
25 geologic properties. These shallower groundwater flows have the greatest interchange with
26 surface waters (see Section 3.2.2) and travel between points in the shortest amount of time.
27 While elevation is the primary factor determining areas that are inundated through overbank
28 flooding, connectivity with the river will generally be higher for riparian/floodplain wetlands

1 located near the river's edge compared with riparian/floodplain wetlands occurring near the
2 floodplain edge.

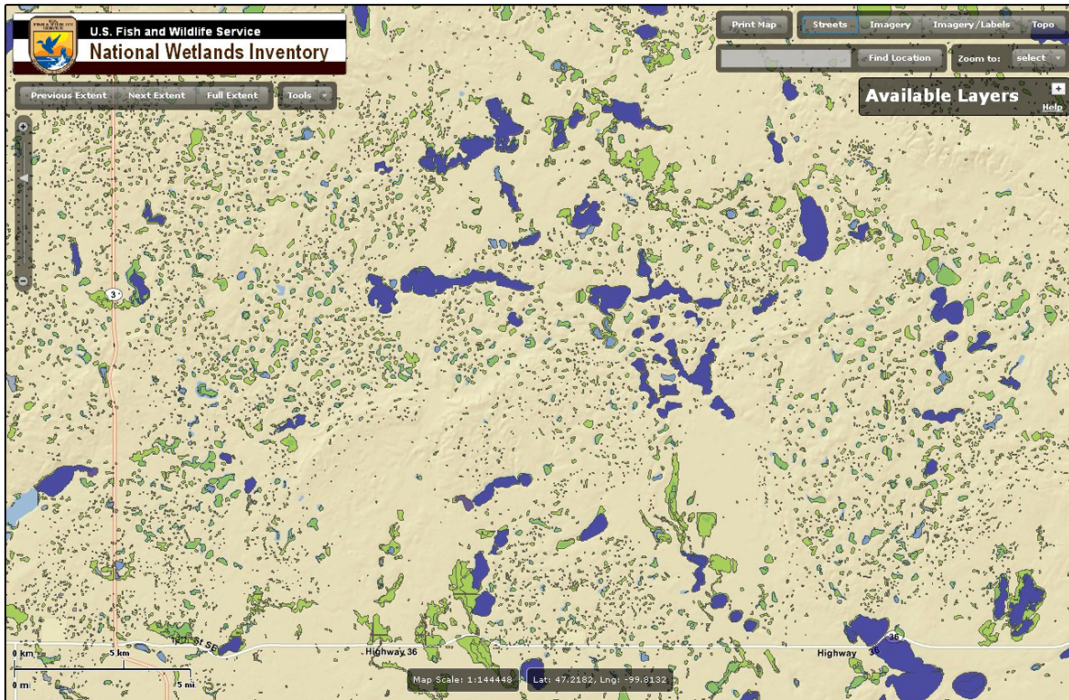
3 Biological connectivity among streams and wetlands is also influenced by distance from
4 the river network. For example, mortality of a given organism due to predators and natural
5 hazards generally increases with the distance it has to travel. The likelihood that organisms or
6 propagules traveling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

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

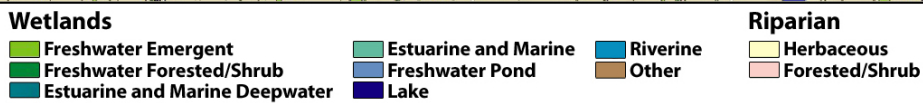
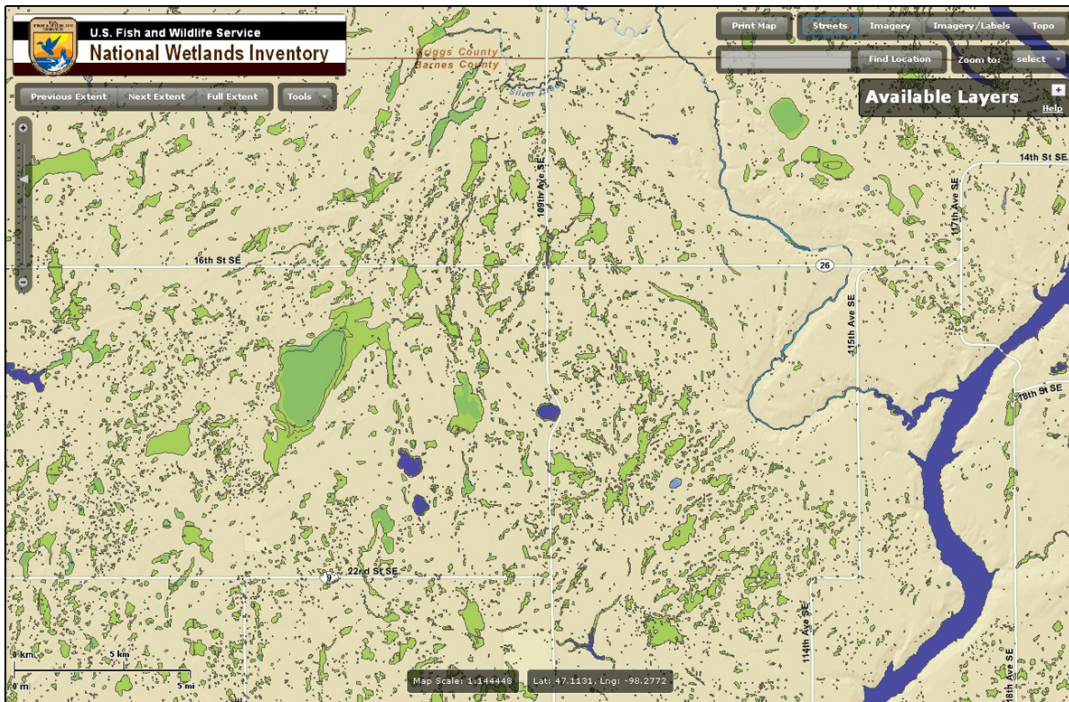
17 Figure 3-20 compares the spatial distribution of wetlands and streams to the river
18 network in six different landscape settings. A comparison of these figures shows landscape
19 settings ranging from no nearby streams and dense small wetlands (see Figure 3-20A), to a few
20 nearby streams with high wetland density (see Figures 3-20B and 3-20C), to less spatially
21 uniform wetlands (see Figure 3-20D), to areas with higher drainage densities and riparian (see
22 Figure 3-20E) or larger, more extensive (see Figure 3-20F) wetlands. The maps on Figure 3-20
23 represent single examples of these different settings, and so might not be representative. They
24 are useful, however, for illustrating the degree to which landscape setting can affect the
25 interspersion—and thus average distance—between wetlands and the river network, and the
26 large variability that can result. In settings with many wetlands and relatively low drainage
27 density (see Figures 3-20B, C, and D), there can be a large range in the distances between
28 individual wetlands and the stream. In contrast, areas with a higher drainage density (see Figure
29 3-20E and F) can have a narrower range of shorter distances. All things being equal, wetlands
30 with shorter distances to the stream network will have higher hydrologic and biological
31 connectivity than wetlands located farther from the same network.

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A. Prairie potholes (Missouri Coteau)



B. Prairie potholes (Drift Prairie)

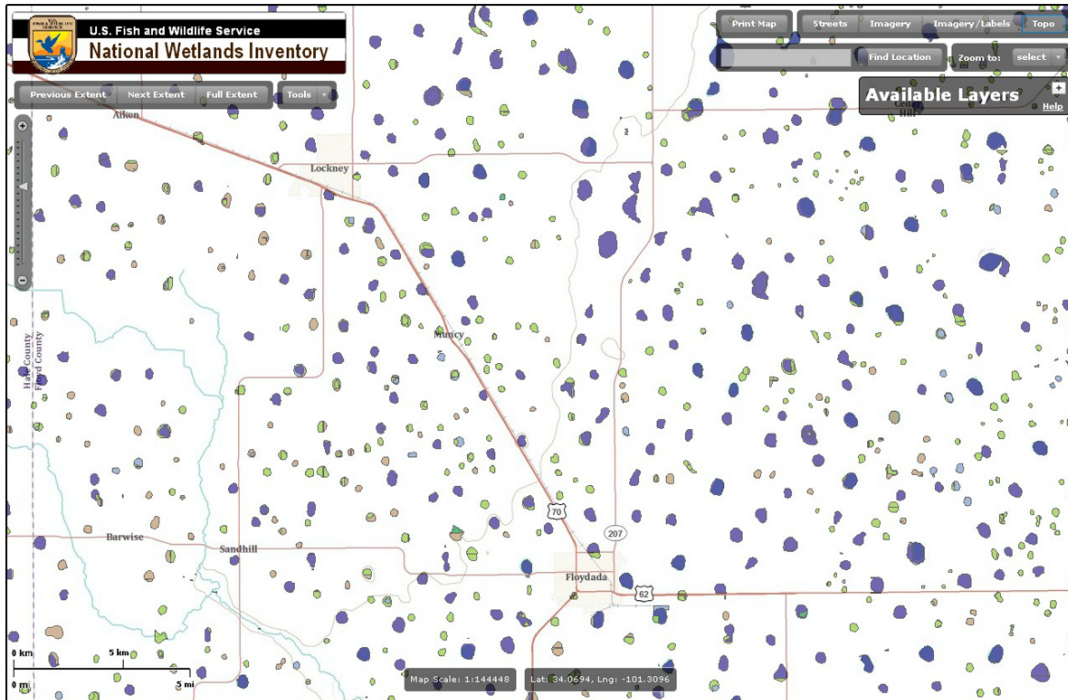


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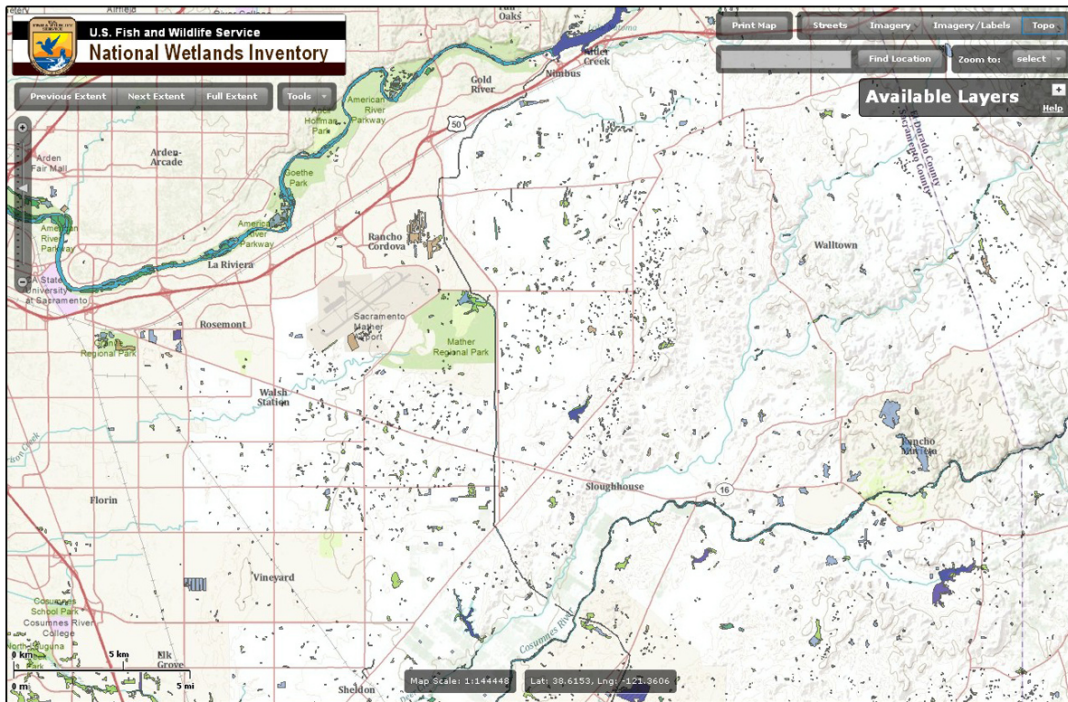
Figure 3-20. Examples of different landscapes showing interspersion of wetlands and streams or rivers.

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C. Playa



D. Vernal pools

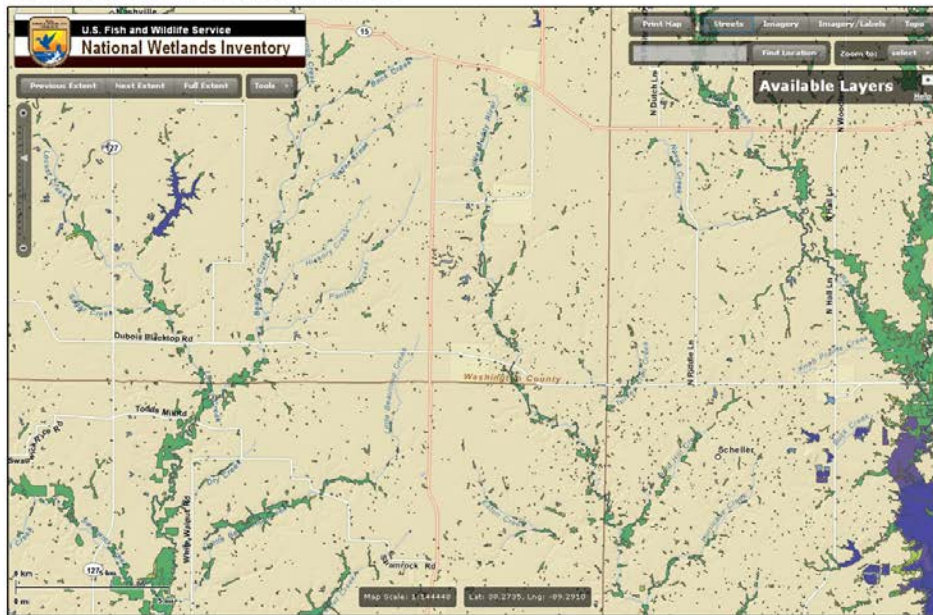


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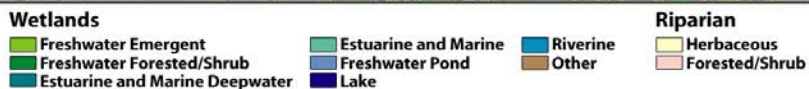
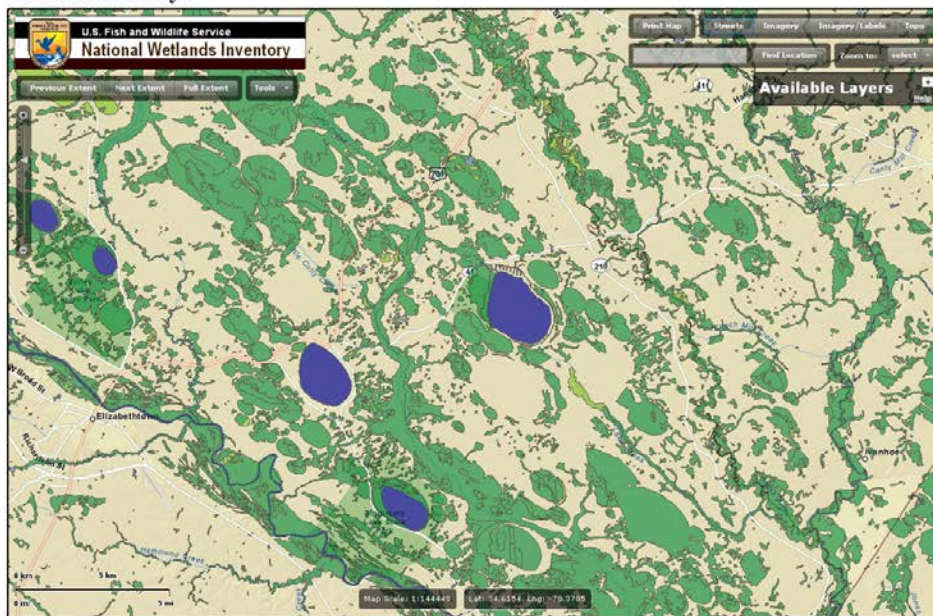
Figure 3–20. Examples of different landscapes showing interspersion of wetlands and streams or rivers (continued).

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E. Bottomland hardwood wetlands



F. Carolina bays



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

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

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1 **3.4.3. Biota**

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

8 Diadromous fauna (e.g., Pacific and Atlantic salmon, certain freshwater shrimps and
9 snails, American eels), which require both freshwater and marine habitats over their life cycles
10 and therefore migrate along river networks, provide one of the clearest illustrations of biological
11 connectivity. Many of these taxa are either obligate or facultative users of headwater streams
12 (Erman and Hawthorne, 1976; Wigington et al., 2006), meaning that they either require
13 (obligate) or can take advantage of (facultative) these habitats; these taxa thereby create a
14 biological connection along the entire length of the river network. For example, many Pacific
15 salmon species spawn in headwater streams, where their young grow for a year or more before
16 migrating downstream, living their adult life stages in the ocean, and then migrating back
17 upstream to spawn. Many taxa can also exploit temporary hydrologic connections between
18 rivers and floodplain wetland habitats, moving into these wetlands to feed, reproduce, or avoid
19 harsh environmental conditions and then returning to the river network (Copp, 1989; Junk et al.,
20 1989; Smock, 1994; Richardson et al., 2005).

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

32
33 **3.4.4. Human Activities and Alterations**

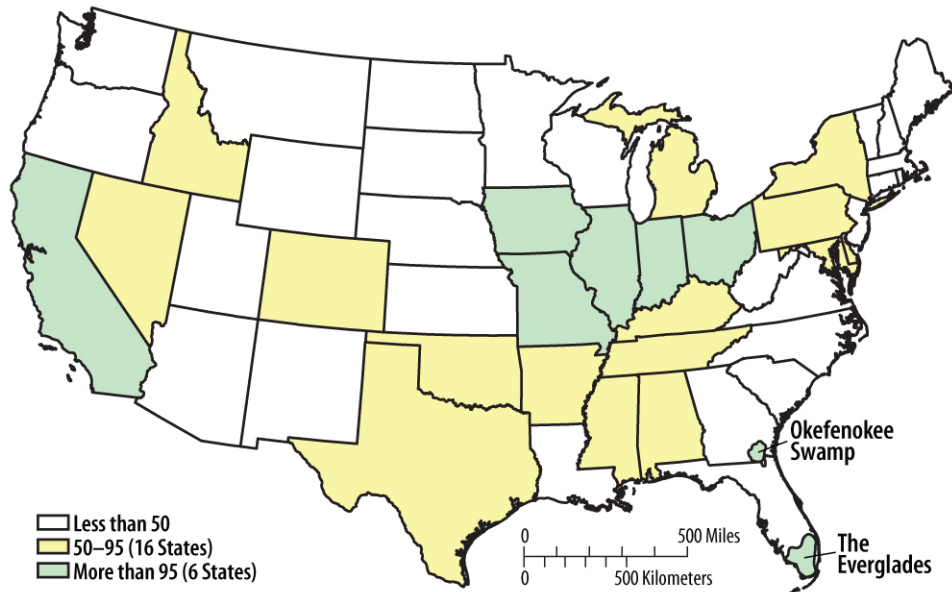
34 Human activities frequently alter connectivity between headwater streams,
35 riparian/floodplain wetlands, unidirectional wetlands, and downgradient river networks, thereby

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

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

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

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



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

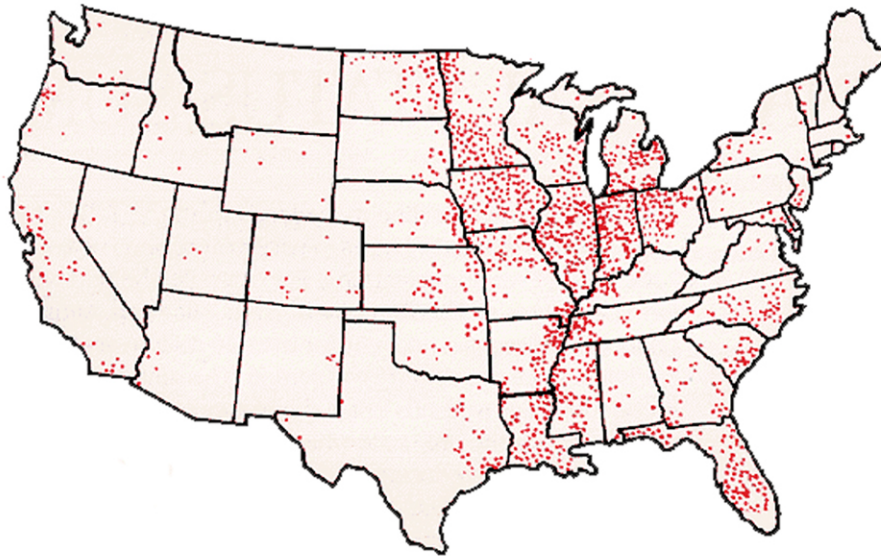


Figure 3-21. Comparison of percent wetland loss between (A) the 1780s and mid-1980s with (B) the distribution of artificially drained agricultural land in 1985. One dot equals 8100 ha.

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

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

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

17 Particularly noteworthy is that restoration of hydrologic connectivity, particularly in
18 systems with widespread human alterations, also might adversely affect downstream waters
19 (Jackson and Pringle, 2010). For example, dam removal can result in the downstream transport
20 of previously sequestered pollutants (Jackson and Pringle, 2010); dam releases to restore flows,
21 without simultaneous restoration of sediment supplies, can result in downstream channel
22 degradation (Germanoski and Ritter, 1988; Schmidt and Wilcock, 2008). Hammersmark et al.
23 (2008) used a modeling study to show how the restoration of incised stream channels can
24 improve connectivity between streams and floodplains and thus restore predisturbance hydrology
25 (i.e., increased floodplain water storage, reduced peak stormflow, and reduced baseflow).

26 27 **3.4.5. Interactions Among Factors**

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

32 During high water conditions in 1995, a temporary surface water connection was
33 observed between two geographically isolated prairie potholes in the region's Drift Prairie.
34 Based on a spatial analysis during similarly wet conditions in 1996, 28% of the wetlands in a
35 40 km² area containing the sites had a temporary surface water connection to at least one other

1 wetland. This included a complex (defined in the study as a group of wetlands interconnected
2 through temporary surface water connections) of 14 wetlands.

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

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

33 Beyond these regional trends in relief and precipitation, local variation in the occurrence
34 of intermittent surface-water connections should be influenced strongly by groundwater
35 dynamics. The groundwater hydrology of prairie potholes has been well investigated at several
36 sites (e.g., Winter et al., 1998; Winter and Rosenberry, 1998). However, the specific

1 groundwater interactions—and hence the effects of groundwater movement on spillage or
2 mixing—are unknown for most prairie potholes. It would generally be expected that, all else
3 being equal, groundwater discharge wetlands should receive more water, and so have a higher
4 probability of spillage, than groundwater recharge wetlands, since recharge should reduce the
5 amount of water available for spillage.

6 A major factor influencing the temporal distribution of intermittent connections within
7 the PPR is wet-dry cycles. These cycles are driven by climatic changes that have occurred
8 throughout the Holocene. For example, there is evidence of 20-, 22-, 50-, 100-, and 200-year
9 climatic cycles (Ashworth, 1999). Wetland hydrology responds dramatically to these wet-dry
10 cycles as groundwater levels and precipitation patterns fluctuate. In 1996, the average monthly
11 Palmer Hydrological Drought Index for central North Dakota was 4.02 (88th percentile),
12 compared with a median of 1.00 for annually calculated monthly averages between 1895 and
13 2001. Moisture levels of this magnitude—and consequently the degree of connectivity observed
14 (Leibowitz and Vining, 2003)—would be expected to occur during wetter portions of wet-dry
15 cycles.

16

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

3 **4.1. ABSTRACT**

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

23
24 **4.2. INTRODUCTION**

25 The purpose of this chapter is to describe the state of knowledge of stream connectivity
26 and its effects on the physical, chemical, and biological condition of downstream waters.
27 Although we recognize that streams also are important sources of water and other materials to
28 nearby terrestrial and groundwater systems (e.g., Gray, 1993; Shentsis and Rosenthal, 2003;
29 Walters et al., 2008), we focus here on surface water connections between streams and rivers, as
30 well as subsurface water interactions integral to surface water connections and downstream water
31 condition. The evidence primarily focuses on the downstream connections of small (headwater)
32 streams to downstream waters, but some evidence is drawn from connections of larger streams to
33 rivers, reservoirs, lakes, and coastal waters. We consider the peer-reviewed evidence for
34 connectivity and its effects on downstream rivers in terms of physical (see Section 4.3), chemical
35 (see Section 4.4), and biological (see Section 4.5) connections between upstream and

1 downstream habitats. While recognizing that many linkages between streams and downstream
2 waters cross physical, chemical, and biological boundaries, we have chosen this format for ease
3 of presentation. We close this general section on stream-river connections with a synthesis of the
4 evidence in terms of the conceptual framework (see Section 4.6), and then consider in greater
5 detail the evidence for connectivity in two specific stream types: prairie streams (see Section 4.7)
6 and arid streams of the Southwest (see Section 4.8). Prairie streams and arid streams of the
7 Southwest were selected for case studies in part because a high proportion of these river
8 networks are composed of intermittent and ephemeral streams.

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

15 The contribution of headwater streams to river networks in terms of stream number,
16 length, or drainage area over large geographic regions has been difficult to determine, even with
17 advances in remote sensing and geographic information systems (GIS). The small size of
18 headwater streams makes distinguishing them from surrounding areas and overlying tree
19 canopies in most regions difficult (Gilvear and Bryant, 2003). Numerous studies have shown
20 that existing U.S. hydrographic databases and topographic maps underestimate the extent of
21 headwater streams (Morisawa, 1957; Gregory, 1976; Hansen, 2001; Heine et al., 2004; Stoddard
22 et al., 2005; Colson et al., 2008; Roy et al., 2009). Therefore, most first-order streams portrayed
23 on databases and maps are second- or third-order streams when ground truthed. For example,
24 over 80% of mapped (1:25,000 scale topographic maps) stream terminuses in a Massachusetts
25 watershed that were surveyed underestimated the upstream extent of the channels (Brooks and
26 Colburn, 2011). On average these unmapped upstream segments were nearly 0.5 km in length
27 and 40% had one or more upstream tributaries (Brooks and Colburn, 2011). Despite the widely
28 known underestimation by databases and maps, first-order streams recognized by the U.S.
29 Geological Survey (USGS) medium-resolution (1:100,000-scale) National Hydrographic
30 Database (NHD) represented 53% (2,900,000 km) of total stream length (Nadeau and Rains,
31 2007b). Moreover, approximately 50% of these first-order streams were classified as not having
32 year-round flow (i.e., nonperennial; Nadeau and Rains, 2007b; see Section 3.2.2). Because most
33 databases and maps do not portray the true extent of headwater and nonperennial streams, these
34 resources do not accurately reflect the true geomorphic definition of stream order and should not
35 be used to define the upper extent of what is and is not a stream within a watershed.
36 Nevertheless, given what we do know from hydrographic databases and about the distribution of

1 streams by size, it is clear that headwater and nonperennial streams represent a large fraction of
2 river networks in the United States.

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

11 **4.3. PHYSICAL CONNECTIONS**

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

18 **4.3.1. Water**

19 The recurrent, concentrated surface flow of water from surface runoff and groundwater
20 develops and maintains river networks, and water is the primary medium carrying other materials
21 from streams to rivers (see Section 3.3). Most (although not all) rivers receive most of their
22 water from tributaries rather than through direct precipitation on or groundwater input to river
23 segments (Winter, 2007; Bukaveckas, 2009). Alexander et al. (2007) modeled flow through
24 stream networks in the northeastern United States and estimated that first-order streams
25 (designated on the 1:100,000-scale NHD river network) provide approximately 70% of the mean
26 annual water volume in second-order streams and about 55% and 40% of the mean water volume
27 in fourth- and higher order rivers, respectively. Overall, first-order streams contribute about 60%
28 of the total volume of mean annual flow to all northeastern streams (Alexander et al., 2007).
29 Contributions of headwaters to downstream baseflow vary among river networks, depending on
30 large-scale factors (see Section 3.4). For example, headwater streams which have stronger
31 connections to groundwater or which consistently receive more precipitation, relative to
32 downstream reaches, will have a larger effect on river baseflows. Hydrologic data from
33 11 nested gages distributed throughout a 176 km²-basin in the Catskill Mountains, NY were used
34 to assess the extent of spatial correlation in baseflow discharge (Shaman et al., 2004). Baseflow
35 discharge in smaller streams (i.e., with watersheds <8 km²) was more weakly correlated with

1 mainstem discharge than discharge in larger streams; the authors concluded that this pattern
2 reflected greater contributions by deep groundwater as drainage area increased (Shaman et al.,
3 2004). Using geochemical tracers and hydrologic data from 32 nested stations in a
4 1,849 km²-basin of the River Dee in Scotland, Tetzlaff and Soulsby (2008) determined that
5 streams draining the upper 54% of the catchment contributed 71% of baseflow. This finding is
6 particularly significant because the upper catchment received only 58% of the total annual
7 precipitation, indicating that groundwater storage in the headwater catchments was important in
8 maintaining downstream baseflows (Tetzlaff and Soulsby, 2008). In contrast, headwater streams
9 (0.11–3.5 km²) making up 33% of the total area in a northern Sweden basin (78 km²) contributed
10 only 18% of the summer baseflow at the basin outlet (Temnerud et al., 2007). The specific
11 discharge contribution (L s⁻¹ km²) for headwater streams, however, varied by an order of
12 magnitude (~0.5–8.0) reflecting the heterogeneity (i.e., mires, lakes, forest) of the study
13 catchment (Temnerud et al., 2007).

14 The role of headwater streams also can be inferred from variation in river hydrologic
15 response over space. Discharge increases with drainage area, and the general assumption is that
16 they have a positive relationship such that drainage area is a common proxy for discharge. The
17 relationship can be written as $Q = kA^c$, where Q is discharge (m³ s⁻¹), k is a constant representing
18 hydrologic factors such as antecedent moisture and precipitation, A is drainage area (km²), and c
19 is the scaling power constant. This scaling power reflects how the rate of discharge increases
20 with drainage area and can be useful for qualitatively assessing the contributions of headwaters
21 to downstream discharge. Where $c \approx 1$, discharge is generated proportionally with increasing
22 drainage area; where $c < 1$, upstream portions of the catchment (where small streams tend to be
23 most abundant) generate more discharge per unit area than downstream portions; where $c > 1$,
24 downstream portions generate more discharge per area than upstream reaches. Data from
25 multiple USGS gages along large, unregulated rivers showed that mean and peak annual
26 discharge does not always increase proportionally with drainage area (Galster, 2007, 2009). Of
27 the 40 rivers examined, only 16 had linear peak annual discharge-area relationships ($c \approx 1$)
28 throughout their period of record (Galster, 2009). Eleven rivers had relationships where $c < 1$,
29 three rivers had relationships where $c > 1$, and ten showed changes in the relationship over their
30 period of record. Rivers having $c < 1$ suggests that these rivers derive a higher proportion of
31 their flow from headwater streams. Rivers having $c > 1$ suggests that the upstream portions
32 might store more water per unit area than downstream areas. In some cases, however,
33 urbanization in the lower portions of the catchment can cause greater flow generation per unit
34 area, leading to a similar relationship (Galster et al., 2006).

35 Despite the variability in area-discharge relationships, most watersheds have a value of c
36 between 0.8 and 1 (Galster, 2007), suggesting that to a first approximation, drainage area can be

1 used to estimate the proportion of flow that arises from headwater streams. For example,
2 Alexander et al. (2007) found that the catchments of first-order streams accounted for 57% of the
3 total drainage area, and 55% of the total annual river flow of the New England states. Caruso
4 and Haynes (2011) reported that first-order catchments made up 61% of the total drainage area
5 of the Upper Colorado River basin. In this case, however, the first-order streams produced a
6 lower proportion (41%) of the total annual river flow than suggested by their total drainage area,
7 explained in part by the fact that 84% of the streams were intermittent. Both studies used the
8 1:100,000-scale NHD, in which first-order catchments generally correspond to second-order
9 catchments at the 1:24,000 scale (Alexander et al., 2007). These results, representing two very
10 different parts of the United States, strongly suggest that headwater streams, even where
11 seasonally dry, generate a large fraction of the nation's stream and river flows.

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

22 Such propagation was recorded following a monsoonal storm event through an arid
23 network of ephemeral channels in the Río Grande, NM (see Figure 4-2). The high intensity
24 storm dropped approximately 18–25% of the annual rainfall over a 2-day period on the stream's
25 approximately 16,000-km² drainage area. Discharge recorded at two gages on the stream and
26 three gages on the Rio Grande downstream of the confluence illustrated lag time and peak
27 hydrograph broadening at least 127 km downstream (Vivoni et al., 2006). The contributions of
28 the stormflow from the ephemeral stream accounted for 76% of the flow at the Rio Grande,
29 despite being considered to have a flood return interval only ranging from 1.11 to 1.84 years
30 across the USGS gages in the network (Vivoni et al., 2006).

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

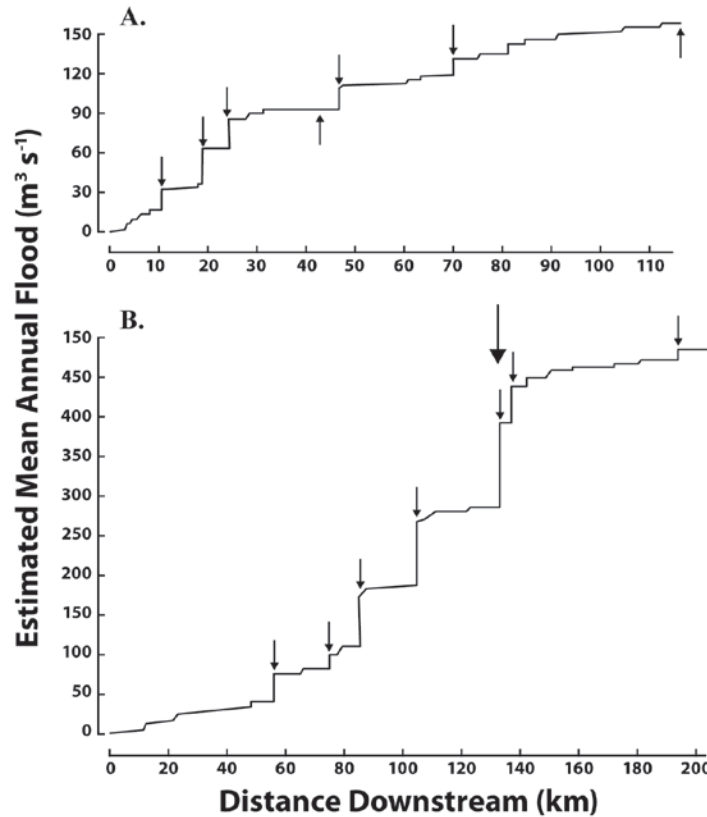
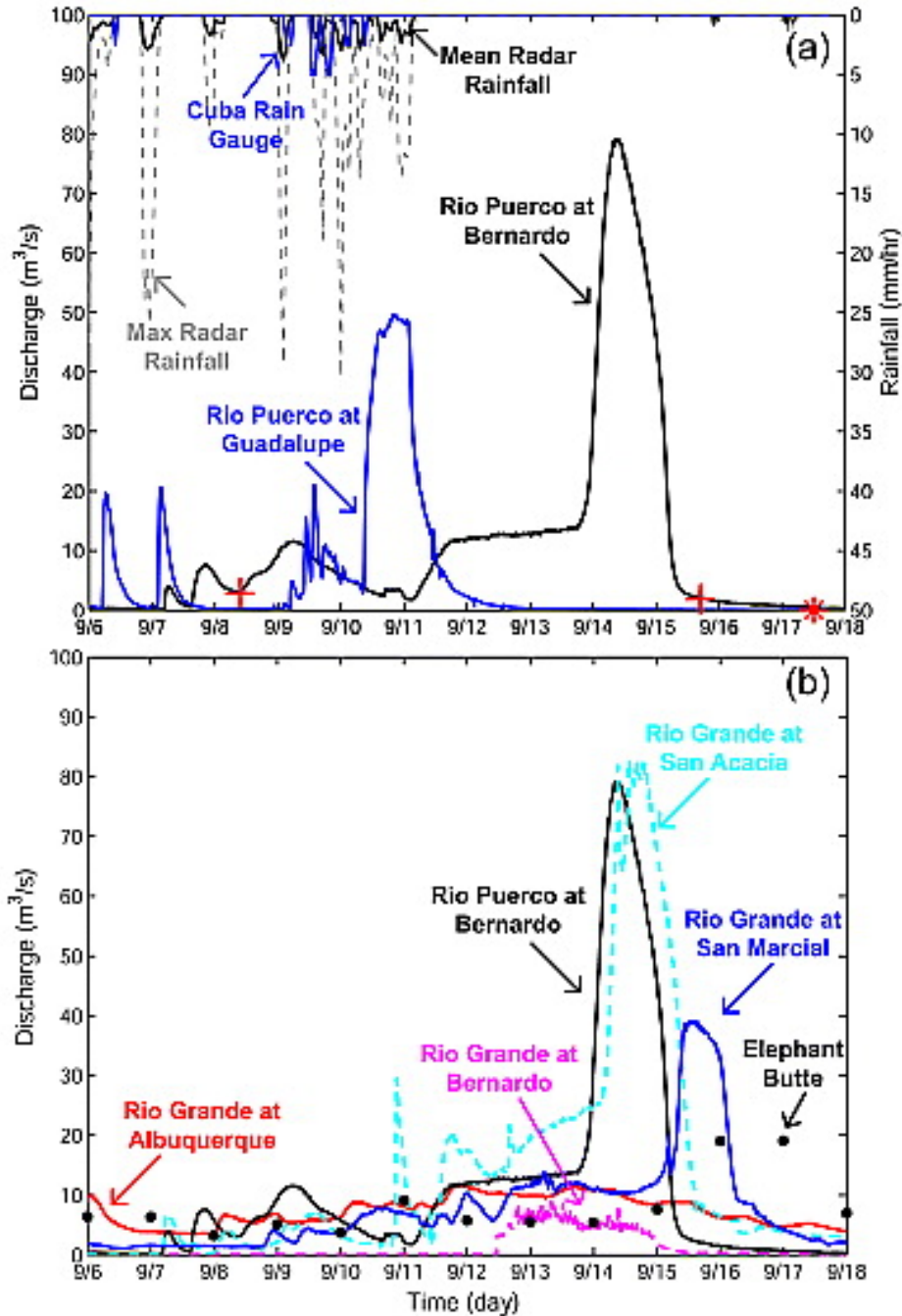


Figure 4-1. Longitudinal pattern of flow along (A) River Derwent and (B) River Trent, illustrating stepped increases in flow associated with contributions from tributaries. Small arrows indicate location of tributary confluences along the mainstem; bold arrow in (B) indicates the confluence of the two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

Modified from Knighton (1998).

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

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



1
2
3 **Figure 4-2. Time series of rainfall and streamflow observations in the Rio**
4 **Puerco and Rio Grande, 6–18 September 2003.**

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

6
7
8
9 Geomorphologic dispersion is the effect of different travel distances over the larger
10 spatial scale of entire river networks (Rodríguez-Iturbe and Valdes, 1979; Gupta et al., 1980;

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

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

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

28 Channel bed and bank permeability also governs the degree to which infiltration is an
29 important pathway between streams and groundwater aquifers. Fine bed and bank sediments
30 slow infiltration; in many semiarid and arid streams, bed sediments become finer in the
31 downstream direction because flow competence declines (Dunkerley, 1992). Because fine
32 sediments can become concentrated in channels following moderate flows, higher flows that
33 scour out fine sediments or submerge more permeable floodplains have higher infiltration rates
34 (Lange, 2005). In Walnut Gulch, Arizona, transmission losses over 54 km of channel resulted in
35 a 57% decrease in flow volume associated with a storm (Renard and Keppel, 1966). Tang et al.
36 (2001) used chemical and isotopic tracers to confirm that ephemeral streams are important areas

1 for floodwaters to recharge groundwater aquifers in desert regions, and infiltration losses
2 accounted for up to half of the flow volume along three ephemeral channels in the southwestern
3 United States (Constantz et al., 2002). Although transmission losses represent disruptions of
4 surface connectivity between streams and downstream waters, such losses are hydrologic
5 pathways that reduce downstream flooding and recharge groundwater aquifers that eventually
6 support springs and flow in downgradient streams and rivers (Izbicki, 2007).

8 **4.3.2. Sediment**

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

15 Sediment in headwater streams originates from adjacent hillslopes and enters these
16 streams via overland flow, bank erosion (Grimshaw and Lewin, 1980), and infrequent
17 disturbances such as landslides and debris flows (e.g., Benda and Dunne, 1987; Swanson et al.,
18 1998; Eaton et al., 2003). Sediment transported within river networks can be divided into two
19 major categories: suspended and bed load. Suspended sediment is fine sediment (clay, silt, and
20 fine sand) that requires slow velocities and little turbulence to remain entrained in the water
21 column; bedload sediment is coarser particles that slide, roll, and bounce along the streambed
22 during faster, more turbulent flows (Church, 2006; Wilcock et al., 2009).

23 The dynamic balance between sediment supply and transport capacity (Lane, 1955; Bull,
24 1991; Trimble, 2010)—with variables of sediment flux and sediment grain size on one side, and
25 discharge and channel slope on the other side—is a principal paradigm of fluvial
26 geomorphology. If one of these variables changes, a compensatory change occurs in at least one
27 of the other variables. For example, if discharge increases, a lower channel slope is needed to
28 transport the same amount of sediment of that grain size; alternatively, to move a load of fine
29 sediment, less discharge or lower channel slope is needed relative to the same load of coarse
30 sediment. Associated with this balance is the relationship between channel geometry (width and
31 depth) and discharge (Leopold and Maddock, 1953), and adjustments to maintain a dynamic
32 balance also can include channel dimensions. This balance is particularly relevant to
33 geomorphologic connectivity in river networks because these variables commonly differ between
34 streams and rivers (Ferguson et al., 2006; Ferguson and Hoey, 2008), with slope and grain size
35 decreasing and discharge and channel size increasing downstream (Church, 2002). Thus,
36 streams affect rivers through changing sediment supply or transport capacity at confluences.

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

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

11 Ephemeral desert streams can exhibit high sediment export efficiency. The amount of
12 bed load per unit stream power from an ephemeral Negev Desert stream was estimated to be
13 substantially higher than from a forested perennial stream (Laronne and Reid, 1993). Despite
14 infrequent flows with short durations, flood waves (bores) in ephemeral desert streams carry
15 substantial amounts of sediment downstream (Hassan, 1990). The transport distance associated
16 with these floods, however, often is insufficient to link them to perennial rivers. For example, a
17 reach-scale study in Walnut Gulch, Arizona estimated sand transport distances of only 401 and
18 734 m in two consecutive years marked by nine floods (Powell et al., 2007). Streams also can
19 store substantial amounts of sediment that are only released during rare export events. A series
20 of experimental sediment introductions (to mimic road surface sediment) into steep, ephemeral
21 second-order streams in southwestern Washington revealed that between 30 and 45% of the
22 sediment (ranging from clay to coarse sand) was exported to the mainstem, 95–125 m
23 downstream, during stormflows representing 66–69% of bank full discharge (Duncan et al.,
24 1987). Virtually all of the fine clay particles introduced were exported from the ephemeral
25 streams to the mainstem, presumably because this fraction remained suspended at even moderate
26 flows (Duncan et al., 1987). Streams in the Coastal Range of Oregon stored 23% of the sediment
27 within a 2.5-km² basin compared with only 9% within the mainstem channel (May and
28 Gresswell, 2003). A long-term sediment budget for the Coon Creek watershed (360 km²), a
29 stream to the Mississippi River in Wisconsin, was constructed over periods coinciding with
30 major land use changes (Trimble, 1999). Over a period when agricultural practices caused major
31 soil erosion (1853–1938), streams acted as net sources of sediment ($42 \times 10^3 \text{ Mg y}^{-1}$); after
32 erosion control, streambank stabilization, and revegetation (1975–1993), streams changed to net
33 sinks of sediment ($9 \times 10^3 \text{ Mg y}^{-1}$; Trimble, 1999).

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

1 (1987) determined that for a stream to create a discernible sediment or channel morphology
2 discontinuity along a mainstem river, the symmetry ratio needed to be at least 0.7. A similar
3 review of 168 confluences across the western United States and Canada found that a symmetry
4 ratio needs to be greater than 0.2 to affect a downstream river's sediment supply or transport
5 capacity (Benda, 2008). Suspended particulate matter (inorganic + organic) and bed particle size
6 were measured above and below eight confluences on the Acheron River in Australia to
7 determine stream contributions (Wallis et al., 2008; Wallis et al., 2009). Suspended particulate
8 matter downstream of confluences approximated the sum of mainstem and stream exports during
9 high flow, but stream contributions were negligible during low flows (Wallis et al., 2009). Four
10 of the eight confluences showed expected changes in bed particle size below confluences with
11 streams, and the bed particle sizes were similar in the mainstem and stream for the remaining
12 confluences so particle size change associated with streams was not discernible (Wallis et al.,
13 2008).

14 Streams, through their connections to rivers at confluences, can disrupt longitudinal
15 trends in discharge of water and sediment in rivers (Best, 1988; Benda et al., 2004; Ribeiro et al.,
16 2012). For example, dams often remove much of the sediment from transport, whereas most
17 streams are sediment sources. The objective of a study on the Agigawa River in Japan was to
18 examine contrasting disruptions associated with a dam (sediment removal) and a stream
19 confluence (sediment discharge) located downstream from the dam (Katano et al., 2009). The
20 stream contributions to the river reversed many of the dam-related changes to the river, including
21 restoring the turbidity level and the proportion of sand and gravel substrate in the river bed
22 (Katano et al., 2009).

23
24

25 **4.3.3. Wood**

26 Large woody debris (typically considered >10 cm diameter and >1 m long) has a strong
27 influence on hydrodynamics, sediment transport and storage, and channel morphology (e.g.,
28 Harmon et al., 1986; Nakamura and Swanson, 1993; Abbe and Montgomery, 1996; Naiman and
29 Decamps, 1997; Montgomery et al., 2003). More specifically, woody debris dissipates energy,
30 traps moving material, and forms habitat for aquatic plants and animals (Anderson and Sedell,
31 1979; Harmon et al., 1986; Abbe and Montgomery, 1996; Naiman and Decamps, 1997; Gurnell
32 et al., 2002). The debris can redirect water movements, create pools, and slow water movement
33 through a channel (Nakamura and Swanson, 1993; Abbe and Montgomery, 1996; Naiman and
34 Decamps, 1997). Wood recruitment to forested streams occurs as a result of chronic tree
35 mortality; episodic disturbances such as fire, debris flows, landslides, and windthrow; and bank
36 erosion. The steeper topography associated with hillslopes along many headwater streams

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1 increases the likelihood that trees will fall toward the channel (Sobota et al., 2006), relative to
2 streams in flatter terrain.

3 Wood tends to accumulate in, rather than be exported from, most forested headwater
4 streams, due to their low discharge and relatively small channel widths (Keller and Swanson,
5 1979; Bilby and Ward, 1989; Gurnell, 2003). For example, wood in a headwater stream in North
6 Carolina was determined to have entered the channel more than 60 years earlier (Wallace et al.,
7 2001) and more than a century earlier in some Pacific Northwest streams (Swanson et al., 1976;
8 Keller et al., 1981). Because of the large occurrence of wood and small size of streams, wood
9 has a stronger influence on hydrologic and geomorphic processes in headwater streams than in
10 most larger rivers (Bilby and Bisson, 1998). Large, infrequent disturbance events are the
11 primary drivers for wood movement in headwater streams (Benda and Cundy, 1990; Benda et
12 al., 2005; Bigelow et al., 2007). Reeves et al. (2003) determined that 65% of the wood pieces
13 and 46% of the wood volume in a fourth-order stream in the Coastal Range in Oregon were
14 delivered downstream by debris flows from headwater streams rather than the riparian zone
15 adjacent to the fourth-order channel. Using data from 131 reservoirs in Japan, investigators
16 identified a curvilinear relationship between watershed area and large woody debris export (Seo
17 et al., 2008), meaning that wood export per unit area increased from small streams (6–20 km²),
18 peaked at intermediate-sized streams (20–100 km²), and decreased from large streams
19 (100–2,370 km²). The amount of wood in low-gradient streams in the Midwest was determined
20 to be supply-limited mainly because human alteration depletes large wood sources and altered
21 hydrology and channel structure enhances transport of small wood downstream (Johnson et al.,
22 2006). Topography and topology also govern wood delivery from headwaters. Downstream
23 segments draining steep, finely dendritic networks will receive a greater proportion of wood
24 from headwater streams than networks that are low gradient and weakly dissected (Benda and
25 Cundy, 1990; Reeves et al., 2003).

26 Several studies have assessed the distribution of wood associated with confluences.
27 Wood volumes were measured upstream and downstream of 13 confluences (symmetry ratios
28 ranged from 0.05 to 0.49) in the Cascade Range of western Washington (Kiffney et al., 2006).
29 Wood volumes tended to peak at or immediately downstream from stream confluences (Kiffney
30 et al., 2006), suggesting that streams are either important sources of wood to mainstems or alter
31 channel form to enhance wood storage at confluences. Elevated wood density, however, was not
32 associated with confluences of eight streams to the Acheron River in Australia (Wallis et al.,
33 2009). The authors concluded that the study streams did not have sufficient capacity for
34 transporting wood to the mainstem, because streams had similar slope to the mainstem but lower
35 discharges (Wallis et al., 2009).

1 Large wood can shorten sediment transport and debris flow runout by entrainment
2 (Lancaster et al., 2003). Woody debris in 13 Coastal Range streams in Oregon had accumulation
3 rates ranging from 0.003 to 0.03 m³ m⁻¹ yr⁻¹, which were subsequently driven by time since the
4 last debris flow (May and Gresswell, 2003). The volume of instream wood was strongly related
5 to the volume of sediment stored. On average, 73% of stream sediment, prone to debris flow
6 transport, was stored behind instream wood (May and Gresswell, 2003). Wood (and associated
7 sediment) movement from headwater streams to downstream segments occurs through
8 infrequent, high-magnitude events (e.g., debris flows, fire). Once in larger streams, wood and
9 sediment can be stored in alluvial fans and floodplains between stormflows that trigger further
10 downstream movement through the network (Benda et al., 2005). Because of the long distances
11 and infrequent triggers associated with wood transport from most headwater streams to rivers,
12 the relevant periods for governing transport are decades to centuries (Benda et al., 1998). Wood
13 entering headwater streams can affect the downstream transport of water and materials in
14 headwater streams, but also can be transported downstream from headwater streams where it is
15 important habitat for aquatic life, a source of dissolved and particulate organic matter (POM),
16 and influential in controlling hydrodynamics and channel morphology of rivers.

17 18 **4.3.4. Temperature (Heat Energy)**

19 Connections between streams and downstream rivers can affect water temperature in
20 river networks (Knispel and Castella, 2003; Rice et al., 2008). Water temperature is an
21 important physical factor governing the distribution and growth of aquatic life, both directly
22 (through its effects on organisms) and indirectly (through its effects on other physicochemical
23 properties, such as dissolved oxygen and suspended sediments; Allan, 1995). The primary
24 factors governing water temperature in streams and rivers are climate (e.g., solar radiation, air
25 temperature), water source (e.g., groundwater, runoff, meltwater), channel characteristics (e.g.,
26 width, bed topography, hydraulic exchange), topography (e.g., aspect, upland shading, canopy
27 cover), and discharge (e.g., volume of water, turbulence; Poole and Berman, 2001; Caissie,
28 2006).

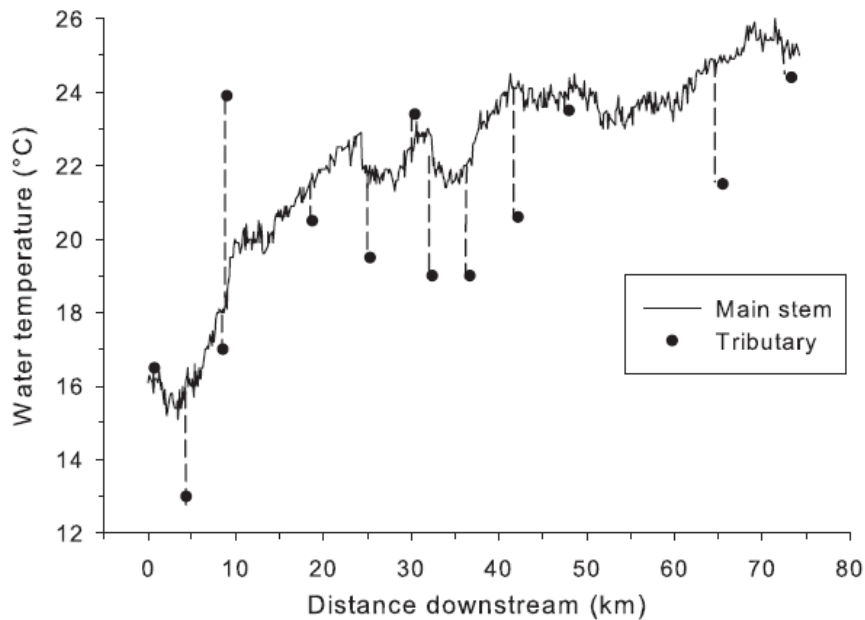
29 Perennial and intermittent streams that derive much of their flow from intermediate or
30 regional groundwater have water temperatures similar to groundwater. Groundwater
31 temperature is largely buffered from seasonal and short-term changes that affect air temperature,
32 so that in temperate climates, groundwater tends to be cooler than air temperature in summer but
33 warmer in winter. Streams deriving water from other sources (e.g., local groundwater, runoff, or
34 snowmelt) have water temperatures and associated fluctuations reflecting these sources.
35 Typically a nonlinear increase in mean daily water temperature occurs from headwaters to large
36 rivers, and a unimodal trend is observed in daily variation (i.e., daily maximum-minimum) of

1 water temperature (Caissie, 2006). Stable groundwater temperatures (in headwater streams) and
2 greater depth and volume of water (in large rivers) buffer water temperatures from the daily
3 changes typical in intermediate-sized streams. The steep increase in water temperature
4 immediately downstream of headwaters is associated with more rapid flux of heat into small
5 streams, as shallow water contacts the surrounding air and receives direct radiation (Caissie,
6 2006). This longitudinal pattern, however, does not hold for all river networks, because some
7 river networks receive substantial deep groundwater contributions at lower reaches. As water
8 moves from streams through stream networks, water temperature is influenced by heat exchange
9 associated with solar radiation and hyporheic exchange (mixing with groundwater). These
10 factors vary with geographic location. For instance, water in headwater streams draining steep,
11 forested regions will be buffered from solar radiation and move downstream rapidly, compared
12 to a headwater stream draining a low-gradient, prairie catchment where shading by riparian trees
13 is minimal (see Section 4.7.2).

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

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

1 differences of streams and the mainstem exceeded 1°C and streams had large symmetry ratios
2 (Cristea and Burges, 2009).
3



4
5
6 **Figure 4-3. Airborne thermal infrared remotely sensed water temperature in**
7 **the mainstem and at tributary confluences of the North Fork John Day**
8 **River, OR, on 4 August 1998.** Line indicates main stem, black dots indicate
9 tributary confluences, and dashed vertical lines indicate location of tributary
10 confluences along the mainstem.

11
12 Reprinted with permission from Torgersen et al. (2008).

13
14
15 In most cases, the effect of the stream on river water temperature was minor in relation to
16 longitudinal changes over the course of the river (Torgersen et al., 2001; Cristea and Burges,
17 2009). Despite having a relatively minor effect on temperature over the length of entire rivers,
18 however, streams provide constant cold-water habitats that are important for aquatic life (see
19 Section 4.5.2).

20 21 **4.4. CHEMICAL CONNECTIONS**

22 Chemical connections are linkages between headwater and other tributary streams to their
23 downstream waters based on the transport of chemical elements and compounds, such as
24 nutrients, dissolved and particulate organic matter, ions, and contaminants. Chemical
25 connectivity between streams and rivers involves the transformation, removal, and transport of

1 these substances; in turn, these processes influence water quality, sediment deposition, nutrient
2 availability, and biotic functions in rivers.

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

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

24 **4.4.1. Nutrients**

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

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

18 The underlying geology of the Mokelumne River in the central Sierra Nevada of
19 California affected the spatial and temporal variability in chemical connections. Holloway et al.
20 (1998) examined water quality in that watershed to identify primary sources of nitrate entering
21 downstream reservoirs. They conducted a paired watershed comparison with two ephemeral
22 streams in adjacent catchments, which were underlain with different rock types (diorite vs.
23 biotite schist) but had similar land use, vegetation, topography, and catchment area. Many
24 samples from the diorite watershed had nitrate concentrations below detection limits (<4 µM),
25 with a median concentration of 3.3 µM; concentrations were not strongly associated with the
26 start or end of the high precipitation period. In the biotite schist watershed, maximum stream
27 concentrations of nitrate (>300 µM) occurred at the start of the high precipitation period, and
28 concentrations decreased over time. An adjacent perennial stream, also in a biotite schist
29 watershed, displayed this same temporal trend, with highest nitrate concentrations at the
30 beginning of the rainy season and decreasing concentrations during the spring. By monitoring
31 the stream network in this watershed, Holloway et al. (1998) concluded that biotite schist streams
32 in watersheds having this geological source of nitrogen, contributed a disproportionately large
33 amount of total nitrate to downstream reservoirs despite draining only a small area of the entire
34 watershed.

35 Chemical connectivity throughout a river network also is dynamic due to environmental
36 and biological processes. Nitrate concentrations were measured at 50 sites across the West Fork

1 watershed of the Gallatin River in the northern Rocky Mountains of southwestern Montana
2 under different hydrologic conditions and across two seasons, growing or dormant (Gardner and
3 McGlynn, 2009). Streams ranged from first-order mountain streams to fourth-order streams near
4 the West Fork-Gallatin River confluence. In the dormant season, the distance over which nitrate
5 concentrations were spatially correlated ranged from 3.2 to 5.5 km. In the growing season, this
6 range decreased to 1.9–2.7 km. This seasonal difference could have resulted from greater
7 biological uptake and use of nitrate during the growing season, limiting its transport by
8 streamflow; when these processes were reduced during the dormant season, greater spatial
9 dependence in nitrate concentrations was detected among sites.

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

19 Peterson et al. (2001) examined chemical connectivity by studying similar network
20 components across different types of stream networks. After measuring nitrogen export from
21 12 headwater tributaries distributed throughout the contiguous United States, Alaska, and Puerto
22 Rico, they found that uptake and transformation of inorganic nitrogen were most rapid in the
23 smallest streams (Peterson et al., 2001). Given the prevalence of headwater streams on the
24 landscape (see Section 4.2) and their hydrologic connectivity to other network components (see
25 Sections 3.2 and 4.3.1), this level of nitrogen processing could improve the water quality in the
26 downstream receiving waters. Other studies also highlight the processing of nitrogen in
27 headwater streams (e.g., Hill et al., 1998; Hill and Lymburner, 1998; Triska et al., 2007).
28 Mulholland et al. (2008) measured in situ rates of nitrate removal by denitrification and used
29 those rates to model how small and large tributaries in a network respond to simulated increases
30 in nitrate loading. At low loading rates, the biotic removal of dissolved nitrogen from water is
31 high and occurs primarily in small tributaries, reducing the loading to larger tributaries and rivers
32 downstream. At moderate loading rates, the ability of small tributaries to remove nitrogen is
33 reduced, but downstream the larger tributaries can remove the excess nitrogen. At high loading
34 rates, removal by small and large tributaries in the network is ineffective, resulting in high
35 nitrogen export to rivers (Mulholland et al., 2008). Similar results were obtained by Wollheim et
36 al. (2008) in the Ipswich River, MA.

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

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

29 Measurement of total spiraling length requires detailed study of tracer dynamics through
30 multiple compartments of the stream ecosystem, but Newbold et al. (1981; 1983a) have shown
31 that it can be approximated by the “uptake length” or distance traveled in the water column
32 before microbial and algal assimilation occurs. Uptake lengths for phosphorus and nitrogen can
33 be estimated precisely only from tracer additions of radioactive or stable isotopes, but they can
34 be roughly estimated from experimental additions that briefly raise the concentration of the
35 natural form of the nutrient. Ensign and Doyle (2006) compiled results of 404 measurements of
36 uptake length of phosphate, ammonium, and nitrate in streams and rivers ranging from first to

1 fifth order. For a given stream order, they estimated the number of cycles that each nutrient had
2 undergone as the ratio of median uptake length to the average length of stream for that stream
3 order (from Leopold et al., 1964). They found roughly that the three nutrient forms cycle
4 between 8 (nitrate) and 40 (ammonium) times within the length of a first-order stream, and
5 between 8 and 90 times within the respective lengths of first- to fourth-order streams.

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

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

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

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

18

19 **4.4.2. Dissolved and Particulate Organic Matter**

20 Headwater streams supply downstream ecosystems with organic carbon in both dissolved
21 and particulate forms, which supports biological activity throughout the river network. Organic
22 carbon enters headwater streams from the surrounding landscape, including wetlands (see
23 Sections 5.3.2.4 and 5.4.3.1), in the form of terrestrial leaf litter and other seasonal inputs (e.g.,
24 catkins), dissolved organic carbon (DOC) in subsurface and surface runoff, and fine particulate
25 organic matter in surface runoff including eroded soil. Ågren et al. (2007) determined that small
26 headwaters exported the largest amount of terrestrial dissolved organic carbon on a per unit basis
27 in the Krycklan watershed in Sweden. Organic carbon is also produced within the stream by
28 photosynthesis. These inputs were first documented and quantified by Fisher and Likens (1973)
29 for a forested headwater stream in New Hampshire. Fisher and Likens (1973) followed the fate
30 of these inputs, concluding that 34% of the inputs were mineralized through respiration by
31 consumers and microbes within the reach; this was the “ecosystem efficiency” of the reach. The
32 remaining 66% was exported downstream constituting, as Fisher and Likens observed, “...
33 inputs to the next stream section where they are assimilated, or passed on (throughput) or both.”
34 Vannote et al. (1980) recognized that the exported carbon was not simply the unutilized fraction
35 but was also greatly modified in character. They proposed, as one of the basic tenets of their
36 River Continuum Concept, that longitudinal variations in the structure of stream ecosystems

1 reflect, in part, the cumulative effects of upstream organic matter processing. Here we focus on
2 a subset of the large body of literature on organic matter dynamics in streams and rivers, citing
3 basic evidence that headwaters modify and export organic carbon that significantly affects
4 downstream ecosystem processes throughout the river network.

5 Most organic matter inputs (66%) to a headwater stream in New Hampshire were
6 exported (Fisher and Likens, 1973), which is comparable to results from other studies. Webster
7 and Meyer (1997) compiled organic matter budgets from 13 North American first- and second-
8 order streams. The median ecosystem efficiency was 31%, implying a median export of 69% of
9 inputs. Much or most of the organic carbon exported from headwater streams has been altered
10 either physically or chemically by ecosystem processes within the headwater reaches. Leaf litter
11 contributes an average of 50% of the organic matter inputs to forested headwater streams
12 (Benfield, 1997), but leaves and leaf fragments (>1 mm) only account for 2% or less of organic
13 matter exports (Naiman and Sedell, 1979; Wallace et al., 1982; Minshall et al., 1983). The
14 conversion of whole leaves to fine particles (<1 mm) involves physical abrasion, microbial
15 decomposition, and invertebrate feeding and egestion (Kaushik and Hynes, 1971; Cummins et
16 al., 1973; Petersen and Cummins, 1974). The rate of that conversion is affected by whether the
17 leaves are in an aerobic environment, such as riffles, or an anaerobic environment, such as
18 depositional pools (Cummins et al., 1980). Aquatic invertebrates that feed on leaves that have
19 entered streams are called shredders (Cummins and Klug, 1979; Cummins et al., 1989).
20 Invertebrate activity is particularly important, as demonstrated by large reductions of fine
21 particle export that followed experimental removal of invertebrates from a headwater stream
22 (Cuffney et al., 1990; Wallace et al., 1991). Strong invertebrate influence on fine particle export
23 also has been inferred from analysis of seasonal (Webster, 1983) and daily (Richardson et al.,
24 2009) variations. Headwater reaches also export organic carbon produced within the stream by
25 photosynthesis, both as dissolved organic carbon (Kaplan and Bott, 1982) and suspended
26 particles (Marker and Gunn, 1977; Lamberti and Resh, 1987).

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

34 The organic carbon turnover length, derived from the spiraling concept (Newbold et al.,
35 1982a; see Section 4.4.1), is a measure of the downstream fate of exported carbon. Carbon
36 turnover length is computed as the ratio of the downstream flux of organic carbon to ecosystem

1 respiration per length of stream. It approximates the average distance that organic carbon is
2 expected to travel before being consumed and mineralized by aquatic biota. Carbon turnover
3 length for first-order streams is on the order of 1–10 km (Newbold et al., 1982a; Minshall et al.,
4 1983), suggesting that organic carbon exported from small streams is likely to be used primarily
5 in the somewhat larger streams of which they are direct tributaries (i.e., second- or third-order
6 streams). The carbon turnover length, however, actually represents a weighted average of widely
7 varying turnover lengths associated with the diverse array of particulate and dissolved forms of
8 organic carbon in stream and river ecosystems (Newbold, 1992). Turnover lengths of specific
9 forms can be estimated if their rates of downstream transport and mineralization (or assimilation)
10 are known. For example, Webster et al. (1999) estimated a turnover length of 108 m for whole
11 leaves in a North Carolina second-order stream whereas the estimate for fine (<1 mm) organic
12 particles was far longer at 40 km. Newbold et al. (2005) obtained similar estimates of 38 and
13 59 km for the turnover lengths of two different size fractions of fine organic particles in a
14 second-order Idaho stream. Similarly, Kaplan et al. (2008) concluded that dissolved organic
15 carbon in a third-order stream in southeastern Pennsylvania consisted of a rapidly assimilated
16 “labile” fraction with a turnover length of 240 m, a more slowly assimilated “semilabile” fraction
17 with a turnover length of 4,500 m, and a “refractory” fraction with immeasurably slow
18 assimilation, implying an indefinitely long turnover length sufficient, at least, to carry the carbon
19 to coastal waters.

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

29 Although turnover length reflects the spatial scale over which upstream exports of
30 organic carbon are likely to support downstream metabolism, it does not provide direct evidence
31 for or quantify the actual use of organic carbon in the downstream reaches. Such evidence,
32 however, is provided by studies of transport and mass balance throughout the river network.
33 Shih et al. (2010) applied the SPARROW model to organic carbon (C) data from
34 1,125 monitoring sites throughout the conterminous United States. They estimated that all river
35 reaches (large and small) delivered an annual average of 72 kg C ha⁻¹ of incremental drainage
36 area, whereas the river systems as a whole exported 30 kg C ha⁻¹. Thus, 58% of the carbon

1 inputs were respired within the river networks, while the rest (42%) were transported
2 downstream. Shih et al. (2010) did not specify the proportion of inputs originating from
3 headwater streams but using their results with some assumptions, we can get a rough estimate
4 that river networks receive approximately a third of their organic carbon from headwater
5 streams. We begin with the proportion of carbon originating from allochthonous sources being
6 0.78 (Shih et al., 2010). If we assume that the proportion of headwater streams in a drainage area
7 is 0.50 (see Section 4.2; Alexander et al., 2007; Caruso and Haynes, 2011). Headwater streams
8 then provide 0.39 ($= 0.78 \times 0.50$) of the total organic carbon supply, with the input from the
9 larger downstream network being 0.61 (i.e., 61%) of the carbon supply. Using the ecosystem
10 efficiency for headwater streams of 31% (Webster and Meyer, 1997), we calculate that the
11 proportion of carbon originating in headwater stream that is delivered downstream is
12 $0.39 \times (1 - 0.31) = 0.27$. The proportion of carbon exported from headwater streams (0.27), plus
13 the proportion of carbon input directly to the downstream network (0.61), equals the carbon input
14 to the downstream network of 0.88. Thus, 0.31 ($= 0.27/0.88 = 31\%$) of the total carbon supplied
15 to downstream reaches originates from headwater streams.

16 Most terrestrial organic matter that enters headwater tributaries is transported
17 downstream (Gomi et al., 2002; MacDonald and Coe, 2007), typically as fine particulate or
18 dissolved organic matter (Bilby and Likens, 1980; Naiman, 1982; Wallace et al., 1995; Kiffney
19 et al., 2000). These small streams also can export significant amounts of autochthonous organic
20 matter via the downstream transport of benthic algae (Swanson and Bachmann, 1976). Both
21 allochthonous and autochthonous organic matter can be transported significant distances
22 downstream (Webster et al., 1999), especially during high flows (Bormann and Likens, 1979;
23 Naiman, 1982; Wallace et al., 1995). For example, Wallace et al. (1995) examined coarse
24 particulate organic matter export in three headwater streams in North Carolina and found that
25 63–77% of export over a 9-year period occurred during the 20 largest floods. This finding
26 suggests that headwater tributaries (including ephemeral and intermittent streams) can provide
27 temporary storage for organic matter (Gomi et al., 2002), which is then transported downstream
28 during storms or snowmelt. Exports also can vary seasonally, increasing in autumn and winter
29 when deciduous trees drop their leaves (Wipfli et al., 2007) and in the spring when flowers and
30 catkins are shed.

31 The amount of organic matter exported from headwater tributaries can be large, and often
32 depends on factors such as abiotic retention mechanisms within the channel (Bilby and Likens,
33 1980), biotic communities (Cuffney et al., 1990), and the quality and quantity of riparian
34 vegetation in headwater catchments (Wipfli and Musslewhite, 2004). For example, Wipfli and
35 Gregovich (2002) found that organic matter export ranged from <1 to 286 g of detritus (dead
36 organic matter) per stream per day in 52 small coastal streams in Alaska. When debris dams

1 were removed from a small stream in New Hampshire, export of fine particulate organic carbon
2 increased by 632% (Bilby and Likens, 1980); this finding illustrates the interdependence of
3 physical and biological connections within the river network.

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

18 **4.4.3. Ions**

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

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

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

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

4 **4.4.4. Contaminants**

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

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

24 In a broader study, Wang et al. (2007) investigated spatial patterns in major cation and
25 anion concentrations related to coalbed methane development in the Powder River basin
26 (33,785 km²) in Wyoming and Montana, using retrospective USGS data (1946–2002). The
27 study indicated that coalbed methane development could have detrimental effects on the Powder
28 River, especially concerning sodium adsorption ratio (sodicity). Although the authors indicated
29 connectivity and adverse affects in stream quality with increased sodium and stream sodicity,
30 data also revealed inconsistent patterns associated with complex spatial variability within the
31 basin (due to the geographic distribution of the coalbed methane wells). In addition, the use of
32 annual medians rather than monthly medians from the entire data set likely smoothed seasonal
33 variation inherent in the data.

34 The spatial extent of metal transport was shown in a study of the upper Arkansas River in
35 Colorado, where the headwaters have been affected by past mining activities (Kimball et al.,
36 1995). Bed sediments sampled from the headwaters to approximately 250 km downstream

1 showed an inverse relationship between sediment concentrations of cadmium, lead, and zinc and
2 downstream distance. That same spatial distribution pattern in metals in bed sediments from
3 headwaters to downstream was observed for the Clark Fork River in Montana, which has been
4 impacted by mining and smelting activities in its headwaters (Axtmann and Luoma, 1991).
5 Based on regression models, metal concentrations in bed sediments from river sites were
6 inversely related to distance downstream, and predictions from those models indicated that
7 sediments with metals originating from the mining and smelting areas in the headwaters were
8 reaching Lake Pend Oreille, more than 550 km downstream. Hornberger et al. (2009) used a
9 19-year data set on sediments from the Clark Fork River with sites spanning from the
10 headwaters to 190 km downstream and found that copper concentrations in bed sediments at
11 downstream sites were positively correlated with concentrations at upstream sites.

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

29 An additional example of intermittent streams contributing highly mineralized, acidic
30 waters to a perennial tributary occurs in a study that characterized acid mine drainage impacts on
31 water and sediment chemistry (particularly major cations, silica, sulfate, selected heavy metals,
32 and acidity) in Lynx Creek, a small intermittent stream in east-central Arizona (Lampkin and
33 Sommerfeld, 1986). Six stations, two above and four below an abandoned copper mine, were
34 monitored (water and sediment samples) monthly for 1 year. Specific conductance, pH, and
35 dissolved ion concentrations varied with proximity to the mining complex. Concentrations of
36 most constituents were higher near the mine and progressively decreased downstream toward the

1 terminus of Lynx Creek due to precipitation and dilution by tributary streams. All heavy metals
2 and sulfate had significantly higher levels at the immediate discharge location versus the
3 above-mine stations; sulfate concentrations downstream of mine-drainage inputs also
4 significantly differed from the rest of the creek. Sediments throughout the creek were high in
5 metals, suggesting downstream transport of contaminated sediments. Acid-mine drainage from
6 the mine had a major but mostly localized impact on Lynx Creek. Evidence of connectivity was
7 apparent, with noticeable increases in dissolved metals, major cations, and sulfate and a
8 three-unit depression in pH.

9 Studies of the distribution, transport, and storage of radionuclides (e.g., plutonium,
10 thorium, uranium) have provided convincing evidence for distant chemical connectivity in river
11 networks because the natural occurrence of radionuclides is extremely rare. The production, use,
12 and release of radionuclides, however, have been monitored for military and energy production
13 for more than 50 years. Like metals, radionuclides adsorb readily to fine sediment; therefore, the
14 fate and transport of radionuclides in sediment generally mirrors that of fine sediment. From
15 1942 to 1952, prior to the full understanding of the risks of radionuclides to human health and
16 the environment, plutonium dissolved in acid was discharged untreated into several intermittent
17 headwater streams that flow into the Rio Grande at the Los Alamos National Laboratory, NM
18 (Graf, 1994; Reneau et al., 2004). These intermittent headwaters drain into Los Alamos Canyon,
19 which has a 152 km² drainage area and joins the Rio Grande approximately 160 km upriver from
20 Albuquerque. Also during this time, nuclear weapons testing occurred west of the upper Rio
21 Grande near Socorro, NM (Trinity blast site) and in Nevada. The San Juan Mountains in the
22 northwestern portion of the upper Rio Grande basin (farther upstream from the site where Los
23 Alamos Canyon enters the Rio Grande) are the first mountain range greater than 300 m in
24 elevation east of these test locations. The mountains therefore have higher plutonium
25 concentrations than the latitudinal and global averages because of their geographic proximity to
26 the test sites. The mountain areas are steep with thin soils, so erosion and subsequent overland
27 movement of plutonium from the testing fallout readily transported it to headwater streams in the
28 upper Rio Grande basin. The distribution of plutonium within the Rio Grande illustrates how
29 headwater streams transport and store contaminated sediment that has entered the basin through
30 fallout and from direct discharge. Los Alamos Canyon, while only representing 0.4% of the
31 drainage area at its confluence with the Rio Grande, had a mean annual bedload contribution of
32 plutonium almost seven times that of the mainstem (Graf, 1994). Much of the bedload
33 contribution occurred sporadically during intense storms that were out of phase with flooding on
34 the upper Rio Grande. Total estimated contributions of plutonium between the two sources to
35 the Rio Grande are approximately 90% from fallout to the landscape and 10% from direct
36 effluent at Los Alamos National Laboratory (Graf, 1994). Based on plutonium budget

1 calculations, only about 10% of the plutonium directly discharged into Los Alamos Canyon and
2 less than 2% of the fallout over the upper Rio Grande basin have been exported to the Rio
3 Grande. Much of the plutonium is adsorbed to sediment and soil that has either not yet been
4 transported to the river network or is stored on floodplains or in tributary channels (Graf, 1994).
5 Approximately 50% of the plutonium that entered the Rio Grande from 1948–1985 is stored in
6 the river and its floodplain; the remaining amount is stored in a downriver reservoir.

8 **4.5. BIOLOGICAL CONNECTIONS**

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

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

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

30 **4.5.1. Invertebrates**

31 Headwater streams provide habitat for diverse and abundant stream invertebrates (Meyer
32 et al., 2007) and serve as collection areas for terrestrial and riparian invertebrates that fall into
33 them (Edwards and Huryn, 1995; Kawaguchi and Nakano, 2001). These aquatic and terrestrial
34 invertebrates can be transported downstream with water flow and ultimately serve as food
35 resources for downstream biota. Many fish feed on drifting insects (Nakano and Murakami,

1 2001; Wipfli and Gregovich, 2002), and these organisms can also settle out of the water column
2 and become part of the local invertebrate assemblage in downstream waters. However, drift has
3 been shown to significantly increase invertebrate mortality (Wilzbach and Cummins, 1989),
4 suggesting that most drifting organisms are exported downstream in the suspended detrital load
5 (see Section 4.3.2).

6 The downstream drift of stream invertebrates (Müller, 1982; Brittain and Eikeland, 1988)
7 and the contribution of terrestrial and riparian invertebrates to overall drift (Edwards and Huryn,
8 1995; Kawaguchi and Nakano, 2001; Eberle and Stanford, 2010) have been well documented.
9 For example, drift estimates in 52 small coastal streams in Alaska ranged from 5 to
10 6,000 individuals per stream per day (Wipfli and Gregovich, 2002). The amount of invertebrate
11 drift often is closely related to stream discharge (e.g., Harvey et al., 2006) and diel invertebrate
12 behavioral patterns that are independent of flow (Rader, 1997). To compensate for loss of
13 individuals to downstream drift, invertebrate populations in headwater streams are maintained
14 and replenished by a combination of high productivity and upstream dispersal (Hershey et al.,
15 1993; Humphries and Ruxton, 2002).

16 As with organic matter, assessing the effect of headwater invertebrate production and
17 export on downstream waters is difficult. Wipfli and Gregovich (2002) estimated that drifting
18 insects and detritus (i.e., particulate organic matter; see Section 4.4.2) from fishless headwater
19 tributaries in Alaska supported between 100 and 2,000 young-of-year salmonids per km in a
20 large, salmon-bearing stream. This estimate of headwater importance in systems where juvenile
21 salmonids move into headwater tributaries to feed and grow is likely conservative (see Section
22 4.5.2). Other studies have shown increased fish growth with increased invertebrate drift
23 (Wilzbach et al., 1986; Nielsen, 1992; Rosenfeld and Raeburn, 2009), indicating that drift does
24 provide a valuable food resource, especially when food is limiting (Boss and Richardson, 2002).

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

1 et al. (2004) found that native amphipods can persist in intermittent reaches but are replaced by
2 nonnative amphipods in perennial reaches.

4 **4.5.2. Fishes**

5 Although some fish species maintain resident headwater populations, many species move
6 into and out of headwater streams at some point in their life cycles (Ebersole et al., 2006; Meyer
7 et al., 2007). Some fish species occur only in small streams, which contribute to regional aquatic
8 biodiversity (e.g., Paller, 1994). However, as with invertebrates, certain fish species can be
9 found throughout a range of stream sizes (Freeman et al., 2007) and flow durations (Schlosser,
10 1987; Labbe and Fausch, 2000), and the fish species found in headwater streams often are a
11 subset of species found in downstream habitats (Horwitz, 1978). Use of headwater streams as
12 habitat is especially obvious for the many diadromous species that migrate between small
13 streams and marine environments during their life cycles (e.g., Pacific and Atlantic salmon,
14 American eels, certain lamprey species), and the presence of these species within river networks
15 provides robust evidence of biological connections between headwaters and larger rivers. Return
16 migration of diadromous fishes provides a feedback loop in which marine-derived nutrients are
17 transported upstream to headwaters, for subsequent processing and export (see Section 4.4.1).
18 Even nonmigratory taxa, however, can travel substantial distances within the river networks
19 (Gorman, 1986; Sheldon, 1988; Hitt and Angermeier, 2008).

20 Hydrologic connectivity must exist for the exchange of fish between upstream and
21 downstream reaches. Fish assemblages tend to be more similar among connected streams, in that
22 assemblages in reaches located more closely together tend to have more species in common than
23 in distantly separated reaches (Matthews and Robinson, 1998; Hitt et al., 2003; Grenouillet et al.,
24 2004). Measures of river network structure also can explain fish assemblage structure, with
25 studies showing that metrics such as link magnitude (the sum of all first-order streams draining
26 into a given stream segment) and confluence link (the number of confluences downstream of a
27 given stream segment) are significant predictors (e.g., Osborne and Wiley, 1992; Smith and
28 Kraft, 2005).

29 For certain taxa, headwater tributaries provide habitat for a specific part of their life
30 cycle. Many salmonids spawn in small streams, including those with intermittent flow (Erman
31 and Hawthorne, 1976; Schrank and Rahel, 2004; Ebersole et al., 2006; Wigington et al., 2006;
32 Colvin et al., 2009); many nonsalmonids also move into these habitats to spawn (Meyer et al.,
33 2007). After spawning, these fish sometimes return downstream for feeding and overwintering.
34 For example, Bonneville cutthroat trout moved from less than 1 km to more than 80 km
35 downstream postspawning, typically within 30 days (Schrank and Rahel, 2004).

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

7 In prairie streams (see Section 4.7), the importance of hydrologic connectivity is
8 especially evident, as many fishes broadcast spawn, or release eggs into the water column, which
9 then develop as they are transported downstream (Cross and Moss, 1987; Fausch and Bestgen,
10 1997); adult fish then migrate upstream prior to egg release (Fausch and Bestgen, 1997). Thus,
11 these fishes require hydrologic connectivity for egg development and upstream migration of
12 adult fish, to maintain populations (Fausch and Bestgen, 1997).

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

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

28 Headwater tributaries also can provide refuge from flow extremes. Fish can move into
29 headwaters (including intermittent streams) to avoid high flows downstream (Wigington et al.,
30 2006); fish also can move downstream during peak flows (Sedell et al., 1990), demonstrating the
31 bidirectionality of biological connections within these systems. Low flows can cause adverse
32 conditions for biota, as well, and residual pools, often fed by hyporheic flow, can enable
33 organisms to survive dry periods within intermittent streams (Pires et al., 1999; May and Lee,
34 2004; Wigington et al., 2006).

35 Biotic conditions within the river network—the taxa found in the system—also can create
36 an adverse environment, as the presence of invasive species or other predators and competitors

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

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

17

18 **4.5.3. Genes**

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

27 Although physical barriers can protect headwater habitats and populations by isolating
28 them from colonization and hybridization with invasive species (see Section 4.5.2), isolation also
29 can have serious adverse effects on native species via reductions in genetic connectivity. For
30 example, Hanfling and Weetman (2006) found that man-made weirs intensified natural patterns
31 of limited headwater immigration, such that headwater (above-barrier) sculpin populations
32 diverged genetically from downstream (below-barrier) populations and lost significant amounts
33 of genetic diversity. This pattern of strong genetic divergence accompanied by loss of headwater
34 genetic diversity above natural and man-made barriers has been documented in multiple fish
35 species and regions (Yamamoto et al., 2004; Wofford et al., 2005; Deiner et al., 2007; Guy et al.,
36 2008; Gomez-Uchida et al., 2009; Whiteley et al., 2010). Loss of headwater-river genetic

1 connectivity might be exerting selection pressure against migrant forms in fish with life cycles
2 requiring movement along the entire river corridor (Morita and Yamamoto, 2002). Ultimately,
3 tradeoffs exist between the risks associated with headwater-river genetic connectivity (e.g.,
4 hybridization with nonnative species and hatchery fish) and those associated with genetic
5 isolation (e.g., reduced reproductive fitness, increased risk of local extinction, deterioration of
6 overall genetic variation, and selection against migratory traits; Fausch et al., 2009).

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

12 Computer simulation approaches examine the spatial and temporal processes of genetic
13 connectivity for realistic behaviors and life histories of species inhabiting complex, dynamic
14 landscapes and riverscapes (Epperson et al., 2010). For example, Morrissey and de Kerckhove
15 (2009) demonstrated that downstream-biased dispersal in dendritic river networks (which by
16 definition have more tributaries than mainstems) can promote higher levels of genetic diversity
17 than other geographical habitat structures. Under these conditions, low-dispersing headwater
18 stream populations can act as reservoirs of unique genetic alleles (units of genetic variation) that
19 occasionally flow into and mix with highly dispersing downstream populations. Although the
20 number of headwater streams (i.e., potentially unique genetic reservoirs) is important in
21 maintaining genetic diversity, networks with more complex hierarchical structures (see
22 Figure 4-4) are more efficient at maintaining genetic diversity than networks in which all
23 tributaries flow directly into the mainstem (Morrissey and de Kerckhove, 2009). In another
24 simulation, Chaput-Bardy et al. (2009) demonstrated that out-of-network gene flow (e.g.,
25 terrestrial dispersal by insects or amphibians) or very high levels of within-network gene flow
26 (e.g., fish that move and reproduce throughout the network) can counteract the effects of network
27 structure; thus, individual species behavior can profoundly affect observed genetic patterns.

28 Most empirical evidence for the role of headwaters in maintaining genetic connectivity
29 and diversity comes from studies of economically important fish species, but correlations of river
30 network structure or landscape alteration with genetic patterns have been reported for other
31 species. Consistent with the model of Morrissey and de Kerckhove (2009), Fer and Hroudova
32 (2008) found higher genetic diversity in downstream populations of yellow pond-lily (*Nuphar*
33 *lutea*), which disperses over long distances via water-mediated dispersal of detached rhizomes.
34 Frequent dispersal and high gene flow among headwater and downstream populations of the
35 giant Idaho salamander (*Dicamptodon aterrimus*; Mullen et al., 2010) are expected to contribute
36 to genetic diversity of upstream and downstream populations.

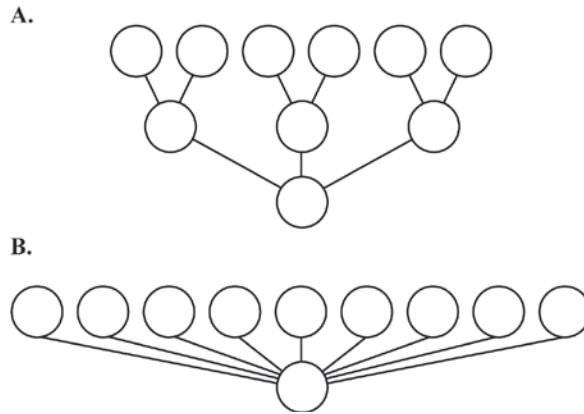


Figure 4-4. (A) A dendritic network with multilevel hierarchical structure, and (B) a uninodal network with all headwater streams feeding directly into a river mainstem.

Modified from Morrissey and de Kerckhove (2009).

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

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

4.6. STREAMS: SYNTHESIS AND IMPLICATIONS

A substantial body of evidence unequivocally demonstrates connectivity between streams and downstream rivers via both structural and functional connectivity (as defined in Wainwright et al., 2011). Streams are structurally connected to rivers through the network of continuous channels (beds and banks) that make these systems physically contiguous, and the very existence of a continuous bed and bank structure provides strong geomorphologic evidence for connectivity (see Section 3.2.1). A stream must be linked to a larger, downstream water body by

1 a channel in order for the two to have surface water (hydrological) connection. While there are
2 streams that lack a channel connection to larger water bodies (i.e., small endorheic basins), these
3 are the exception. Streams that link larger water bodies through networks of continuous bed and
4 bank are the rule. Streams are functionally connected to rivers by the movement of water and
5 other materials through this network of channels. Even losing-stream reaches that at times lack
6 sufficient flow for hydrological connection can still influence downstream waters by functioning
7 as sinks for water and materials carried by water. The river network and its flow of materials
8 represent the integration of its streams' cumulative contributions to downstream waters.

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

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

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

Source Function
<ul style="list-style-type: none">Streams supply water downstream through baseflow and floods that influence discharge and habitat (4.3.1, 4.7.2.5, 4.7.3.1.1, 4.8.4.2, 4.8.5.1).
<ul style="list-style-type: none">Streams supply downstream waters with sediment (4.3.2, 4.4.4, 4.7.3.1.3, 4.8.4.2).
<ul style="list-style-type: none">Streams supply downstream waters with nutrients and other ions (4.4.1, 4.4.3, 4.7.4.2.1, 4.8.4.2).
<ul style="list-style-type: none">Streams can transport to downstream waters contaminants that adversely affect organisms (4.4.4, 4.7.3.1.3).
<ul style="list-style-type: none">Streams supply dissolved and particulate organic matter that can fuel heterotrophy in downstream waters and influence physicochemical conditions (4.3.3, 4.4.2, 4.7.3.2.2, 4.8.4.2).
<ul style="list-style-type: none">Organisms actively and passively move from streams to downstream waters (4.5, 4.7.2.4, 4.7.3.3).
Sink Function
<ul style="list-style-type: none">Streams can divert surface flow from downstream waters via infiltration into underlying alluvium and evapotranspiration to the atmosphere (4.3.1, 4.8.3, 4.8.4.2, 4.8.5.1).
<ul style="list-style-type: none">Streams can divert nitrate from downstream waters via denitrification (4.4.1, 4.7.3.2.1)
<ul style="list-style-type: none">Streams can divert sediment and associated contaminants from being transported to downstream waters through deposition on floodplains (4.3.2, 4.4.4).
Refuge Function
<ul style="list-style-type: none">Streams can offer protection from temperature extremes, drying, predators, and competition with nonnative species for organisms that inhabit downstream waters (4.5, 4.7.3.3).
Transformation Function
<ul style="list-style-type: none">Streams mediate the form of nutrients before entering downstream waters via nutrient spiraling (4.4.1, 4.7.3.2.1)
<ul style="list-style-type: none">Streams mediate the form of organic matter before entering downstream waters via carbon spiraling (4.4.2, 4.7.3.2.2)

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

Lag Function
<ul style="list-style-type: none"> Streams can delay water from arriving at downstream waters through local and network structures, thus reducing flood magnitudes, but increasing baseflows in downstream waters (4.3.1, 4.3.3, 4.7.3.1.1, 4.8.3, 4.8.4.2).
<ul style="list-style-type: none"> Streams can delay sediment from arriving at downstream waters through local and network structures (4.3.3, 4.3.2, 4.4.4).
<ul style="list-style-type: none"> Streams can delay nutrients from arriving at downstream waters through local and network structures and biological uptake (4.4.1, 4.7.2.4, 4.7.3.2.1).
<ul style="list-style-type: none"> Streams can delay organic matter from arriving at downstream waters through local and network structures and biological uptake (4.3.3, 4.4.2, 4.7.3.2.2).

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3 **4.7. CASE STUDY: PRAIRIE STREAMS**

4 **4.7.1. Abstract**

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

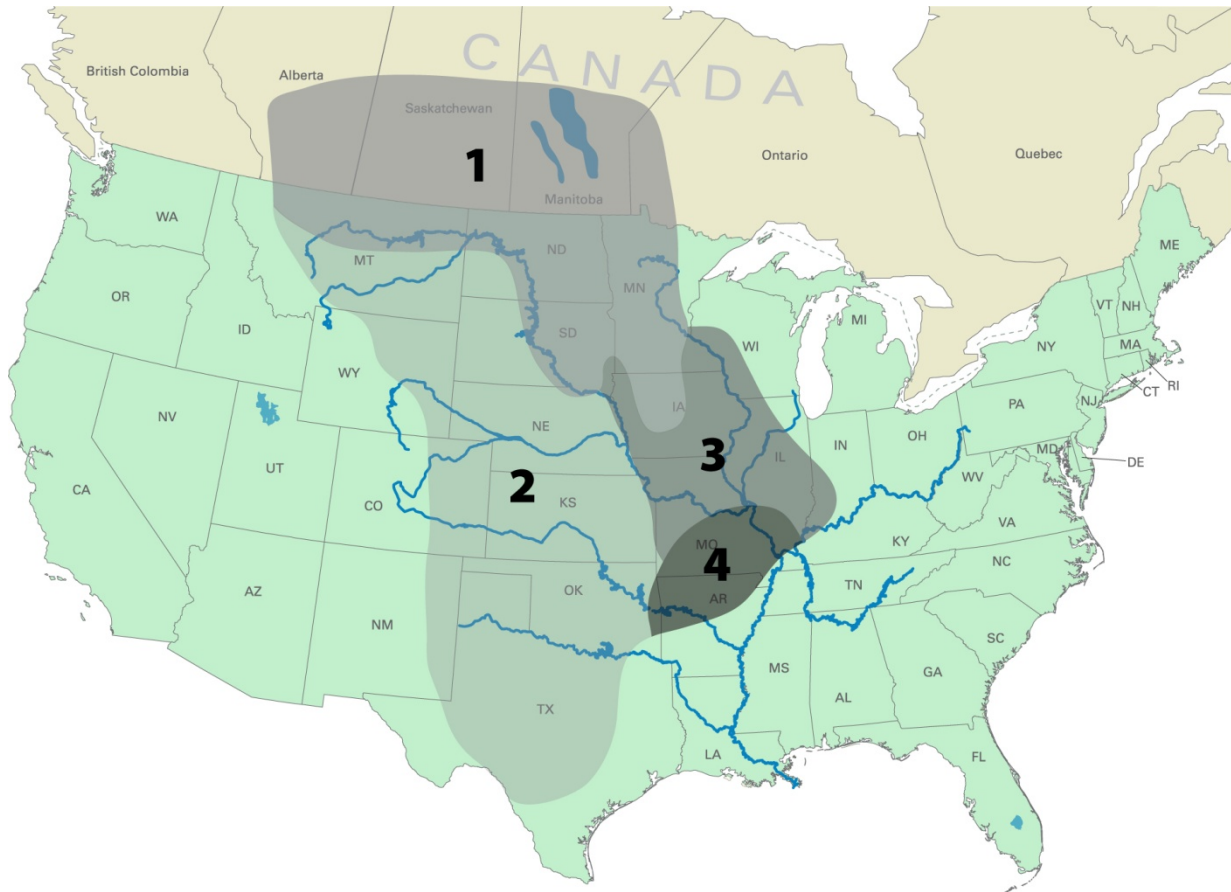
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13 **4.7.2. Introduction**

14 **4.7.2.1. Geography and Climate**

15 Prairies are temperate grasslands located in the Great Plains physiographic region of the
16 central United States and Canada (see Figure 4-5). Grasses and forbs (broad-leaf plants other
17 than grasses) dominate the region, particularly in upland areas. Shrubs and trees can be found in
18 lowlands, and are commonly called gallery forests. Native prairie ecosystems once covered
19 approximately 1.62 million km² in North America but have been almost completely lost since
20 European settlement, mainly replaced by row-crop agriculture (Samson and Knopf, 1994).
21 Because of drastic alterations to much of the historical eastern plains (Iowa, Illinois, Missouri,

1 Indiana, and Minnesota), our discussion centers principally on river networks in the high plains
2 subregion of the Great Plains (see Subregion 2 in Figure 4-5), where drier climate and thin, rocky
3 soil have limited row-crop agriculture.
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8 **Figure 4-5. Map of the United States showing physiographic subregions and**
9 **major rivers of the Great Plains. (1) Glaciated prairie; (2) high plains; (3)**
10 **eastern plains; and (4) Ozark Plateau.**

11 Modified from Covich et al. (1997).
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15 Prairies generally can be characterized by their relatively low topographic relief, although
16 areas such as the Flint Hills in eastern Kansas, the Arikaree Breaks in northwestern Kansas, and
17 the Arbuckle Mountains in south-central Oklahoma have relatively steep terrain compared to that
18 of western Kansas or the Oklahoma panhandle (Osterkamp and Costa, 1987; Matthews, 1988).
19 The underlying geology consists of extensive limestone deposits, but other areas are
20 characterized by sandstone and shale deposits or unconsolidated sands, silts, and clays (Brown
21 and Matthews, 1995). Soils in the Great Plains are predominately loess, but some areas such as

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

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

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

23 24 **4.7.2.2. Hydrology and Geomorphology**

25 The hydrology of most prairie river networks is highly variable (Matthews, 1988; Brown
26 and Matthews, 1995; Dodds et al., 2004). These systems are frequently subjected to the
27 extremes of drying and flooding, and intermittent or flashy hydrology is prevalent in river
28 networks throughout most of the Great Plains (Matthews, 1988; Zale et al., 1989; Poff, 1996;
29 Dodds et al., 2004). The topology of most prairie river networks is dendritic due to the relatively
30 flat landscape and uniform geology (Brown and Matthews, 1995). Prairie river networks tend to
31 have high drainage density (see Section 3.4.2), and are therefore efficient at transferring rainfall
32 from uplands to downstream reaches (Gregory, 1976; Osterkamp and Friedman, 2000). Flood
33 magnitudes tend to be higher in the semiarid Great Plains than in other regions, despite
34 comparable rainfall intensities, due to low infiltration and vegetation interception (Osterkamp
35 and Friedman, 2000). Although floods tend to occur in late fall through late spring, they can
36 occur any time during the year (Brown and Matthews, 1995; Poff, 1996). Like most river

1 networks, those draining prairie landscapes often contain ephemeral, intermittent, and perennial
2 streams. Although many headwater prairie streams are ephemeral or intermittent (Matthews,
3 1988; Brown and Matthews, 1995; Dodds et al., 2004), some have perennial spring-fed reaches
4 located at the network origins or distributed between intermittent reaches along headwater
5 streams (Matthews et al., 1985; Sawin et al., 1999; Dodds et al., 2004; Bergey et al., 2008).

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

13 The High Plains (Ogallala) aquifer system and other aquifers (e.g., Edwards-Trinity) are
14 important hydrologic features interconnected with Great Plains river networks. The High Plains
15 aquifer system is the largest (450,658 km²) and most intensively pumped U.S. aquifer,
16 underlying much of the Great Plains from southern South Dakota and southeastern Wyoming to
17 central Texas (Sophocleous, 2005; Ashworth, 2006; Sophocleous, 2010). The High Plains
18 aquifer is composed of blanket sand and gravel derived mainly from alluvial deposits and ancient
19 marine sands. It is unconfined regionally, but locally can be confined where beds of silt, clay, or
20 marl are present. Regional movement of water through the aquifer is from west to east, but
21 locally the water moves toward major tributaries. Northern areas of the Great Plain are underlain
22 by glacial deposit aquifers that can be a mixture of till (unsorted material ranging from clay to
23 boulders) and outwash (stratified sand and gravel) that was deposited by glacial meltwater.

24 Most headwater streams originating in the prairie have riffle-pool morphology with
25 alluvial gravel; only headwater streams originating in the western mountains have high gradient,
26 cobble-boulder channels (Brown and Matthews, 1995). Southern prairie headwater streams tend
27 to have finer substrate than those in the northern and central Great Plains (Brown and Matthews,
28 1995). Larger streams tend to have broad sand beds that are frequently braided (but see
29 Section 4.7.2.5). In contrast to headwater streams in forested regions, the riparian areas of
30 prairie headwater streams typically lack overhanging trees. Grasses and shrubs are the dominant
31 riparian vegetation, so channels lack woody debris and are generally well lit. Because of intense
32 flooding, prairie streams tend to form wide, deep channels relative to their drainage areas,
33 regardless of flow permanence (Hedman and Osterkamp, 1982; Brown and Matthews, 1995).
34 Because of similarity in topography, climate, geology, and soils, stream geomorphology across
35 the Great Plains is largely comparable (Miller and Onesti, 1988). High plains channels,
36 however, tend to be slightly steeper in gradient and more sinuous than wider and deeper channels

1 of the eastern plains (Miller and Onesti, 1988). During floods, the relatively incised channels
2 and lack of woody debris in prairie headwater streams make them less retentive of organic matter
3 and other materials than those of high-gradient forested channels; their pool-riffle morphology,
4 high sinuosity, and seasonal drying, however, can enhance retention (Brown and Matthews,
5 1995).

7 **4.7.2.3. Physicochemistry**

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

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

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

1 4.7.2.4. Ecology

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

11 Algae are foundational components of prairie streams, acting to retain nutrients and
12 provide an important energy source to consumers (Gelwick and Matthews, 1997; Dodds et al.,
13 2000; Evans-White et al., 2001; Evans-White et al., 2003). Flooding and drying in prairie
14 streams reset algal assemblages, spur successional sequences, and maintain high levels of
15 primary production (Power and Stewart, 1987; Dodds et al., 1996b; Murdock et al., 2010). Algal
16 assemblages are composed primarily of diatoms (e.g., *Cymbella*, *Cocconeis*, *Pinnularia*,
17 *Achnanthes*, *Navicula*, and *Gomphonema*), filamentous green algae (e.g., *Cladophora*,
18 *Spirogyra*, *Rhizoclonium*, *Stigeoclonium*, *Zygnema*, and *Oedogonium*), and cyanobacteria (e.g.,
19 *Oscillatoria*, *Nostoc*).

20 Because of high light availability, algal primary production in prairie streams can at times
21 be substantially higher than in forested headwaters (Hill and Gardner, 1987a; Dodds et al.,
22 1996b; Mulholland et al., 2001; Bernot et al., 2010). Gallery forests farther downstream provide
23 shade and contribute organic matter. Shade from the gallery forests lowers light transmission to
24 algae, resulting in lower algal primary production in these reaches than in unshaded prairie
25 headwater reaches. Thus, in contrast to conventional longitudinal paradigms like the River
26 Continuum Concept, the organic matter driving prairie headwater streams is derived mainly from
27 within the channel (autochthonous production), whereas leaf litter and other detritus from
28 adjacent gallery forests (allochthonous production) dominate in intermediate-sized streams
29 (Gurtz et al., 1982; Gurtz et al., 1988; Wiley et al., 1990). Despite having greater primary
30 production than forested headwaters, prairie streams, like forested ones, tend to also be net
31 heterotrophic systems (Mulholland et al., 2001), but those influenced by agricultural activities
32 (e.g., elevated nutrients, channelization) may at times be net autotrophic (Prophet and Ransom,
33 1974; Gelroth and Marzolf, 1978; Wiley et al., 1990).

34 Invertebrates in prairie streams are represented by various aquatic insect groups (e.g.,
35 Diptera, Coleoptera, Plecoptera, Ephemeroptera, Trichoptera), crustaceans (crayfish, isopods,
36 amphipods), mollusks, and oligochaetes. Consumers of fine benthic organic matter, epilithic

1 algae, and other invertebrates tend to dominate invertebrate communities (Gray and Johnson,
2 1988; Harris et al., 1999; Stagliano and Whiles, 2002). Diversity and abundance of invertebrates
3 tend to increase with flow permanence, but there is generally high overlap in species
4 composition, with intermittent stream assemblages representing a nested subset of those from
5 perennial streams (McCoy and Hales, 1974; Miller and Golladay, 1996; Fritz and Dodds, 2002).

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

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

19 Longitudinal organization of fish assemblages has been widely recognized in Great
20 Plains river networks (e.g., Harrell et al., 1967; Smith and Powell, 1971; Schlosser, 1987), and
21 like macroinvertebrates these assemblages often are nested such that intermittent headwater
22 communities are subsets of those in downstream perennial segments. Unlike algae and
23 macroinvertebrates, fish inhabiting intermittent headwater streams do not have terrestrial or
24 drying-resistant life stages. Fish, however, are highly mobile and avoid desiccation by moving
25 into downstream perennial reaches or perennial spring-fed pools in upstream segments (Deacon,
26 1961; Fausch and Bramblett, 1991). Periodic floods are important for creating perennial refugia
27 and providing connectivity between habitats for the dispersal of fish and their eggs in prairie
28 stream networks (see Section 4.7.3.3; Labbe and Fausch, 2000; Franssen et al., 2006).

30 **4.7.2.5. Human Alterations**

31 Human alterations to prairie river networks have affected physical, chemical, and
32 biological connectivity in these systems both directly and indirectly. Crop and livestock
33 agriculture are predominant land uses in the Great Plains (Galat et al., 2005; Matthews et al.,
34 2005) and represent major nonpoint sources of nutrients, sediment, and pesticides (Battaglin et
35 al., 2003; US EPA, 2006; Alexander et al., 2008). Livestock concentrate in and near streams for

1 shade, food, and water, leading to bank erosion, increased soil bulk density, sedimentation, and
2 elevated fecal bacteria concentrations (Armour et al., 1991; Strand and Merritt, 1999).

3 To support these agricultural enterprises, water has been diverted from channels, mined
4 from regional aquifers, and stored in reservoirs. Groundwater withdrawals in the Great Plains
5 are the highest in the United States (Sophocleous, 2010), causing many once perennial river
6 segments to regularly dry out completely during summer months, particularly in the drier
7 western portions of the Great Plains (Cross and Moss, 1987; Ferrington, 1993; Falke et al.,
8 2011). Nearly all river networks in prairie regions have been altered by impoundments for
9 irrigation storage and flood control, from small farm ponds in headwaters to large reservoirs on
10 river mainstems (Smith et al., 2002; Galat et al., 2005; Matthews et al., 2005). Decline in flood
11 magnitude, altered flow timing, and reduced flow variability and turbidity are evident in many
12 prairie rivers compared to historically documented conditions (e.g., Cross and Moss, 1987;
13 Hadley et al., 1987; Galat and Lipkin, 2000). Reductions in peak discharge derived from prairie
14 streams have contributed to the narrowing of the region's once broad and shallow river channels
15 (e.g., Friedman et al., 1998; Wohl et al., 2009). Dynamic mosaics of sand bars common in most
16 prairie rivers have become stabilized and coalesced islands. The establishment of trees along
17 prairie river riparian zones was limited by floods prior to settlement, but now dense zones of
18 native and invasive trees and shrubs further reduce flows through high evapotranspiration
19 (Johnson, 1994; Dahm et al., 2002).

21 **4.7.3. Evidence**

22 **4.7.3.1. *Physical Connections***

23 **4.7.3.1.1. *Water***

24 As in other river systems, water is the primary medium by which materials are
25 transported from streams to rivers in prairie networks. Floods are common in Great Plains
26 streams (e.g., Fausch and Bramblett, 1991; Hill et al., 1992; Fritz and Dodds, 2005), and
27 propagation of these floods from streams to downstream rivers demonstrates hydrologic
28 connectivity. Fritz and Dodds (2004, 2005) characterized the hydrology of intermittent streams
29 draining native tallgrass prairie in a study that coincided with the highest flow on record (on May
30 13, 1995, with a return interval of at least 50 years). Kings Creek and one of its headwater
31 streams (N01B) are both headwater streams draining into the Kansas River, downstream of the
32 USGS gaging station at Fort Riley and upstream from the confluence of the Big Blue and Kansas
33 Rivers and the USGS gaging station at Wamego (see Figure 4-6). The peak flow rising and
34 descending limbs were very rapid at Kings Creek and N01B compared to those recorded for the
35 Kansas River at Wamego, where the peak arrived approximately 12 hours later (see Figure 4-7).

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

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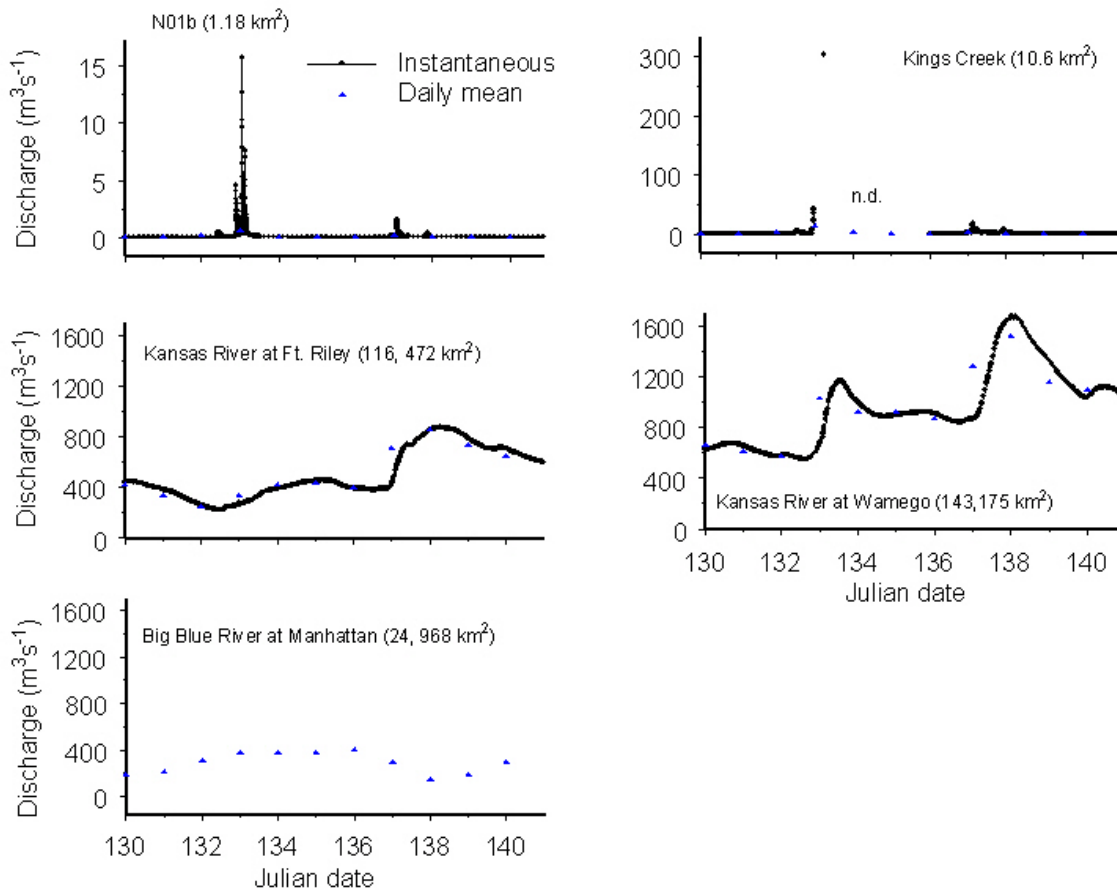
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11 **Figure 4-6. Map showing the location of Kings Creek and N01B, intermittent**
12 **tributaries to the Kansas River.**

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15 A flood occurring June 14–20, 1965 on the Platte River (Colorado and Nebraska) is
16 among the largest U.S. floods in recorded history, with a recurrence interval of 900 to
17 1,600 years (Matthai, 1969). This flood originated from runoff of intense rainfall (360 mm in
18 4 hours) over headwater portions of the drainage south of Denver, CO. Normal annual
19 precipitation for this area is approximately 400 mm. Flows in Plum Creek, one of the
20 intermittent headwater streams to the Platte River that received the heaviest rains, rose from
21 $<5 \text{ m}^3 \text{ s}^{-1}$ to $4,360 \text{ m}^3 \text{ s}^{-1}$ in only 40 minutes. Under the Federal Flood Control Act of 1944,
22 detention impoundments were extensively constructed on headwater streams in the Great Plains
23 to retard flooding in downstream rivers (Schoof et al., 1978; Van Haveren, 1986). Headwater
24 impoundments reduced runoff to the Washita River in Oklahoma by 36%, but channel dredging

This document is a draft for review purposes only and does not constitute Agency policy.



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

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

15 Machavaram et al. (2006) examined hydrologic connectivity between intermittent prairie
16 streams, a headwater pond, and a perennial stream reach approximately 10 km downstream using
17 chemical and isotopic tracers in a southeastern Kansas system. They found that, following
18 precipitation, 20% of downstream water originated from the upstream pond, which was fed by
19 ephemeral and intermittent streams; elevated oxygen stable isotope tracer associated with the

1 pond water took 26–31 hours to reach the downstream site (Machavaram et al., 2006). Streams
2 connected to lakes and wetlands contributed proportionally more flow to a southeastern
3 Minnesota river in summer, when other water sources were minimal, than in spring (Lenhart et
4 al., 2010). Flow from these streams has a delayed or lagged release because of storage in lakes
5 and wetlands, and stream flow backed up because of high mainstem flows (Lenhart et al., 2010).

7 **4.7.3.1.2. *Temperature (heat energy)***

8 Water temperatures represent a substantial stress to biotic communities in Great Plains
9 rivers (see Section 4.7.3.3). Rivers to the north experience cold winters, and those to the south
10 and west experience hot summers. Streams, particularly those strongly connected to more stable
11 groundwater, can provide thermal refugia for avoiding temporary hypothermic and hyperthermic
12 stress (see Section 4.7.3.3.2). Wide, shallow channels with little overhead canopy can result in
13 high water temperatures under summer low flows. Over a 1-km reach of the South Canadian
14 River in Oklahoma, summer (August 18–19, 1976) maximum mainstem water temperatures
15 were 36–37°C, with cooler water (32–35°C) in backwater pools and a tributary stream
16 (Matthews and Zimmerman, 1990). Mean water temperatures of seven streams immediately
17 upstream from confluences with the Missouri River (at the Kansas-Missouri border) did not
18 differ from water temperatures in the mainstem river, 200–300 m downstream of the
19 confluences, except during March when streams were warmer than the river (Braaten and Guy,
20 1999). Mean water temperature was determined to be homogeneous with no relationship
21 between drainage area and water temperature across two agriculturally dominated drainages in
22 Illinois, where most flow was derived from surface and shallow subsurface runoff (agricultural
23 tiles) rather than deeper groundwater (Wiley et al., 1990).

25 **4.7.3.1.3. *Sediment***

26 Great Plains rivers are naturally turbid (Jewell, 1927; Cross and Moss, 1987; Huntzinger,
27 1995), with suspended sediment derived from the fine soils through which these river networks
28 flow. Turbidity and suspended sediment concentration increase in prairie networks with
29 increasing discharge and drainage area (Hill and Gardner, 1987b; Wiley et al., 1990; Lenhart et
30 al., 2010), and can vary seasonally (Lenhart et al., 2010). Seasonal turbidity levels at tributary
31 mouths and adjacent mainstem reaches, however, were not related across seven Missouri River
32 confluences in Kansas and Missouri (Braaten and Guy, 1999), suggesting that these streams did
33 not influence river turbidity at baseflow conditions. In contrast to other studies in the prairie
34 region, no relationship was found between suspended particle concentration and stream size
35 among 22 sites ranging in land use and network position (second- to eighth-order) in the Kansas

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

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

14 15 **4.7.3.2. *Chemical Connections***

16 **4.7.3.2.1. *Nutrients and other chemicals***

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

22 Small prairie streams also can be important in preventing downstream nutrient transport.
23 Studies conducted in Kings Creek, a stream draining a 1,060-ha tallgrass prairie catchment in
24 Kansas, indicate that small prairie streams are highly nitrogen retentive (Tate, 1990; Dodds et al.,
25 1996a; Dodds et al., 2000). For example, Dodds et al. (1996a) found that nitrogen transport
26 through four second- and third-order streams in the Kings Creek watershed ranged from 0.01 to
27 6.0% of the total nitrogen supplied by precipitation, the balance being retained by the stream
28 system. Similar patterns of nutrient retention have been demonstrated at larger spatial scales, as
29 well. Alexander (2000; 2008) modeled the contribution of different-sized streams and rivers
30 (including prairie streams) to nutrient loading in the Gulf of Mexico. They found that large
31 rivers deliver more of their nitrogen and phosphorus loads to the Gulf of Mexico than small
32 streams (Alexander et al., 2008), largely due to increased instream nutrient uptake and removal
33 by small streams (Alexander et al., 2000). Despite their relative retentiveness, however, small
34 streams do make substantial contributions to downstream nutrient loading due to their large
35 numbers, with small to mid-sized streams in the western regions of the Mississippi River basin

1 (which includes the Great Plains) delivering approximately 25–50% of their nitrogen loads to the
2 Gulf (Alexander et al., 2008).

3 Correlations between water quality and upstream land use also indicate that prairie stream
4 headwaters affect downstream reaches. Dodds and Oakes (2006, 2008) examined relationships
5 between water quality and watershed land use at different spatial scales, along one fifth-order
6 prairie stream network (2006) and across 68 small prairie streams (2008) in eastern Kansas. In
7 the single drainage study, they found that concentrations of total nitrogen and nitrate were
8 significantly related to riparian cover in the 2 km upstream of sampling sites, even when
9 controlled for catchment land cover at each site (Dodds and Oakes, 2006). In the cross-drainage
10 study, riparian cover along first-order streams was more closely correlated with total nitrogen,
11 nitrate, ammonium, total phosphorus, atrazine, dissolved oxygen, and fecal coliform
12 concentrations than riparian cover 2 or 4 km immediately upstream of sites across the
13 68 drainages (Dodds and Oakes, 2008). Nutrients are elevated in most prairie streams and rivers
14 and nutrient concentrations in these systems are related to nonpoint land uses (Dodds and Oakes,
15 2004). These, along with widespread nature of headwater streams in river networks, are highly
16 indicative that streams have strong chemical connection, functioning as important links between
17 the surrounding lands to downstream waters.

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

31 **4.7.3.2.2. *Dissolved and particulate organic matter***

32 Differences in DOC inputs along the prairie stream longitudinal gradient provide further
33 indirect evidence of chemical connections between prairie stream headwaters and downstream
34 reaches. McArthur et al. (1985b) isolated bacteria from stream sediments of grassland reaches
35 and gallery forest reaches of a prairie stream and exposed them to leachates derived from grasses
36 and bur oak (a common gallery forest species). Grassland bacteria only grew when provided

1 with grass leachates as a carbon source, whereas gallery forest bacteria grew when provided with
2 either grass or bur oak leachates. This finding suggests that either (1) grass-derived DOC-
3 consuming bacteria are transported downstream and then coexist with bacteria consuming forest-
4 derived DOC, or (2) grass-derived DOC is transported downstream, and local bacterial
5 communities have adapted to use more refractory DOC exported from upstream reaches
6 (McArthur et al., 1985b).

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

20 Stagliano and Whiles (2002) found that the standing stock of FPOM in a perennial reach
21 of a tallgrass prairie stream was insufficient to support the annual secondary production (i.e., the
22 rate of heterotrophic biomass formation) of collector-gatherers (Cummins and Klug, 1979), the
23 dominant group of macroinvertebrates feeding on deposited FPOM. The replenishment of
24 FPOM standing stocks, at least in part from upstream sources via algal senescence, the transport
25 and settlement of suspended POM, and the breakdown and transport of coarse POM, likely
26 accounted for this apparent imbalance: turnover of FPOM standing stocks was estimated to occur
27 every 20 days (Stagliano and Whiles, 2002). Whiting et al. (2011) examined organic matter
28 dynamics and trophic structure along a tallgrass prairie stream network (first- to fifth-order).
29 They found that collector-filterers (macroinvertebrates that feed upon suspended POM;
30 Cummins and Klug, 1979) in upstream reaches consumed <1% of suspended POM flux;
31 gatherers that feed upon fine and very fine POM dominated secondary production in downstream
32 reaches; and predators in downstream forested reaches consumed 107% of locally derived
33 macroinvertebrate production. Predators in the upstream and middle reaches consumed 65% and
34 74% of available macroinvertebrate production, respectively. These findings support the idea
35 that downstream secondary production depends in part on the export of energy sources (i.e.,
36 particulate organic matter and invertebrates) from upstream reaches.

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

16 Coarse particulate organic matter can connect prairie stream headwaters to downstream
17 reaches. Johnson and Covich (1997) examined detrital inputs along a second- to fifth-order
18 prairie stream network in Oklahoma. They found that leaves in the stream originated from
19 farther upstream than expected, with the percentage of whole leaves at a site best explained by
20 riparian forest cover in reaches 500 and 1,000 m upstream. The percentage of leaf fragments
21 >1 mm was best explained by downstream distance along the stream network (Johnson and
22 Covich, 1997), suggesting increased processing and fragmentation of leaves as they move down
23 the longitudinal gradient.

24 25 **4.7.3.3. *Biological Connections***

26 **4.7.3.3.1. *Invertebrates***

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

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

1 stretch of Kings Creek in Kansas. They found that initial recovery of invertebrate taxa richness
2 in intermittent reaches, and taxa richness of invertebrate drift and aerially colonizing insects,
3 were negatively related to distance from upstream perennial water (Fritz and Dodds, 2002,
4 2004). Distance from upstream refugia, however, was not a significant predictor of invertebrate
5 diversity measures across annual time scales (Fritz and Dodds, 2005); they speculated that
6 movement of water along the entire stream network (i.e., maintenance of hydrologic
7 connectivity) makes proximity to colonists less important over longer time scales. These
8 findings suggest that recovery from disturbance in these systems depends on biological
9 connectivity via both downstream drift of colonizers and downstream (and potentially upstream)
10 movement of aerially dispersing, egg-depositing adults (Miller and Golladay, 1996; Dodds et al.,
11 2004).

12

13 **4.7.3.3.2. Fishes**

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

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

33 This pelagic-spawning reproductive strategy also necessitates upstream movement by
34 adult fish, if populations are to be maintained in small prairie streams (Fausch and Bestgen,
35 1997; Durham and Wilde, 2008). Prairie stream fishes generally are highly vagile, with adults
36 capable of long-distance migrations. For example, individuals of one species of prairie fish

1 (*Hybognathus placitus*) in the South Canadian River, NM were observed to move approximately
2 250 m upstream over a 15-minute period, illustrating that prairie fishes can move substantial
3 distances over relatively short periods (Fausch and Bestgen, 1997).

4 The effect that impoundment of prairie streams and rivers has had on the region's native
5 fish assemblages highlights the importance of hydrologic connectivity in these systems. Many
6 studies have documented statistically significant associations between impoundment of prairie
7 streams and loss of native fishes (e.g., Winston et al., 1991; Luttrell et al., 1999; Schrank et al.,
8 2001; Falke and Gido, 2006; Matthews and Marsh-Matthews, 2007). For example, Schrank et
9 al. (2001) found that, across 26 streams in the Flint Hills region of Kansas, sites from which
10 Topeka shiners (*Notropis topeka*) had been extirpated had significantly more small
11 impoundments on them and higher largemouth bass (*Micropterus salmoides*) catch-per-unit-
12 effort than sites at which the shiners were extant. Fewer studies have specifically examined the
13 mechanisms by which impoundments affect these changes, although impoundments likely
14 disrupt both the downstream transport of developing eggs and larvae (Platania and Altenbach,
15 1998) and the upstream and downstream movement of adult fish.

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

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

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

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

7 **4.7.4. Prairie Streams: Synthesis and Implications**

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

- 15
16
17 • Studies have demonstrated significant physical, chemical, and biological connections
18 from prairie headwater streams to larger rivers, despite extensive alteration of
19 historical prairie regions by agriculture, water impoundment, water withdrawals, and
20 other human activities (Matthews and Robinson, 1998; Dodds et al., 2004), and the
21 challenges these alterations create for assessing connectivity.
- 22 • The most compelling evidence for connectivity along prairie river networks comes
23 from examples of streams as sources of water via flood propagation (e.g., Matthai,
24 1969; Fritz and Dodds, 2004, 2005), sources of contaminated sediment transport
25 (Horowitz et al., 1988; Marron, 1989), sites of nutrient lags and transformation (e.g.,
26 Dodds et al., 1996a; Alexander et al., 2008), the downstream transport of prairie fish
27 eggs and larvae (e.g., Platania and Altenbach, 1998; Perkins and Gido, 2011), and
28 refugia for prairie fishes (e.g., Fausch and Bestgen, 1997; Franssen et al., 2006).
- 29 • Impoundments for irrigation storage and flood control have altered flood magnitude,
30 altered flow timing, and reduced flow variability and turbidity across the prairie
31 regions (e.g., Cross and Moss, 1987; Hadley et al., 1987; Galat and Lipkin, 2000).
32 The effect that impoundment of prairie streams and rivers has had on the regions'
33 native fish assemblages highlights the importance of hydrologic connectivity in these
34 systems. Maintenance of fish populations often depends on dispersal out of
35 intermittent reaches before drying occurs and recolonization of these habitats once
36 water flow resumes—both of which require hydrologic connectivity along the stream
37 network—and many fishes also require different habitats during different life stages
38 (Labbe and Fausch, 2000; Falke et al., 2010).
- 39

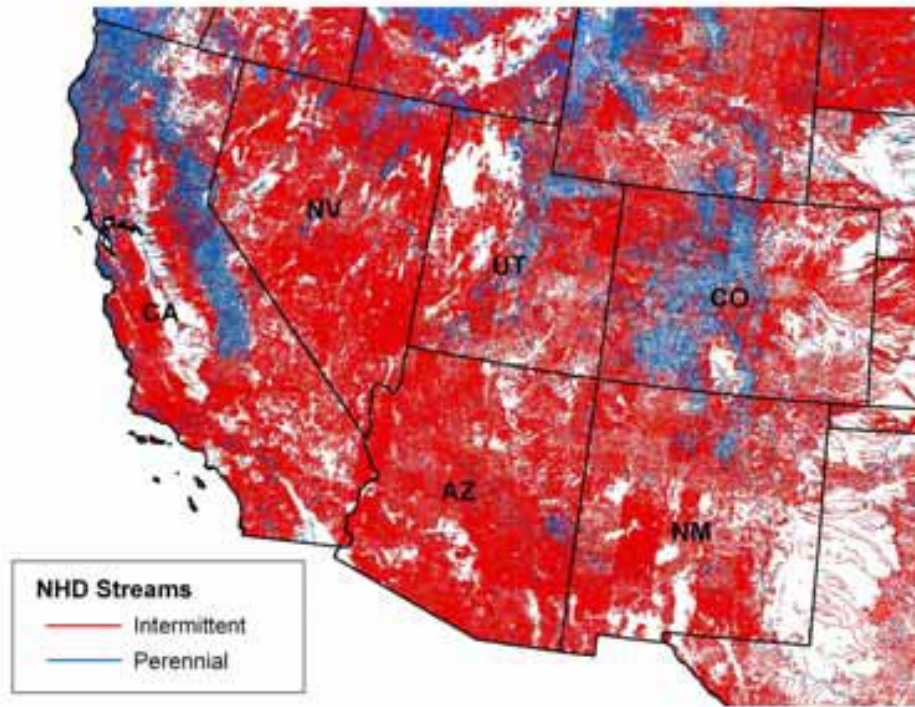
1 **4.8. CASE STUDY: SOUTHWESTERN INTERMITTENT AND EPHEMERAL**
2 **STREAMS**

3 **4.8.1. Abstract**

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

24
25 **4.8.2. Introduction**

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



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2
3 **Figure 4-8. Geographic distribution of intermittent (includes ephemeral) and**
4 **perennial streams in the southwestern states, illustrated using the National**
5 **Hydrography Dataset (NHD) stream map (<http://nhd.usgs.gov/>).** Note that
6 the NHD may not accurately reflect the total extent of ephemeral or intermittent
7 streams, as it does not include stream segments less than one mile in length,
8 combines intermittent and ephemeral streams, and is based on 1:100,000 scale
9 topographic maps.

10
11
12 **4.8.3. Southwestern Rivers**

13 Understanding the unique characteristics of southwestern American rivers is necessary to
14 evaluate the influence of ephemeral and intermittent streams on these rivers (Levick et al., 2008).
15 Southwestern rivers differ in many ways from rivers in the humid eastern United States or in the
16 Midwest and West. Southwestern rivers typically can be divided into two main parts,
17 particularly in the basin and range geologic province. One part comprises rivers in the
18 mountainous upper basins that receive higher precipitation, often as snow, and the second part
19 comprises those rivers located in arid or semiarid plateau regions and plains dominated by
20 ephemeral streams (Blinn and Poff, 2005). For example, more than 80% of the Gila River
21 corridor in New Mexico and Arizona meanders through desert scrublands. Precipitation is
22 seasonal. In summer, precipitation is strongly influenced by atmospheric moisture flowing from
23 the Gulf of Mexico and the Gulf of California (Mexican monsoon), where local heating triggers
24 high-intensity air-mass thunderstorms (summer monsoon). In fall, tropical depressions, often

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1 remnants of hurricanes, can bring infrequent but long-duration rainfall events; such storms are
2 responsible for many of the larger floods in the region (Webb and Betancourt, 1992). Cyclonic
3 storms from the Pacific Ocean, resulting in large frontal systems, dominate winter precipitation
4 in the form of snow in higher elevations and typically as low-intensity rainfall in lower
5 elevations (Blinn and Poff, 2005). Figure 4-9 illustrates the 2003 calendar year hydrograph from
6 the White River near the Fort Apache USGS gaging station (upper) in east central Arizona, and
7 the San Pedro River near Tombstone, in southeast Arizona (lower). Although the two gaging
8 stations differ in elevation by less than 200 m, the watershed contributing to the White River is
9 substantially larger and higher in elevation than the San Pedro watershed, resulting in
10 long-duration spring runoff from snowmelt. Monsoon-generated, short-duration runoff
11 dominates the San Pedro watershed but monsoonal influence also is apparent in the White River
12 hydrograph. Runoff generated from late monsoon precipitation in September caused a major
13 increase in discharge in the White River and a minor increase in the San Pedro. Most perennial
14 and intermittent rivers in the Southwest are groundwater-dependent, flowing primarily in a
15 baseflow regime and supported by discharge from a connected regional and/or alluvial aquifer.
16 As discussed in more detail below, part of baseflow also is sustained or augmented by slow
17 drainage of a shallow alluvial aquifer from past flooding. In arid and semiarid regions, the
18 riparian areas that perennial and intermittent streams support occupy a small percentage of the
19 overall landscape but they harbor disproportionately greater percentage of the biodiversity than
20 the areas surrounding them (Goodrich et al., 2000; Stromberg et al., 2005). Reservoir
21 construction, irrigation withdrawals, and groundwater pumping have converted many historical,
22 perennially flowing reaches into intermittently flowing reaches (Blinn and Poff, 2005).

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

36

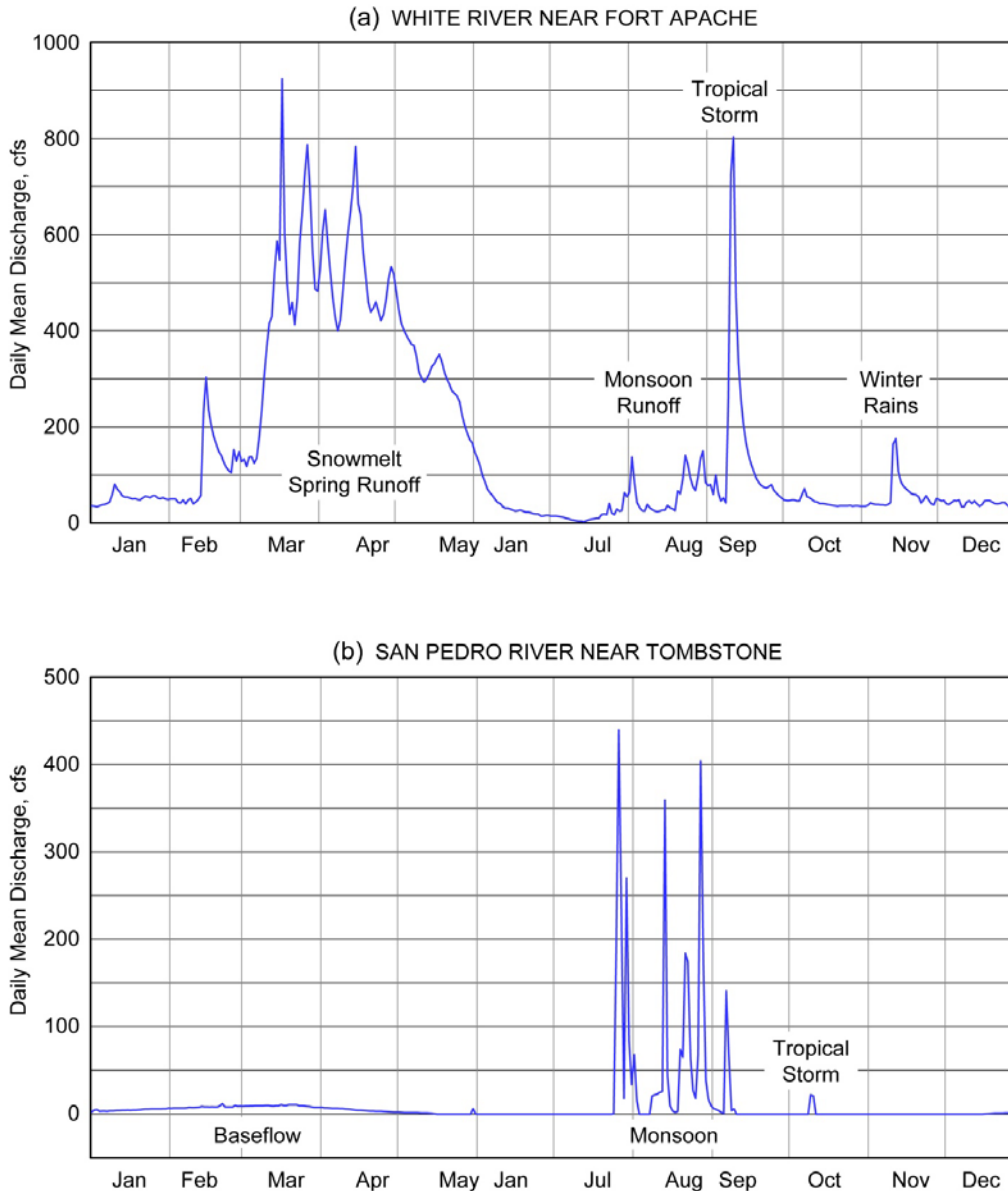


Figure 4-9. 2003 calendar year hydrographs from (a) the White River near Fort Apache, Arizona and (b) the San Pedro River near Tombstone, AZ.

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Mountains with deeper soils or those consisting of fractured rock will have higher infiltration capacities, less frequent occurrences of overland flow, and serve as recharge areas for regional groundwater (Wilson and Guan, 2004; Blasch and Bryson, 2007; Wahi et al., 2008). Mountains with shallow soils and more consolidated rock will shed streamflow and shallow groundwater off the mountain block onto the valley, which often consists of deep alluvium, particularly in the basin and range geologic province. This is where mountain front recharge occurs. High-elevation perennial streams often become intermittent or ephemeral at this

1 transition, with their downstream disappearance of surface flow dependent on the flow rates
2 coming off the mountain block and the permeability of the valley alluvium into which they enter.
3 During periods of high flow, they can reconnect with other perennial stream reaches maintained
4 by groundwater flow (Blinn and Poff, 2005; Blasch and Bryson, 2007; Yuan and Miyamoto,
5 2008).

6 Runoff generation in arid and semiarid valley floors and lowlands is dominated by the
7 infiltration excess mechanism where precipitation rates exceed infiltration rates. In the arid and
8 semiarid Southwest, this situation typically is triggered by high-intensity convective
9 thunderstorms. Generally, such storms are relatively short in duration, resulting in ephemeral
10 flows with short runoff duration (Goodrich et al., 1997). As water flows down dry ephemeral
11 channels, it infiltrates into the channel bottom and sides (i.e., channel transmission losses occur)
12 where channel substrate is porous. If restricting soil or geologic layers underlying the channel do
13 not substantially inhibit downward motion, channel transmission losses will recharge either the
14 regional or alluvial groundwater (Tang et al., 2001; Constantz et al., 2002; Harrington et al.,
15 2002; Coes and Pool, 2005; Vivoni et al., 2006; Blasch and Bryson, 2007). In this influent
16 stream environment typical of many southwestern streams, the volume of transmission water
17 losses in ephemeral channels increases as watershed size increases, resulting in a losing stream
18 environment as opposed to a gaining stream environment encountered in wetter hydroclimatic
19 regimes (Goodrich et al., 1997). As noted above and discussed in Phillips et al. (2004), these
20 ephemeral tributary channels are the dominant source of recharge in valley floors, and at the
21 basin scale they can provide substantial recharge during wet years. Typically, as stream drainage
22 area increases, the alluvium under and adjacent to streams begins to serve as important shallow
23 aquifers that receive and store streamflow infiltration during hydrologic events and sustain
24 baseflow and riparian communities between storms (Stromberg et al., 2005; Dickinson et al.,
25 2010).

26 The magnitude of aquifer recharge has high temporal variability in the Southwest.
27 Winter precipitation, which has a predominant effect on mountain block and mountain front
28 recharge in the Arizona-New Mexico portion of the Southwest, is correlated with El
29 Niño/Southern Oscillation (Woolhiser et al., 1993) at interannual time scales. Over decadal
30 climate cycles, winter precipitation is also related to the Pacific Decadal Oscillation (Pool, 2005).
31 The magnitude of ephemeral channel recharge varies widely from year to year, depending on the
32 strength of the monsoon season (Goodrich et al., 2004) and the occurrence of relatively
33 infrequent prolonged precipitation events resulting from tropical depressions. Floods and large
34 runoff events caused by any of these mechanisms can have a long-lasting influence (6 to
35 10 months) on baseflow of southwestern rivers by recharging near-stream alluvial aquifers and
36 thereby sustaining streamflow as they drain (Brooks and Lemon, 2007).

1 **4.8.4. San Pedro River**

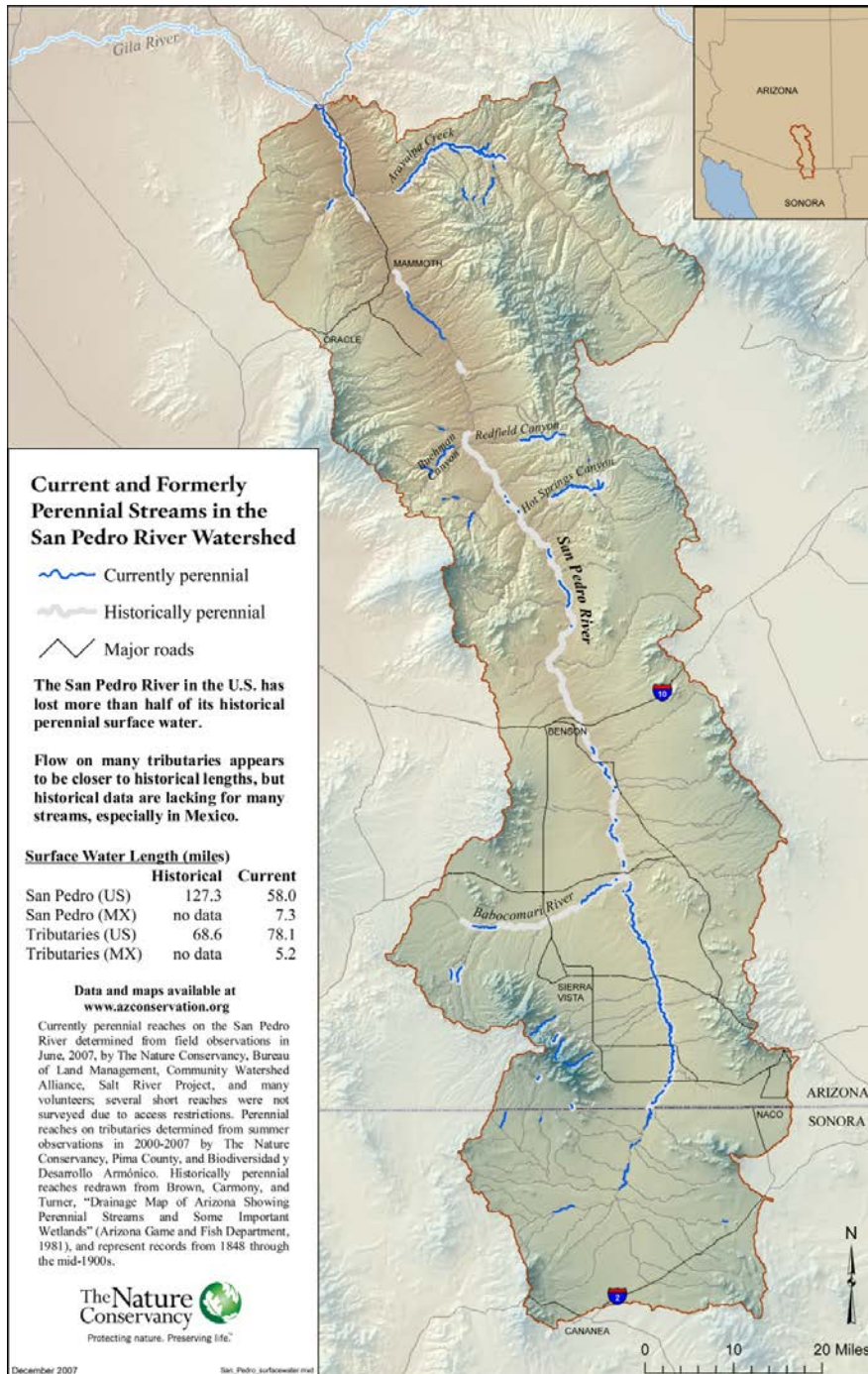
2 **4.8.4.1. Basin Characteristics**

3 Because of a rich research and long-term monitoring history, the San Pedro Basin and
4 River in southeastern Arizona represents an excellent case study of the hydrologic behavior and
5 connectivity of southwestern rivers (Goodrich et al., 2000; Stromberg and Tellman, 2009;
6 Brookshire et al., 2010). The San Pedro River originates in Mexico, flowing undammed north to
7 its confluence with the Gila River. The San Pedro Basin is comprised of 49% nonperennial
8 (includes ephemeral and intermittent), 31% perennial, and 20% artificial path (human canals or
9 diversions) reaches in the U.S. portion of the basin as derived from the USGS NHD¹. However,
10 the most recent wet-dry, ground-based mapping of reaches in the San Pedro conducted by The
11 Nature Conservancy in June 2012, historically the time of lowest streamflow, found only 29% of
12 the reaches surveyed in the basin were wet, including the portion in Mexico
13 (http://azconservation.org/downloads/category/san_pedro_river). It is the only unimpounded
14 significant river in Arizona and is the last remaining stream in southern Arizona that has long
15 perennial reaches (Kennedy and Gungle, 2010; see Figure 4-10). Most tributaries to the river are
16 ephemeral at their confluence with the mainstem. The river basin, located in the Basin and
17 Range Province, has a valley that is generally 30–50 km wide, comprising sedimentary fill
18 deposits, and slopes upward from the river to mountains with elevation ranging from 2,000 to
19 2,900 m.

20 Annual precipitation within the basin ranges from 300 to 750 mm with highest amounts
21 occurring in the mountains. Vegetation includes desert scrub, grasslands, oak woodland
22 savannah, mesquite woodland, riparian forest, coniferous forest, and agriculture (Kepner et al.,
23 2000; Kepner et al., 2004). Brush and grasses typical of southwest semiarid landscapes
24 (Goodrich et al., 1997) dominate the valley floor vegetation.

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

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



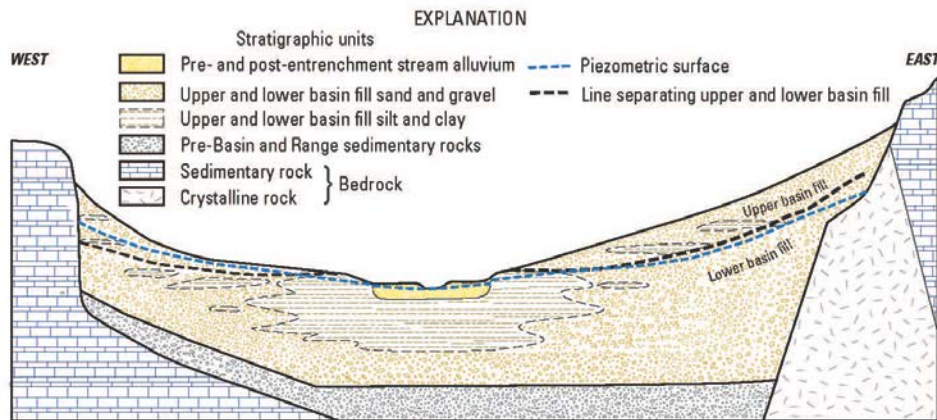
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Figure 4-10. San Pedro River basin map showing major physiographic features and current and historical perennial reaches.

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

1 summer monsoon season via infiltration excess that produces overland flow. The hydrogeology
 2 of the San Pedro River basin is typical of many alluvial basins in the Southwest (Dickinson et al.,
 3 2010). Groundwater flows through the basin-fill aquifer (regional aquifer) from recharge areas
 4 near the mountains and beneath ephemeral tributaries to perennial reaches of the San Pedro River
 5 (Wahi et al., 2008; Dickinson et al., 2010). A narrow band of highly permeable stream alluvium
 6 is incised into the basin-fill along the major stream channels (see Figure 4-11). The stream and
 7 floodplain alluvium is an important alluvial aquifer that receives discharge from the basin-fill
 8 aquifer and streamflow via streambank infiltration occurring during high stream stages.

9 This bank and alluvial aquifer storage supports riparian vegetation during periods lacking
 10 runoff (Dickinson et al., 2010). The San Pedro River network with associated shallow alluvial
 11 aquifers (mainstem and portions of some tributaries) support extensive riparian vegetation
 12 communities (Stromberg et al., 2005) that provide habitat for more than 350 species of birds,
 13 80 species of mammals, and 40 species of reptiles and amphibians (Kennedy and Gungle, 2010).
 14 Alluvial aquifers are also zones of extensive hyporheic exchange (Stanford and Ward, 1988;
 15 Fernald et al., 2001).



18
 19
 20 **Figure 4-11. Generalized east-west section and stratigraphic units in the**
 21 **middle San Pedro watershed.**

22 From Dickinson et al. (2010).

23
 24
 25
 26 **4.8.4.2. Ephemeral Stream Connections to and Influence on the San Pedro River.**

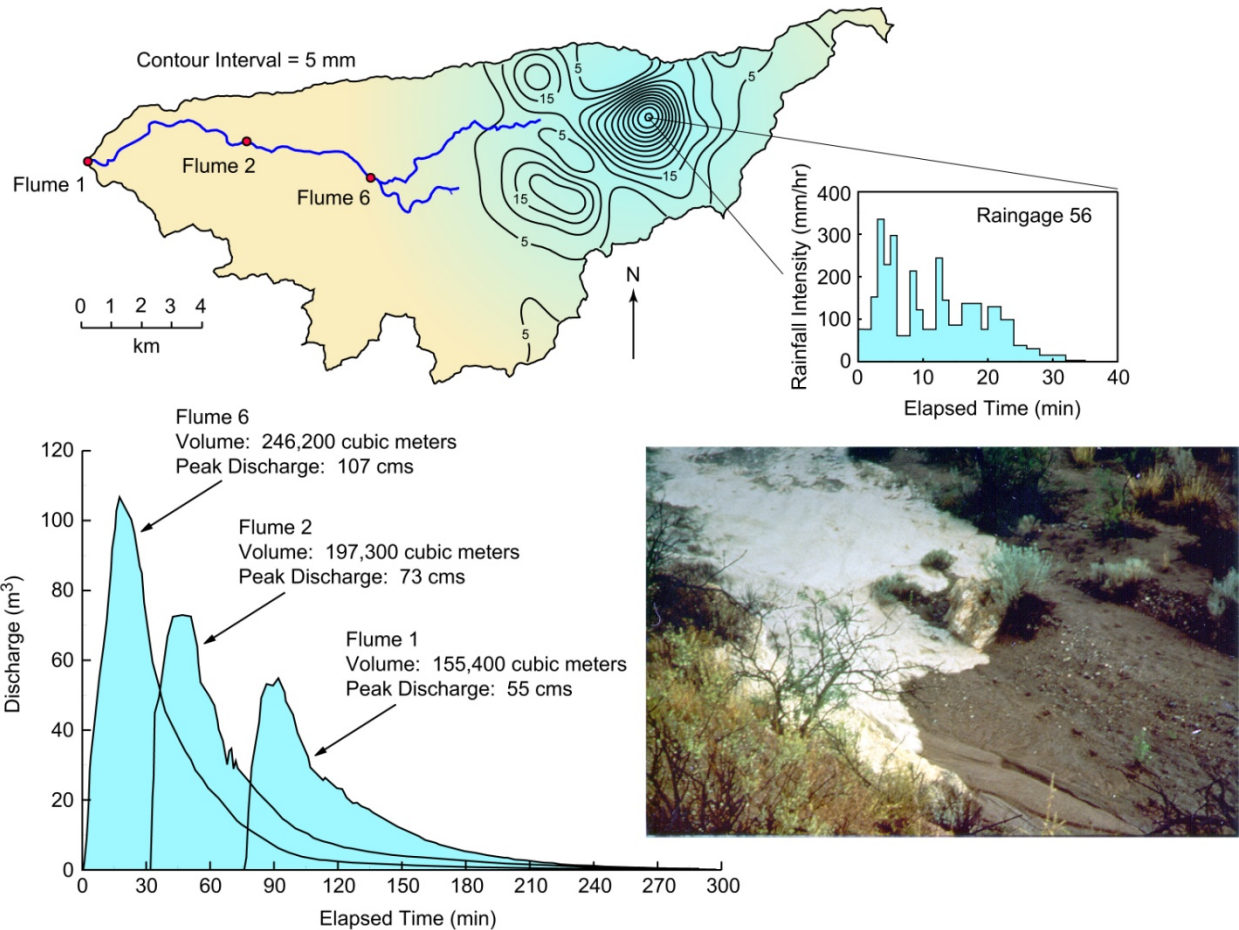
27 Overland runoff generation and associated ephemeral streamflow is common in San
 28 Pedro tributary streams. Goodrich et al. (1997) examined hundreds of hydrologic events in
 29 different-sized catchments at the USDA-ARS WGEW and found that the relationship between

1 watershed area and runoff volume was increasingly nonlinear as drainage area increased. The
2 authors found a critical threshold watershed area of approximately 36–60 ha, at which runoff
3 responses became much less linear and channel transmission losses increased more rapidly with
4 increasing watershed area. This relationship is very different from commonly observed
5 relationships in humid streams of the East, where runoff is generally proportional to watershed
6 area (see Section 4.3.1). Two reasons were given for this variability in runoff produced per unit
7 watershed area: (1) the spatial variability and limited spatial extent of runoff producing
8 precipitation, and (2) the loss of runoff water by infiltration into the bed of ephemeral channels
9 (transmission losses). Figure 4-12 illustrates this process. During a major rainstorm on 27
10 August, 1982, most of the precipitation occurred in the upper watershed. As overland flow
11 occurred and became concentrated in the ephemeral tributary network, streamflow dramatically
12 diminished as the runoff hydrograph traveled downstream through the channel network.

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

23 The influence of stormflows from ephemeral tributary streams extends to the San Pedro
24 River mainstem. As stormflow is exported from the tributaries to the mainstem and water moves
25 downstream, transmission losses and bank recharge occur within the mainstem river itself and
26 supply water to the alluvial aquifer of the mainstem (Kennedy and Gungle, 2010). Using
27 geochemical tracers (chloride, sulfate, and stable isotopes of hydrogen and oxygen in water),
28 Baillie et al. (2007) found two main sources of water in the alluvial aquifer for the upper San
29 Pedro River: (1) regional groundwater recharged along the Huachuca Mountains (mountain
30 block, mountain front) to the west, and (2) local recharge from monsoon floodwaters. Alluvial
31 groundwater composition varied between gaining and losing reaches. Locally recharged
32 floodwater comprised 60 to 85% of the alluvial groundwater in losing reaches but only 10 to
33 40% in gaining reaches. Baseflow also contained a significant component of monsoon
34 floodwater throughout the year, from 80% in upstream reaches to 55% after passing through
35 several gaining reaches.

36



1
2
3 **Figure 4-12. Spatial and temporal distribution of precipitation and**
4 **discharge at nested flumes at Walnut Gulch Experimental Watershed for**
5 **rainstorm on August 27, 1982.**
6

7 Photograph shows ephemeral streamflow in a Walnut Gulch ephemeral stream.
8 From Levick et al. (2008).
9

10
11 Ephemeral tributary stormflows are also sources of sediment and alluvium for the main
12 San Pedro River. Only the largest, less frequent events can flush sediment completely through
13 ephemeral tributaries (Lane et al., 1997). For example, in an arid watershed in Israel, Lekach et
14 al. (1992) found that more than 90% of the bedload yield originated from the mid-catchment
15 channels during larger runoff events. Ephemeral tributary stormflows and their associated
16 sediment loads influence the character of river floodplains and alluvial aquifers (Nanson and
17 Croke, 1992; Shaw and Cooper, 2008).

18 Extensive riparian plant communities along the mainstem San Pedro River depend on the
19 availability of water in the alluvial aquifer along the river, including water derived from
20 ephemeral stream stormflows (Stromberg et al., 2005; Baillie et al., 2007). These riparian areas,

1 in turn, strongly influence river attributes through stream shading, channel stabilization, nutrient
2 cycling, inputs of invertebrates and other organisms, and inputs of detritus, wood, and other
3 materials (Gregory et al., 1991; National Research Council, 2002; Naiman et al., 2005).

4 The nutrient and biogeochemical status of the San Pedro River is heavily influenced by
5 ephemeral tributary stormflow inputs. Brooks and Lemon (2007) performed synoptic sampling
6 on a 95-km reach of the San Pedro River to identify the effects of regional hydrology and land
7 use on dissolved carbon and nitrogen concentrations. They found that, during the summer
8 monsoon season, baseflow increased 5- to 10-fold, and dissolved organic matter and inorganic
9 nitrogen increased 2- to 10-fold. The fluorescence index of water samples indicated a large input
10 of terrestrial solutes with the onset of monsoon runoff inflows, and both chloride and oxygen
11 isotope tracer values indicated that streamwater and alluvial groundwater were well mixed along
12 the entire 95-km reach. Meixner et al. (2007) used chloride tracer samples and mixing analyses
13 to examine sources of San Pedro River water during six summer floods in 2001 (wet year) and
14 2002 (dry year). Results of mixing models indicated that both a groundwater-soil water
15 end-member and a precipitation end-member (indicative of overland flow) contributed to the
16 floods. The highest percentage of groundwater-soil water in the flood flow (46%) occurred
17 during an early 2001 flood and the lowest during large monsoon floods of 2002. They noted that
18 groundwater probably made lower contributions than soil water to streamflow, because high
19 river stage during flood events created hydraulic gradients from the river to alluvial groundwater
20 in the riparian area (water moved from the river to alluvial groundwater via bank storage, see
21 Figure 3-13B). During the first floods of each year, nitrate and dissolved organic carbon
22 increased dramatically in the river, whereas dissolved organic nitrogen did not exhibit increases
23 in 2001 but did in 2002. During floods, nitrate-nitrogen ($\text{NO}_3\text{-N}$) concentrations in river water
24 were 0.2–0.5 mg $\text{NO}_3\text{-N L}^{-1}$ higher in 2002 than during 2001. This result was consistent with
25 higher observed nitrate-nitrogen concentrations in soil water of the riparian zone (alluvial
26 aquifer) in 2002 than in 2001.

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

30 31 **4.8.5. Other Southwestern Rivers**

32 **4.8.5.1. *Physical Connections***

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

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

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

22 Shaw and Cooper (2008) studied the 14 ephemeral stream reaches in the Little Colorado
23 River Basin in northeast Arizona. As derived from the USGS National Hydrography Dataset,
24 this basin contains a higher percentage of ephemeral and intermittent stream reaches (70%) as
25 compared to 54% of such reaches in the Upper San Pedro. Shaw and Cooper (2008) related
26 watershed characteristics of the Little Colorado to downstream reaches and the riparian plant
27 communities of those reaches. They found that as the watershed area draining to the studied
28 reaches increased, the overall basin channel slope decreased which resulted in less erosive
29 capacity due to channel transmission losses as well as a decrease in the variability of alluvial
30 groundwater in these channels. This resulted in “decreased disturbance potential and increased
31 moisture availability in the downstream direction,” and these reaches had a greater abundance of
32 obligate riparian vegetation. Shaw and Cooper (2008) went on to develop a stream classification
33 system that related the functional linkages between contributing upstream watersheds, stream
34 reaches, and riparian plant ecology. Type I stream reaches have relatively small drainage areas
35 (less than 10 km²), which have the greatest disturbance potential with in-channel and near-
36 channel plants resembling those of surrounding upland species. Between 10 and 100 km²,

1 Type II streams exhibit “more moderate shear stresses and more persistent alluvial groundwater”
2 with riparian vegetation that is a mixture of upland and riparian species. At larger areas (greater
3 than 100 km²), Type III reaches are “controlled mainly by upstream hydro-climatic conditions”
4 with wetland tree and shrub communities. Shaw and Cooper (2008) concluded that the
5 connection of streamflow and groundwater regimes to riparian vegetation in the larger Type III
6 watersheds, draining greater than 100 km², to upstream reaches far removed from larger regional
7 floodplain rivers “... were driven by climatic patterns from distant portions of the upper
8 watershed and were relatively insensitive to local rainfall.” This finding reinforces the fact that
9 stream-reach characteristics are influenced and connected, often episodically, to distant portions
10 of the contributing watershed.

11 12 **4.8.5.2. Fish and Aquatic Insects**

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

19 As discussed in the previous section, the interplay between stormflow from ephemeral
20 tributary streams, water from alluvial aquifers, and water from regional groundwater control the
21 distribution and timing of flowing water in southwestern rivers. Native fish species of
22 southwestern streams and rivers are adapted to these dynamic environments (John, 1964; Meffe,
23 1984). Rinne and Miller (2006) compared fish assemblage data in river networks for two
24 southwestern rivers, the Gila River (New Mexico and Arizona) and the Verde River (Arizona)
25 over 7 to 12 years. They included river hydrology and geomorphology data in their analysis and
26 found that variable streamflows and higher flow volumes favor native fish species over
27 nonnatives. They also noted that the presence of unconstrained alluvial valley river reaches with
28 shallow pools favored native fish. Furthermore, when humans alter the hydrologic dynamics of
29 ephemeral and intermittent tributaries such that flows connecting them to the river network are
30 more frequent or more consistent, nonnative fish can invade (Turner and List, 2007). Recent
31 nonnative invasion and a corresponding decline in native fish species diversity was observed in
32 the lower reaches of the Aravaipa Creek, a tributary of the San Pedro River, which historically
33 was rarely connected to the mainstem (Eby et al., 2003).

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

1 In this case, the disturbance was a flash flood. Using signal detection theory, they found that for
2 13 of 15 insect populations, the observed insect response times “were an optimal compromise
3 between the competing risks of abandoning versus remaining in the stream, mediated by the
4 rainfall-flood correlation of the local environment.” They concluded that these aquatic insect
5 populations are able to evolve in their responses to changes in the flow disturbance regime,
6 providing evidence that these aquatic populations can adapt to “among-stream differences in
7 flow regime.”
8

9 **4.8.6. Southwestern Intermittent and Ephemeral Streams: Synthesis and Implications**

10 Rivers of the arid and semiarid Southwest are products of a highly variable and dynamic
11 environment. Even before groundwater pumping dewatered numerous river reaches,
12 southwestern rivers commonly had distributions of reaches with perennial, intermittent, and
13 ephemeral streamflow conditions. Many tributary streams to southwestern rivers are ephemeral,
14 but they exert strong influences on the structure and function of the rivers. Some of the major
15 ways in which ephemeral streams are connected with and influence rivers are as follows:
16
17

- 18 • Flows from ephemeral streams are a major driver of the dynamic hydrology of
19 southwestern rivers. Ephemeral tributary streamflows are especially important drivers of
20 downstream floods during monsoon seasons.
- 21 • Mainstem river native fishes and invertebrates are adapted to the variable flow regimes
22 that ephemeral tributary streams strongly influence. Ephemeral flows prevent or mitigate
23 invasion by introduced species.
- 24 • Ephemeral tributary streams supply water to mainstem river alluvial aquifers; these
25 alluvial aquifers aid in sustaining river baseflows.
- 26 • Ephemeral streams export sediment to rivers during major hydrologic events; the
27 sediment contributes to materials that comprise alluvial aquifers and shape the fluvial
28 geomorphology of rivers.
- 29 • Ephemeral tributaries export nutrients to the mainstream rivers during hydrologic flow
30 events; nutrients occur in many forms and are contributors to the productivity of rivers.
- 31 • Water, sediment, and nutrients exported to the river from ephemeral tributaries support
32 mainstem river riparian communities; the riparian communities profoundly influence
33 river attributes through shading and allochthonous inputs of organic matter, detritus,
34 wood, and invertebrates to the river.

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

4

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

5.1. ABSTRACT

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

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

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

- 11
12 1. A wetland having a surface water outflow to a stream network (e.g., a wetland that
13 serves as a stream origin) is connected to the stream network and has an impact on
14 downstream waters.
- 15 2. Many unidirectional wetlands interact with groundwater, which can travel long
16 distances and affect downstream waters.
- 17 3. Even hydrologically isolated wetlands can influence downstream rivers by preventing
18 water and other materials from entering the river network.
- 19 4. Within a watershed or region, wetlands and open-waters that are closer to rivers and
20 streams will have a higher probability of being connected than more distant areas,
21 assuming that conditions governing type and quantity of flows (e.g., slope, soil, and
22 aquifer permeability) are similar.

23 24 **5.2. INTRODUCTION**

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

31 In Chapter 3, we provided definitions for wetlands, gave a rationale for distinguishing
32 between wetlands in bidirectional and unidirectional settings, and discussed general hydrologic
33 and biological mechanisms by which wetlands can connect to and affect streams and rivers.
34 Given that streams and rivers are the endpoints of interest, we limit our discussion of
35 bidirectional wetlands to those occurring in riparian and floodplain settings. Below, we provide
36 a detailed review of the contributions of riparian/floodplain wetlands (see Section 5.3) and

1 unidirectional wetlands (see Section 5.4) to rivers, followed by conclusions concerning these
2 wetlands and their effects on rivers (see Section 5.5). Examples of some of the functions
3 discussed in these two sections are found in Table 5-1. The chapter ends with four case studies
4 on specific types of wetlands or lentic waters representing different landscape settings and
5 geographic regions: oxbow lakes (see Section 5.6), Carolina and Delmarva bays (see
6 Section 5.7), prairie potholes (see Section 5.8), and vernal pools (see Section 5.9).

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

16 **5.3. RIPARIAN AND FLOODPLAIN WETLANDS**

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

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

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

Source Function
<ul style="list-style-type: none"> Riparian/floodplain wetlands and unidirectional wetlands connected to the stream network by channelized flow—ranging from ephemeral to permanent—are sources of downstream water (5.3.1.1, 5.4.2.1, 5.6.3.1, 5.7.2.3, 5.8.3.1).
<ul style="list-style-type: none"> Wetlands that serve as origins for streams (e.g., seeps) can be sources of groundwater discharge, contributing to stream baseflow (5.2.3, 5.4.2.1).
<ul style="list-style-type: none"> Unidirectional wetlands lacking a channel outlet can be sources of water via overland flow to the stream network if wetland storage capacity is exceeded (5.4.2.1, 5.9.3.1, 5.8.3.1). They can also provide water via subsurface drains (“tile drains”) or surface ditches (5.4.2.1, 5.7.3.1, 5.8.3.1).
<ul style="list-style-type: none"> Riparian/floodplain wetlands and unidirectional wetlands can be sources of nutrients and sediments to downstream waters (5.3.2, 5.4.3, 5.7.3.2, 5.8.3.2).
<ul style="list-style-type: none"> Riparian areas are a source of allochthonous inputs, the primary energy input into the food webs of small forested streams (5.3.2.4). They are also sources of woody debris that can affect stream morphology and flow regime, and provide habitat for aquatic organisms (5.3.1.2).
<ul style="list-style-type: none"> Riparian areas and unidirectional wetlands can be sources of dissolved organic matter utilized by aquatic food webs, with additional potential effects on pH and mercury concentrations of downstream waters (5.3.2.1, 5.3.2.6, 5.3.3.1, 5.4.3).
<ul style="list-style-type: none"> Riparian/floodplain wetlands and unidirectional wetlands can be sources of organisms, including plants, invertebrates, amphibians, reptiles, and fish, to downstream waters transported via passive or active dispersal (5.3.3, 5.4.4, 5.6.3.3, 5.8.3.3, 5.9.3.2).
<ul style="list-style-type: none"> Riparian/floodplain wetlands can provide feeding habitat for riverine organisms, such as fish, during periods of overbank flow (5.3.3.2, 5.6.3.3).
Sink Function
<ul style="list-style-type: none"> Riparian/floodplain wetlands and unidirectional wetlands can be sinks for water by intercepting overland or subsurface flow, if available water storage capacity of the wetlands is not exceeded. This can reduce or attenuate flow to downstream waters and flooding (5.3.1.1, 5.4.2.3, 5.8.3.1).
<ul style="list-style-type: none"> Riparian areas and unidirectional wetlands can be sinks for sediment and chemical contaminants, such as pesticides, metals, mercury and excess nutrients carried by overland or subsurface flow, potentially reducing loading to downstream waters (5.3.1.2, 5.3.2, 5.3.2.6, 5.4.3.2).
<ul style="list-style-type: none"> Riparian areas can be sinks for water, sediment, pesticides, and nutrients from overbank flow events, reducing or attenuating downstream peak flows and materials entrained in the water column (5.3.1.1, 5.3.2, 5.6.3.2). They can also be sinks for seeds and plant fragments deposited via overbank flow (5.3.3.1).
<ul style="list-style-type: none"> Riparian/floodplain wetlands and unidirectional wetlands can be sinks for nitrogen by converting nitrogen to molecular nitrogen through denitrification, which is then lost to the atmosphere (5.3.2.2, 5.4.3.2).

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

Refuge Function
<ul style="list-style-type: none"> Riparian/floodplain wetlands and unidirectional wetlands can provide refuge for fish, aquatic insects, or other lotic organisms, from predators or other environmental stressors, facilitating individual or population survival (5.3.3.2, 5.4.4).
<ul style="list-style-type: none"> Riparian/floodplain wetlands and unidirectional wetlands can provide refuge during certain life stages for lotic organisms. For example, they are breeding sites for frogs and other amphibians that reside in streams as adults (5.4.4, 5.7.3.3, 5.9.3.2; see Table 5-2), and unidirectional wetlands are additionally nesting and nursery sites for American alligators that otherwise primarily reside in streams (5.4.4).
Transformation Function
<ul style="list-style-type: none"> Microbial communities in riparian/floodplain wetlands and unidirectional wetlands can transform elemental mercury to methylmercury prior to entering a stream. Methylmercury is a particularly toxic and mobile form that bioaccumulates in aquatic food webs (5.3.2.6, 5.4.3.1).
<ul style="list-style-type: none"> Riparian/floodplain wetlands and unidirectional wetlands can transform nitrate to molecular nitrogen through denitrification (5.3.2.2, 5.4.3.2).
Lag Function
<ul style="list-style-type: none"> Riparian/floodplain wetlands can temporarily store water following overbank flow, which then can move back to the stream over time as baseflow (5.3.1.1).
<ul style="list-style-type: none"> Riparian/floodplain wetlands and unidirectional wetlands can contribute to groundwater recharge under low water table conditions, which ultimately contributes to baseflow (5.4.2.2, 5.4.2.3 5.8.3.1).
<ul style="list-style-type: none"> Unidirectional wetlands can increase the time for stream discharge to rise and fall in response to a precipitation event due to wetland storage capacity (5.4.2.3).

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

13 As addressed in Chapter 3, much of the theory developed to explain how riverine systems
14 work has focused on linkages between system components (e.g., Vannote et al., 1980; Newbold

1 et al., 1982a; Newbold et al., 1982b; Junk et al., 1989; Ward, 1989; Benda et al., 2004; Thorp et
2 al., 2006). Indeed, central tenets of stream hydrology and ecology are the intimate connectivity
3 between a river and its riparian area/floodplain, and the substantial influence this bidirectional
4 exchange has on the hydrology, chemistry and biology of the river system (Junk et al., 1989;
5 Tockner et al., 2000; Naiman et al., 2005). For instance, the Flood Pulse Concept, first
6 articulated by Junk et al. (1989) and extended by Tockner et al. (2000), is a fundamental
7 paradigm in riverine ecology, depicting the lateral expansion and contraction of the river in its
8 floodplain and the resulting exchange of matter and organisms. Many fish populations, for
9 example, are adapted to use floodplain habitat for feeding and spawning during high water (Junk
10 et al., 1989; Bayley, 1991; Pezold, 1998). Riparian/floodplain wetlands are widely recognized as
11 having frequent connections to streams and rivers and significant influence on water, sediment,
12 and solute fluxes to streams (Naiman et al., 2005; Vidon et al., 2010) and are similarly affected
13 by material and energy fluxes from streams. For instance, the restoration of 70 km of the
14 Kissimmee River channel in Florida includes reestablishing the links between the river and
15 >100 km² of river and floodplain habitats, with a focus on restoring interactions between
16 hydrology, nutrients, dissolved and particulate organic matter, and wetland vegetation (Dahm et
17 al., 1995). Dahm et al. (1995) expect over 11,000 ha of wetland scrub habitat to be restored from
18 current pasture/upland scrub/human-influenced habitats based on reestablishing the hydrology of
19 the system. Riparian/floodplain wetlands also influence streams as an area of nutrient and
20 sediment deposition, and by shading, stabilizing streambanks, and providing habitat for diverse
21 organisms (Naiman et al., 2005; Vidon et al., 2010). This section provides further details on the
22 connections between riparian wetlands and streams and rivers, and the resulting effects.

23

24 **5.3.1. The Physical Influence of Riparian Areas on Streams**

25 **5.3.1.1. Hydrology**

26 Riparian areas have a diverse set of hydrologic inputs and outputs that connects them to
27 streams and rivers (see Figure 3-6A). These inputs and outputs are described in Section 3.2 and
28 reviewed by various authors (National Research Council, 2002; Naiman et al., 2005; Vidon et
29 al., 2010). Many studies document that riparian floodplains help attenuate flood pulses in
30 streams, by both capturing water from overland flow and storing excess water from streams.
31 Bullock and Acreman (2003) reviewed the wetland literature and reported that floodplain
32 wetlands reduced or delayed floods in 23 of 28 studies. Walton et al. (1996) found that peak
33 discharges between upstream and downstream water gages on the Cache River in Arkansas were
34 reduced 10–20%, primarily due to floodplain water storage. A study by Gamble et al. (2007)
35 reported that 12 floodplain wetlands in Ohio stored an average of 3,654 m³ ha⁻¹ of water. They

1 further developed equations relating volume to area and depth for more than 650 regional
2 wetlands and reported that these systems could store approximately 1–2% of the daily flow of
3 larger streams and approximately 40% of the daily flow of small streams (Gamble et al., 2007).
4 As streamflow decreases after hydrologic events, the water temporarily stored in riparian areas
5 can flow back into the channel, supporting stream baseflow (Whiting and Pomeranets, 1997;
6 Chen and Chen, 2003). Although not all riparian/floodplain wetlands store the same amount of
7 water, almost all of them have the potential to perform this function. In addition to the water
8 storage capacity of floodplain and riparian wetlands, riparian vegetation also can influence water
9 levels in the stream by capturing and transpiring water. Phreatophytes (plants that obtain their
10 water from the saturated zone) can intercept groundwater and overland flow before it enters a
11 stream and decrease stream flow by directly taking up stream water through their roots.
12 Meybloom (1964) studied two streams in the Prairie region of the United States to understand
13 how associated floodplain vegetation affects streamflow fluctuations. When the two streams
14 decreased in flow, the floodplain vegetation accounted for 20 and 100% of this reduction
15 (Meyboom, 1964).

16

17 **5.3.1.2. *Geomorphology (Sediment-Vegetation Interactions)***

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

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

1 deep (Dillaha et al., 1989; Magette et al., 1989; Naiman and Decamps, 1997). Thus, riparian
2 areas can buffer stream channels against excessive sediment input.

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

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

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

34 **5.3.1.3. Temperature and Sunlight**

35 Riparian areas can modify stream temperatures, and particularly in forested areas, the
36 amount of light available for photosynthesis. Surface water temperatures are often highly related

1 to groundwater and riparian soils. Excepting groundwater flowpaths discharging directly to the
2 stream, groundwater often moves through the alluvium of the riparian area, exchanging heat and
3 equalizing its temperature prior to reaching the stream (Brosofske et al., 1997; Naiman and
4 Decamps, 1997; Poole and Berman, 2001; Naiman et al., 2005). Additionally, riparian areas
5 play a major role in modifying stream temperatures when vegetation shades the stream (Barton et
6 al., 1985; Gregory et al., 1991; Blann et al., 2002). Dense, overhanging vegetation greatly
7 reduces the intensity of light, whereas open canopies allow light to penetrate (Gregory et al.,
8 1991). This radiant energy, or lack thereof, has a strong influence on stream temperature (Barton
9 et al., 1985; Gregory et al., 1991; Blann et al., 2002). The maximum temperature of a stream in
10 Oregon, for example, was 7°C higher in a reach where the riparian vegetation was removed
11 compared to its temperature when it was forested. Fifteen years of regrowth in the harvested
12 area was required for the stream temperature to return to preharvest levels (Johnson and Jones,
13 2000).

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

25 Shading of the stream by riparian vegetation also has a direct influence on the instream
26 net primary productivity (NPP) of aquatic plants and other photosynthetic organisms, such as
27 algae, by altering light availability (Gregory et al., 1991). Net primary production is greatest in
28 open reaches and is significantly less in reaches that are forested and shaded (Gregory et al.,
29 1991). For example, Gregory et al. (1991) reported that net primary production in open streams
30 in Oregon averaged 210 mg carbon (C) m⁻² d⁻¹, whereas forested reaches of streams with
31 deciduous vegetation averaged 58 mg C m⁻² d⁻¹. Reduced net primary production leads to lower
32 densities of herbivores in streams (Hawkins and Sedell, 1981; Gregory et al., 1991). Shading
33 can be limiting to streams (Hill and Knight, 1988; Gregory et al., 1991), but it can also be
34 beneficial by reducing excessive algal production in nutrient-enriched waters. Algae can lead to
35 excessive biological oxygen demand and turbidity and can decrease water quality in downstream
36 systems (Volkmar and Dahlgren, 2006).

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

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

5.3.2.1. Hyporheic/Soil Processing of Nutrients

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

Riparian areas can have significant impacts on nutrients and other exports from watersheds (Gregory et al., 1991) and can be considered areas of major nutrient transformation as subsurface waters move through them (Dahm et al., 1998). Riparian areas remove nutrients such as nitrogen and phosphorus from water as it flows from uplands to streams (Lowrance et al., 1997; Dosskey, 2001; Mayer et al., 2007). The ability of a riparian area to act as either source or sink of nitrogen, phosphorus, organic matter, pesticides, and mercury is largely controlled by the

1 substance's concentration in riparian soils (Gregory et al., 1991), soil redox conditions, and
2 hydrology (Vidon et al., 2010). For example, riparian plant communities can release seasonal
3 pulses of dissolved leachates derived from stream litter (Fisher and Likens, 1973). Riparian
4 areas are therefore central to watershed water quality management (Burt, 1997; Lowrance et al.,
5 1997).

6

7 **5.3.2.2. Nitrogen**

8 Riparian areas can remove dissolved nitrogen in subsurface flowpaths that would
9 otherwise flow into streams (Vidon et al., 2010). Removal occurs via plant uptake and microbial
10 transformations (i.e., assimilative uptake, assimilatory nitrate reduction to ammonium, and
11 dissimilatory nitrate reduction to ammonium or nitrogen gases such as dinitrogen, nitric oxide,
12 and nitrous oxide via denitrification). Indeed, a study has demonstrated that intact riparian and
13 hyporheic zones are critical in decreasing the amount of dissolved inorganic nitrogen that finds its
14 way from headwaters to larger, downstream waterways (Triska et al., 2007). Riparian areas are
15 often responsible for the removal of more than half of the nitrogen from surface and shallow
16 subsurface water transporting ammonium and nitrate through the rhizosphere (Vidon et al.,
17 2010). However, leaching from nitrogen-fixing plants (e.g., red alder, *Alnus rubra*) in riparian
18 systems can also be a major source of nitrogen to stream systems (Compton et al., 2003).

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

24 Some studies have examined denitrification potential in riparian surface soils 0–20 cm in
25 depth (Vidon et al., 2010). The highest denitrification potentials occur where high organic
26 matter levels, denitrifying microbes, and saturated soil conditions are present (Vidon et al.,
27 2010). Rates of denitrification have been shown to be greater in riparian soils nearer to streams
28 (Gregory et al., 1991). High soil moisture and deposited organic matter enhance microbial
29 activity, thereby tending to increase denitrification (Vidon et al., 2010).

30 As subsurface flow passes through riparian areas, vegetative demand for dissolved
31 nutrients also can reduce nutrient loads (Vidon et al., 2010). More than three-quarters of the
32 dissolved nitrate transported from agricultural fields to a Maryland river (Vidon et al., 2010)
33 were removed by riparian forests. Nitrate N was removed at a rate of 45 kg ha⁻¹ yr⁻¹ as
34 subsurface flow moved from agricultural fields through riparian zones to nearby streams
35 (Peterjohn and Correll, 1984). In the coastal plains of Georgia, riparian forests retained more
36 than 65% of the nitrogen and 30% of the phosphorus contributed from nearby agriculture (Vidon

1 et al., 2010). In southern Pennsylvania, a forested riparian area had a subsurface NO_3^- budget
2 with an average removal of $90 \text{ kg NO}_3^- \text{ ha}^{-1} \text{ yr}^{-1}$, which was 26% of the total nitrate input
3 (Newbold et al., 2010).

4 **5.3.2.3. Phosphorus**

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

18 Although riparian soils generally act as sources of phosphorus when soils are anoxic or
19 when mineral dissolution releases phosphorus (Baldwin and Mitchell, 2000; Chacon et al.,
20 2008), riparian areas act as phosphorus sinks in oxic soils (Carlyle and Hill, 2001). Portions of
21 riparian areas where agricultural sediments are deposited are phosphorus sources to streams if
22 the phosphorus is desorbed and leached but can be sinks by adsorbing dissolved phosphorus if
23 sediment phosphorus concentrations are low (Dillaha and Inamdar, 1997; Sharpley and
24 Rekolainen, 1997). Riparian areas can also act as phosphorus sinks when upland surface runoff
25 travels through the riparian area or where phosphorus in fine-grained sediment is deposited
26 overbank onto the riparian area (Dillaha and Inamdar, 1997). These sediments, however, can
27 become sources of phosphorus if they are later saturated with water and iron and manganese are
28 reductively dissolved during anoxic conditions, thus causing them to desorb phosphorus (Reddy
29 and DeLaune, 2008).

31 **5.3.2.4. Carbon and Allochthonous Inputs**

32 Both production and consumption of organic and inorganic carbon occur in riparian
33 areas. In areas with reducing conditions, microbes generally oxidize organic carbon and reduce
34 available electron acceptors, releasing carbon dioxide gas and making the soils more alkaline
35 (Vidon et al., 2010). This process can result in chemical gradients in which electron acceptor

1 concentrations decrease and alkalinity increases along subsurface flowpaths (Burns, 1996; Cirmo
2 et al., 2000; Bailey Boomer and Bedford, 2008). Riparian areas, especially those in low-lying
3 flatlands, tend to have low subsurface flow velocities resulting in anoxic conditions, shallow
4 water tables, and slow organic matter decomposition, as is often seen in riparian wetlands. This
5 is why riparian areas are active areas for biogeochemical transformations (Vidon et al., 2010).

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

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

32 33 **5.3.2.5. Pesticides**

34 The roots in riparian areas can be important for the removal of pesticides from shallow
35 subsurface flow, because the labile organic matter and organic residues that accumulate near
36 roots can increase microbial biomass and activity (Vidon et al., 2010). Pesticides and their

1 metabolites can be mineralized and adsorbed where there is high surface area contact and
2 sufficient contact time with roots (Krutz et al., 2006). A study of the pesticides alachlor and
3 atrazine in a riparian area notes the importance of plant uptake in the fate of these pesticides, and
4 suggests that vegetated buffer zones help to protect water supplies (Paterson and Schnoor, 1992).
5 Studies examining specific pesticides—for example, isoproturon (Benoit et al., 1999),
6 metolachlor (Staddon et al., 2001), and atrazine (Mudd et al., 1995)—found that the presence of
7 vegetation, associated root zones, and accumulated organic matter increased the removal of those
8 pesticides (Vidon et al., 2010). Pesticide-degrading microbial populations increase after repeated
9 chemical applications (Gonod et al., 2006), suggesting that riparian areas can become better at
10 degrading pesticides that enter these zones (Vidon et al., 2010). In addition, microbial biomass
11 has been shown to be positively correlated with the loss of the herbicides 2,4-D
12 (2,4-dichlorophenoxyacetic acid) and dicamba, suggesting a relationship between the amount of
13 microbial biomass in the soil and the capacity of an ecosystem to degrade pesticides (Voos and
14 Groffman, 1996).

15

16 **5.3.2.6. Mercury**

17 Mercury enters the global atmosphere primarily through waste incineration and coal
18 combustion. It can directly enter wetland systems or can be deposited on terrestrial areas and
19 then transported into riparian areas and wetlands via rainfall and runoff (St. Louis et al., 1994).
20 Riparian soils and wetlands are important both for mercury mobilization (Mierle and Ingram,
21 1991; Driscoll et al., 1995) and the production of methylmercury (MeHg), a particularly toxic
22 and mobile form of the element. Mercury methylation occurs in the presence of anoxic,
23 saturated soils high in organic matter, mercury-methylating microbes, and mercury from either
24 atmospheric deposition or soils (St. Louis et al., 1996). The redox conditions found in the
25 presence of a fluctuating water table are thought to be a strong driver of mercury methylation
26 (Heyes et al., 2000; Branfireun and Roulet, 2002; Branfireun, 2004). Export of mercury and
27 methylmercury can expose organisms in downstream aquatic ecosystems to potential toxicity
28 (Thurman, 1985; Driscoll et al., 1995). Mercury bioaccumulates in fish, and consumption of fish
29 is the main human pathway for exposure to mercury (Rypel et al., 2008).

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

35

1 **5.3.3. Biological Connections Between Riparian Areas and Streams**

2 The dynamic nature of river systems is most apparent in riparian areas, where a shifting
3 landscape mosaic supports diverse communities of aquatic, amphibious, and terrestrial species
4 adapted to periodic or episodic inundation of riparian areas and floodplains (Robinson et al.,
5 2002). In unregulated rivers, floodplain inundation greatly increases the area and diversity of
6 aquatic habitats (Junk et al., 1989; Tockner et al., 2000). It also allows rapid cycling of nutrients
7 imported from river channels (see Section 5.3.2), resulting in high primary productivity of plants
8 and algae (Junk et al., 1989; Tockner et al., 1999). The combination of diverse habitat types and
9 abundant food resources makes floodplains important foraging, hunting, and breeding sites for
10 fish (Copp, 1989), aquatic life stages of amphibians (Richardson et al., 2005), and aquatic
11 invertebrates (Smock et al., 1992; Smock, 1994). Many of these organisms have growth stages
12 or reproductive cycles timed to coincide with seasonal hydrologic connectivity between rivers
13 and floodplains. Thus, lateral fluctuations in hydrologic connectivity can increase overall levels
14 of species productivity and biodiversity in river systems (Junk et al., 1989). Here, we review
15 examples of adaptation to and exploitation of riparian habitats by aquatic species of plants, fish,
16 mammals, and invertebrates.

17 18 **5.3.3.1. Vascular Plants and Phytoplankton**

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

1 typically high flow velocities along riparian areas, and fragments can survive and reestablish
2 downstream at rates above 90% (Truscott et al., 2006).

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

9 Hydrologic connectivity between channels and riparian/floodplain wetlands can
10 significantly enhance riparian vegetation diversity (Jansson et al., 2005) and determine
11 floodplain wetland community structure (Boschilia et al., 2008). In the case of nonnative
12 species, however, connectivity can facilitate invasion, resulting in changes in riparian vegetation
13 community structure. In an intermittent stream in Illinois, tubers of the nonnative Chinese yam
14 (*Dioscorea oppositifolia*) were dispersed via stormflow and overbank flow and became
15 established along a narrow upstream riparian area and wider channel and floodplain more than 1
16 km downstream; the presence of the nonnative plant significantly reduced native plant cover
17 (Thomas et al., 2006). Vegetation community composition, in turn, can affect the function of
18 riparian areas as nutrient sources or sinks to the river network (e.g., see Sections 5.3.2.2 and
19 5.3.2.4). Invasion by nonnative riparian plants also can result in altered stream invertebrate
20 diversity among other effects (Lecerf et al., 2007).

21 Seeds of aquatic and riparian plants also can be actively dispersed by animals that
22 consume them. For instance, seeds of the aquatic emergent bur-reed (*Sparganium emersum*)
23 were found to be ingested and viably excreted by common carp (*Cyprinus carpio*; Pollux et al.,
24 2007), which elsewhere have been observed using channel and floodplain wetland habitat (King
25 et al., 2003). Absent hydrologic connections, riparian floodplain and wetland vegetation can
26 disperse and exchange seeds via terrestrial animal vectors and the wind. Animals that travel
27 overland can also disperse ingested seeds or seeds adhering to fur or limbs between
28 riparian/floodplain wetlands and the river network (see Section 5.3.3.2 for discussion of animal
29 movement). Many macrophyte species have evolved for dispersal by wind, including some of
30 the most invasive in North America, cattail (*Typha spp.*) and reed canary grass (*Phalaris*
31 *arundinacea*; Barrat-Segretain, 1996; Soons, 2006 and references therein). Given the proximity
32 of riparian/floodplain wetlands and the river network itself, dispersal of pollen and seeds
33 between these habitats could be quite frequent. For instance, seeds of some 20 species found in
34 floodplain wetlands in bald cypress swamps in Illinois were caught in aerial seed traps, and
35 dispersal of three species averaged more than $100 \text{ seeds m}^{-2} \text{ yr}^{-1}$ (Middleton, 2000).

1 Phytoplankton also moves via water between floodplain wetlands and the river network.
2 A river with overbank flow can homogenize the phytoplankton communities in floodplain
3 wetlands separated by more than 5 km (Angeler et al., 2010), and phytoplankton communities in
4 river networks can be bolstered by high productivity conditions in temporarily connected
5 floodplain wetlands. For example, a portion of flow from California's Sacramento River is
6 seasonally diverted from the main channel into the Yolo Bypass, an adjacent 240-km² floodplain.
7 From January to June 2003, 14 and 31% of total diatom and total green algae biomass,
8 respectively, was produced in the floodplain (Lehman et al., 2008). This considerable
9 contribution of carbon to the aquatic food chain, which ultimately supports downstream fisheries,
10 resulted from the high net primary productivity of the floodplain. This observation is
11 particularly impressive because the median flow through the floodplain during the period of
12 measurement (23 m s⁻¹) was just 3% of the median flow through the main channel. Considered
13 collectively, these studies indicate that riparian/floodplain wetlands can be both sources and
14 sinks for phytoplankton and water-, animal- and wind-dispersed vascular plants with respect to
15 the river network.

16 17 **5.3.3.2. Vertebrates**

18 Animals, including many fish and mammals, move between riparian/floodplain wetlands
19 and the river network. When hydrologically connected, there is strong and abundant evidence
20 that fish can move between the main river channel and riparian/floodplain wetlands that, in some
21 cases, are seasonal or temporary. Such wetlands provide refuge, feeding, and rearing habitat for
22 many fish species and function as sources by augmenting recruitment to the river network;
23 examples include fish taxa in forested floodplain wetlands of the southeastern and southwestern
24 United States and salmonids of the northwestern United States such as Coho salmon
25 (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*; e.g., Wharton et al.,
26 1982; Matheney and Rabeni, 1995; Pease et al., 2006; Henning et al., 2007; Jeffres et al., 2008).
27 In one section of the mainstem Rio Grande in New Mexico, over 90% of the larval and juvenile
28 fish of six different captured species were from riparian areas with zero water velocity
29 (backwaters, former side channels, and isolated pools; Pease et al., 2006). Oxbow lakes are also
30 important habitats for fish feeding and rearing. Based on a 5-year study of fish in oxbow lakes,
31 Shoup and Wahl (2009) concluded that the entire floodplain should be considered a single
32 functioning unit that supports the overall biological integrity of a river (see also Section 5.6).
33 The use of riparian/floodplain wetlands by fish depends on many factors intrinsic to the
34 particular river system (e.g., periodicity and duration of floodplain inundation) and the
35 characteristics of the resident or migratory fish community (King et al., 2003).

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

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

15 Besides providing a form of biological connectivity that can link riparian/floodplain
16 wetlands and downstream waters, vertebrates in riparian areas can affect stream characteristics
17 and influence various forms of connectivity. Perhaps the most familiar example of this is the
18 beaver (*Castor canadensis*). Although it would seem that beaver damming should reduce
19 hydrologic connectivity through impoundment, their influence can be more complex. For
20 example, a study by Westbrook et al. (2006) found that beaver dams in the Colorado River
21 affected depth, extent, and duration of inundation resulting from a 10-year flood event. In
22 addition, beaver dams attenuated declines in water tables during drier summer periods in 25% of
23 their 58-ha study area. However, they concluded that the main hydrologic effects occurred
24 downstream, rather than near the dam (Westbrook et al., 2006). The hydraulic head generated by
25 the dam raised the water level above adjacent banks, resulting in lateral and downstream
26 spreading of flows during high- and low-flow periods; these effects extended over hundreds of
27 meters. For example, mottled soils occurred throughout the study area, suggesting that the dams
28 caused waterlogged soils for extended periods of time. Increased overbank flooding increases
29 hydrologic connectivity between riparian areas and streams. In contrast, when dams were
30 absent, flooding was limited to the area immediately adjacent to the stream channel. Beaver
31 dams can also affect stream biogeochemistry. For example, beaver dams modify nutrient cycling
32 and decomposition dynamics and can affect downstream transport of materials (Naiman et al.,
33 1988), e.g., they can serve as a source of methylmercury (Roy et al., 2009). Beaver dams can
34 also have an effect on fish species, such as coho salmon (Pollock et al., 2004).

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

1 (2012) provide evidence from analyses at three western National Parks for a trophic cascades
2 model where large predators can affect the morphology of river channels through intermediate
3 effects on ungulate browsers and riparian plant community structure. For example, extirpation
4 of wolves (*Canis lupus*) at Yellowstone National Park by the mid-1920s led to an increase in elk
5 (*Cervus canadensis*) numbers. This caused suppression and mortality of riparian willow (*Salix*
6 *spp.*) communities, ultimately resulting in changes to stream morphology such as bank erosion,
7 decreased sinuosity, increased active channel width, and increased amount of unvegetated
8 alluvium (Beschta and Ripple, 2012). Based on results from the three National Parks and other
9 sites, Beschta and Ripple (2012) concluded that the removal of apex predators due to extirpation
10 increased ungulate herbivory which altered riparian plant communities, thereby increasing bank
11 erosion that led to either widening of the active channel or channel incision. This, in turn,
12 reduced the frequency of overbank flows, which decreases hydrologic connectivity between the
13 riparian area and downstream waters.

14

15 **5.3.3.3. *Invertebrates***

16 Stream macroinvertebrates (e.g., insects, crayfish, mollusks) and microinvertebrates (e.g.,
17 daphnia, copepods, rotifers, gastropods) colonize nutrient-rich riparian areas and floodplains in
18 large numbers during seasonal or episodic immersion by rivers and streams (Junk et al., 1989; Ilg
19 et al., 2008). Macroinvertebrates and microinvertebrates (also called meiofauna) are the
20 intermediate link between primary producers (e.g., algae), detritus pools (e.g., leaf litter), and
21 predators (e.g., fish, amphibians) in river food webs (Malmqvist, 2002; Woodward and Hildrew,
22 2002; Stead et al., 2005; Woodford and McIntosh, 2010). The distribution of invertebrate
23 populations in dynamic river systems is governed by the location of resources required for
24 different needs and life stages, and invertebrates actively disperse to find and exploit resources
25 wherever they become available (Malmqvist, 2002). As with vascular plants, hydrologic
26 connectivity between channels and riparian/floodplain wetlands can significantly influence
27 macroinvertebrate community structure in riparian areas (Paillex et al., 2009).

28 Invertebrates have evolved two basic strategies to exploit habitats adjacent to streams and
29 rivers: (1) rapid colonization of flooded areas and short life cycles that complete before
30 floodplains dry down again, or (2) use of aquatic refugia or dormant life stages to persist in
31 permanent waters, the hyporheic zone, or floodplain soils between inundations (Tronstad et al.,
32 2007). To evaluate the relative importance of each strategy in the same river system, Jenkins and
33 Boulton (2003) compared the abundance and species composition of microinvertebrates
34 emerging from floodplain sediments to those transported by floodwater from instream habitats at
35 reach and catchment scales. Initially, most colonizers of newly flooded riparian habitats came
36 from distant upstream reaches of the river network, washed downstream by floodwaters. After a

1 few days, however, species hatching from eggs diapausing in soils greatly increased the diversity
2 and size of the river/floodplain community. This study illustrates two important points about
3 biological connectivity of river/riparian habitats:

- 4
5
6 1. Stream invertebrate communities are made up of species adapted to different stresses
7 in their environment (in this case, resilient species adapted to high flows and resistant
8 species adapted to desiccation).
- 9 2. Floods that periodically connect different parts of the river network generate potential
10 for gene flow across time and space by mixing individuals from different locations
11 (e.g., upstream/downstream, channel/floodplain) and different years (e.g., eggs that
12 might have diapaused for tens or even hundreds of years).

13
14 The findings by Jenkins and Boulton (2003), that resting egg banks in riparian soils are
15 important to the persistence of aquatic species and the composition of river communities, were
16 validated in a separate study by Frisch and Threlkeld (2005), who compared flood-pulse
17 colonization from a field study with laboratory hatching of copepod microcrustaceans from egg
18 banks of inundated soils in Mississippi. The laboratory samples showed that in the absence of
19 hydrologic connections, egg banks were sufficient for persistence of copepod populations; the
20 field samples showed that when hydrologic connections were present, water dispersal and
21 hatching from dormant stages were both important colonization pathways for copepods. In a
22 perched floodplain in Missouri, Fisher and Willis (2000) showed that flood-pulsed movement of
23 water and organisms between river channels and floodplains was bidirectional. Adaptations by
24 stream-dwelling invertebrates to variable moisture conditions, and rapid two-way dispersal to
25 exploit temporary or seasonal hydrologic connections, are strong evidence of long-term
26 biological connectivity between rivers and riparian areas.

27 Invertebrates that disperse by aerial means take advantage of flooded riparian habitats as
28 well. Tronstad et al. (2007) investigated aerial colonization of floodplains by insects during
29 multiple flood pulses having different inundation periods in an unregulated river in Alabama's
30 coastal plain. Floating colonization trays placed in floodplain waters in June, August,
31 November, and April were colonized by at least 41 genera in 21 families across 7 orders of
32 flight-capable insects. Insect densities varied across the period and reached a maximum in
33 August of about 80,000 individuals m^{-2} , most of which were seeking mates or oviposition sites
34 rather than foraging or hunting. High densities (21,291 individuals m^{-2}) of passively dispersing
35 (e.g., via wind or animal vectors) microcrustaceans also were observed. Vanschoenwinkel et al.
36 (2009) erected nine windsocks (sampling devices for aerially dispersing organisms) near
37 temporary rock pools for 1 month, during which 850 viable propagules (dormant eggs, larvae,

1 and adults) from 17 invertebrate taxa were collected. Results from these studies illustrate that
2 aerial dispersal from multiple taxonomic orders and phyla is a significant source of stream
3 invertebrate colonists in newly inundated floodplain habitats.
4

5 **5.4. UNIDIRECTIONAL WETLANDS**

6 **5.4.1. Introduction**

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

29 Below, we examine the physical (see Section 5.4.2), water quality (see Section 5.4.3),
30 and biological (see Section 5.4.4) effects of unidirectional wetlands on rivers and other
31 downstream waters. We then briefly consider the issue of geographic isolation in unidirectional
32 wetlands (see Section 5.4.5).
33

1 **5.4.2. The Physical Influence of Unidirectional Wetlands on Streams**

2 Section 3.4.1 provided a general description of how unidirectional wetlands can connect
3 to downstream waters via surface and groundwater flow (see Figure 3-18). In this section, we
4 give further details on these connections and discuss how such connections impact streamflow.
5

6 **5.4.2.1. Surface Water Connections**

7 Unidirectional wetlands can be connected by perennial surface flows to river networks.
8 For example, seeps are likely to have perennial connections to streams that provide important
9 sources of baseflow, particularly during summer (Morley et al., 2011). In a study in Maine,
10 seeps were found to provide 40–80% of streamwater during baseflow periods (Morley et al.,
11 2011). In other cases, surface connections between unidirectional wetlands and streams can be
12 intermittent or ephemeral. Rains et al. (2006; 2008) showed that California vernal pools, situated
13 on both clay and hardpan soils, connected with streams through channels containing transient
14 water flow. The series of vernal pools on the clay soils were filled with water for 200 days of the
15 year, and water spilled from these wetlands through the ephemeral channel for 60% of those days
16 (Rains et al., 2008). Drainage of wetlands via ditching can also produce surface water outflows
17 from depressional wetlands directly to streams (see Section 3.4.4).

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

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

4 **5.4.2.2. Groundwater Connections**

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

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

34 Whether a wetland recharges groundwater, is a site of groundwater discharge, or both, is
35 determined by topography, geology, soil features, and seasonal position of the water table
36 relative to the wetland. Shedlock et al. (1993), for instance, concluded that groundwater

1 discharged into a bog along Lake Michigan via a breach in the sediments underlying the wetland.
2 In dry periods when water tables are low, water tends to move out of wetlands into the
3 groundwater, while in wetter periods with higher water tables, water can flow in the opposite
4 direction from shallow groundwater into the wetlands (Phillips and Shedlock, 1993; Pyzoha et
5 al., 2008). Lide et al. (1995) observed both groundwater flow into and from a Carolina bay
6 wetland, with discharge to the wetland when the water table was high and recharge to the
7 groundwater when the water table was low. This exchange and temporary storage of water
8 represents a lag function that can make wetlands particularly important for groundwater recharge
9 during dry periods. Rosenberry and Winter (1997) indicated that groundwater discharge to a
10 wetland often alternates with flow from the wetland to groundwater, and the direction of flow is
11 controlled by the balance of recent precipitation with current evapotranspiration demands.

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

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

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

1 channel, unless the wetland feeds a losing stream that is completely disconnected from the river
2 network.

4 **5.4.2.3. *Effects of Unidirectional Wetlands on Streamflow***

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

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

27 The ability of wetlands to reduce flooding via storage varies with topography, wetland
28 type, antecedent moisture conditions, and available water storage capacity. Using stable
29 hydrogen and oxygen isotopes of water, McEachern et al. (2006) found that snowmelt in boreal
30 forests was discharged rapidly in a sloped catchment. In contrast, in a lowland catchment much
31 of the snowmelt was stored by wetlands, particularly by bogs with stream channel outlets. In
32 northern Canada, stream runoff was positively correlated with slope and the presence of channel
33 fens, but negatively correlated with lowland depressional bogs (Quinton et al., 2003). In a Light
34 Detection and Ranging (LiDAR)-based assessment of depressional wetlands in Florida, Lane and
35 D'Amico (2010) found an average potential wetland water storage capacity of 1,619 m³ ha⁻¹,
36 with values ranging from 1,283 m³ ha⁻¹ for palustrine scrub-shrub wetlands to 2,906 m³ ha⁻¹ for

1 palustrine aquatic-bed wetlands. A literature review study concluded that depressional wetlands
2 lacking a surface outlet (see Figure 3-18B, C, and D) overwhelmingly reduced or attenuated
3 flooding, but the results were more mixed for wetlands with surface water channel connections
4 to streams (Bullock and Acreman, 2003). Only half of the reviewed studies on wetlands that are
5 stream origins (see Figure 3-18A) reported reduced or delayed flooding, while a substantial
6 number of studies (27 of 66, or 41%) found that stream-origin wetlands actually increased flood
7 peaks.

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

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

25 Other wetlands, however, may actually reduce flows during dry periods. Bullock and
26 Acreman (2003) concluded that this was the case in two-thirds of the studies they surveyed.
27 Antecedent moisture conditions and available wetland storage could partially explain this
28 finding, in combination with relatively high evaporation rates from wetland-dominated
29 landscapes (Bullock and Acreman, 2003). One study cited in their review (Boelter and Verry,
30 1977) noted that two storms of nearly equal volume and intensity produced different runoff
31 responses from the same peatland. One storm occurring in the spring at a time of already high
32 water tables led to runoff. The other, in midsummer at a time of low water tables, increased the
33 water depth in the peatland but did not exceed the wetland's water storage capacity, precluding
34 runoff. This mechanism has been observed in simulations of prairie pothole hydrology, in which
35 wetlands reduced streamflow until storage capacity was exceeded (Haan and Johnson, 1968).
36 Thus, wetlands may function as a sink in dry periods if storage capacity is not exceeded and

1 evaporation rates surpass groundwater recharge. Where storage capacity is exceeded during
2 storm events in otherwise dry periods, catchments containing extensive wetlands can require
3 more time for water discharge to rise and fall in response to storm events (Lindsay et al., 2004).
4 This finding suggests that catchments with wetlands take longer to fill and exceed water holding
5 capacity than catchments without wetlands and so, in this case, they provide a lag function by
6 releasing water downstream more slowly.

8 **5.4.3. Effects of Unidirectional Wetlands on Water Quality**

9 Unidirectional wetlands can affect water quality of rivers and other aquatic systems
10 through processes that can be generalized as source and sink functions, often mediated by
11 transformational processes (see Section 5.3.2 for details on specific mechanisms). In some
12 cases, unidirectional wetlands directly modify the water quality in downstream waters through
13 their relative lack of surface water connections; this modification is accomplished by removal,
14 sequestration, or transformation of pollutants such as nitrogen, phosphorus, and metals through
15 processes described by Ewel and Odum (1984), Mitsch et al. (1995), Reddy and DeLaune
16 (2008), and Kadlec and Wallace (2009), among others. Although unidirectional wetlands can
17 lack surface water connections to downstream waters, surface and near-surface hydrologic
18 connections to downstream waters do occur in many unidirectional systems (Sun et al., 1995;
19 Whigham and Jordan, 2003; Wilcox et al., 2011; see Section 3.4.2 and Figure 3-18), providing
20 pathways for materials transformed in unidirectional wetlands (such as methylmercury or
21 degraded organic matter) to reach and affect other aquatic systems.

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

1 **5.4.3.1. Unidirectional Wetlands as Sources for Downstream Waters**

2 Like all wetlands, unidirectional wetlands contain diverse microbial populations that have
3 adapted to hydrologic, physical, and chemical extremes (Reddy and DeLaune, 2008). Microbial
4 populations abound in wetland systems; for instance, Boon (1991) reported that Australian
5 wetlands contained 100 times more microbes in the water column than nearby rivers, with up to
6 157×10^9 cells L⁻¹. Functions that occur in unidirectional wetlands can affect streams, rivers,
7 and lakes when compounds that are transformed in wetland environments move to downstream
8 waters through overland flow or shallow groundwater (Winter and LaBaugh, 2003; see Section
9 3.2.2). Two processes that occur in unidirectional wetlands (as well as in riparian/floodplain
10 wetlands) are useful to illustrate the influence of unidirectional wetlands on downstream waters:
11 the methylation and transport of the bioaccumulating pollutant mercury, and the breakdown and
12 transport of organic compounds to receiving waters.

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

29 Export of dissolved organic matter can have potentially negative effects on downstream
30 waters because contaminants, such as MeHg and other trace metals, can be adsorbed to it
31 (Thurman, 1985; Driscoll et al., 1995). Dissolved organic matter, however, is also an important
32 source of energy for downstream aquatic communities (Hobbie and Wetzel, 1992; Reddy and
33 DeLaune, 2008). Wetlands are the principal source of DOC to downstream waters in forested
34 ecosystems (Mulholland and Kuenzler, 1979; Urban et al., 1989; Eckhardt and Moore, 1990;
35 Koprivnjak and Moore, 1992; Kortelainen, 1993; Clair et al., 1994; Hope et al., 1994; Dillon and
36 Molot, 1997; Gergel et al., 1999). Over prolonged periods, reductions in DOC export (e.g.,

1 through wetland conversion or degradation or alterations in hydrology) decrease the ability of
2 downstream waters to support primary productivity, due to reduced export of entrained carbon,
3 nitrogen, sulfur, and phosphorus (Hedin et al., 1995; Nuff and Asner, 2001). Changes in DOC
4 export also affect the pH and buffering capacity of downstream aquatic systems (Eshelman and
5 Hemond, 1985) and their exposure to damaging UV-B rays (Schindler and Curtis, 1997). Boreal
6 forest basins composed of unidirectional wetlands in central Ontario were found to export
7 between 11.4 and 31.5 kg carbon ha⁻¹ yr⁻¹ to downstream waters (Creed et al., 2003).
8 Furthermore, near-surface lateral transport of DOC explained 88% of the variation in basin DOC
9 export to lake systems where it directly affected pH and buffering capacity. Other studies have
10 similarly shown a relationship between the proportion of wetlands in a drainage area and the
11 average annual concentration of DOC in the receiving streams of that area, and other areas of the
12 boreal forest/Precambrian Shield (Urban et al., 1989; Eckhardt and Moore, 1990; Koprivnjak and
13 Moore, 1992; Clair et al., 1994; Hope et al., 1994; Dillon and Molot, 1997).

14 The export of dissolved organic compounds from unidirectional wetlands can also have
15 an effect on the acidity of downstream waters. Gorham et al. (1986) addressed watershed factors
16 associated with lake and forest acidification in Nova Scotia, Canada. In addition to atmospheric
17 deposition of acid precipitates, they found that the ratio of unidirectional muskeg peatlands to
18 lakes was significantly correlated with lake acidification, as muskeg wetland-dominated
19 watersheds exported high-molecular-weight organic acids via either overland or shallow
20 groundwater flow. Further linking unidirectional wetlands to lakes, Gorham et al. (1986)
21 reported that even small amounts of humic DOC can greatly affect lake water pH; the pH of
22 waters with a dissolved organic carbon value of 4.5 mg DOC L⁻¹ (the log-normal mean) was
23 100 times more acidic than waters with a dissolved organic carbon of <1 mg DOC L⁻¹ (the
24 minimum concentration).

25

26 **5.4.3.2. *Unidirectional Wetlands as Sinks and Transformers for Downstream Waters***

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

1 Unidirectional wetlands act as sinks and transformers for various pollutants. For
2 instance, high levels of human sewage were applied to a forested unidirectional wetland site for
3 4.5 years (Ewel and Odum, 1984 and chapters therein). More than 95% of the phosphorus,
4 nitrate, ammonium, and total nitrogen (N) were removed by the wetland during the study period
5 (Dierberg and Brezonik, 1984), and 66–86% of the nitrate removed was attributed to the process
6 of denitrification. In another example, P retention in unidirectional marshes of the lower Lake
7 Okeechobee basin ranged from 0.3 to 8.0 mg soluble reactive P m⁻² d⁻¹ (Dunne et al., 2006).
8 This retention represents a sizeable amount of phosphorus removal, because only about 7% of
9 the watershed comprised unidirectional marsh. Unidirectional wetland flats studied in Maryland
10 and Delaware had microbially mediated denitrification enzyme activity (an indicator of potential
11 denitrification) rates of 0.06–0.76 mg N kg⁻¹ d⁻¹ (Jordan et al., 2007). Because flats comprise
12 greater than 70% of the wetland area in the basin, this value indicates a significant denitrification
13 capacity. A unidirectional bog in Massachusetts was reported to sequester nearly 80% of the
14 system's various nitrogen inputs, including precipitation that had a range of 1.2–1.9 mg N L⁻¹
15 (Hemond, 1983). Prairie pothole wetlands in the upper Midwest were found to remove >80% of
16 the nitrate load via denitrification (Moraghan, 1993). A large unidirectional prairie marsh was
17 found to remove 86% of nitrate, 78% of ammonium, and 20% of phosphate through assimilation
18 and sedimentation, sorption, and other mechanisms (Davis et al., 1981). Geographically isolated,
19 unidirectional wetland systems in Michigan were found to remove NO₃-N and sulfate (SO₄²⁻) at
20 rates of 0.04–0.55 mg NO₃-N L⁻¹ ha⁻¹ and 0.06–0.30 mg SO₄²⁻ L⁻¹ ha⁻¹. These rates are
21 significant, considering that nitrate-nitrogen pollution of groundwater in Michigan was reported
22 to average 0.50 mg NO₃-N L⁻¹ (Whitmire and Hamilton, 2008). Together, these studies indicate
23 that sink removal of nutrients by unidirectional wetlands is significant and geographically
24 widespread.

25 Other pollutants and compounds can be mitigated by unidirectional wetland sink and
26 transformation processes. For instance, microbial methanogenesis was found to completely
27 remove the pesticide atrazine from a mountainous bog in North Carolina (Kao et al., 2002). The
28 environmental contaminants cobalt (Co) and nickel (Ni) can be phytoremediated by wetland
29 plants common in forested unidirectional wetlands of the Southeast; plant concentrations were
30 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
31 in Massachusetts that Hemond (1980) extensively studied acted as a sink and annually stored
32 54 mg magnesium m⁻², 36 mg potassium m⁻², and 46 mg lead m⁻²; the bog also provided
33 acid-rain buffering for downstream waters. Based on the literature, Boon (2006) concluded that
34 wetland microbial communities can mediate processes that degrade diesel fuel and other
35 hydrocarbons, pesticides, heavy metals and metalloids, and chlorinated solvents that can pollute
36 groundwater.

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5.4.4. Biological Connections Between Unidirectional Wetlands and Streams

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

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

1 geographically isolated wetlands and river networks, depending on temporally dynamic habitat
2 availability (Murkin and Caldwell, 2000 and references therein; Haukos et al., 2006).

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

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

26 Recent evidence suggests that invertebrate hitchhiking on birds and mammals is more
27 common than previously thought (Figuerola and Green, 2002; Figuerola et al., 2005). Allen
28 (2007) trapped zooplankton dispersing from a pond in Illinois and found that animals wider than
29 3 cm were the primary vector of reproductive adult zooplankton forms. These results suggest
30 that animals moving among water bodies can be an important factor structuring unidirectional
31 wetland invertebrate metapopulations. Frisch et al. (2007) found that diapausing invertebrate
32 eggs that dispersed by hitchhiking on birds had higher incidences of hatching in January (59.4%)
33 than in November (11.5%). These invertebrates included nematodes, microcrustaceans (i.e.,
34 rotifers, ostracods, copepods), and insects (i.e., tipulids, chironomids, and hemipterans). This
35 study indicates that winter migrations of aquatic birds can be an important mechanism for spring
36 colonization of habitats separated by hundreds or even thousands of kilometers.

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

7 Amphibians and reptiles also move between streams or rivers and unidirectional wetlands
8 to satisfy part of their life-history requirements (see Table 5-2). For example, Subalusky et al.
9 (2009a; 2009b) reported movement of adult female alligators (*Alligator mississippiensis*) from
10 creeks to shallow, seasonal limesink wetlands for nesting and use of the wetlands as nurseries for
11 juveniles. Subadults then shift to habitats within the river network through overland movements
12 to the creek (Subalusky et al., 2009a; Subalusky et al., 2009b). Lamoureux and Madison (1999)
13 used radio tracking to follow movements of green frogs (*Rana clamitans*) for 9 months in New
14 York. Green frogs, which breed in wetlands and then move into terrestrial habitats, are
15 susceptible to freezing temperatures. In late autumn, the frogs moved from upland habitats near
16 breeding ponds to rapidly flowing streams and seeps to overwinter. Boreal toads (*Bufo boreas*
17 *boreas*) disperse long distances (>1 km) in streams through home ranges (Adams et al., 2005).
18 The American toad (*Anaxyrus [=Bufo] americanus*) and Eastern newt (*Notophthalmus*
19 *viridescens*) are widespread habitat generalists that move among streams and wetlands to take
20 advantage of both habitats, feed on aquatic invertebrate prey, and avoid predators (Babbitt et al.,
21 2003; Green, 2005; Hunsinger and Lannoo, 2005; Petranka and Holbrook, 2006; see Table 5-2).
22

23 **5.4.5. Geographic Isolation of Unidirectional Wetlands**

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

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

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

Common name	Scientific name	Habitat use
Green frog	<i>Rana clamitans</i>	Breeds in wetlands and pools; overwinters in streams (Lamoureux and Madison, 1999)
Leopard frog	<i>Rana pipiens</i>	Breeds in wetlands and pools; overwinters in streams (Rorabaugh, 2005)
Bullfrog	<i>Rana catesbeiana</i>	Uses seasonal pools as complementary nonbreeding habitat (Gahl et al., 2009)
Columbia spotted frog	<i>Rana luteiventris</i>	Breeds in streams and wetlands; overwinters in streams (Pilliod et al., 2002)
Southern leopard frog	<i>Rana sphenoccephala</i>	Breeds in shallow pools and wetlands; adults inhabit many shallow freshwater habitats, including temporary pools, cypress ponds, ponds, lakes, ditches, streams, river edges and floodplains, slightly brackish coastal wetlands (Butterfield, 2005)
Pacific chorus frog	<i>Pseudacris regilla</i>	Breeds in wetlands, ponds, temporary pools, streams, lakes, rivers, and other aquatic habitats (Rorabaugh and Lannoo, 2005)
American toad	<i>Anaxyrus [=Bufo] americanus</i>	Breeds in lakes, ponds, streams, ephemeral wetlands, prairie potholes, ditches, or floodplain pools (Green, 2005)
Fowler's toad	<i>Anaxyrus [=Bufo] fowleri</i>	Breeds in ponds, temporary pools, streams, ditches, lake shores, or shallows of rivers (Green, 2005)
Two-toed amphiuma	<i>Amphiuma means</i>	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	<i>Siren lacertina</i>	Breeds in shallow pools and streams, adults live in lakes, streams, ponds, and wetlands (Gibbons and Semlitsch, 1991; Hendricks, 2005)
Eastern newt	<i>Notophthalmus viridescens</i>	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)

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This document is a draft for review purposes only and does not constitute Agency policy.

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

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

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

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

27 Finally, it is noted that it is precisely this isolation that is responsible for many of the
28 services that geographically isolated wetlands provide to downstream waters. In particular,
29 many of the sink and lag functions that are supplied by these wetlands result from their relative
30 isolation with respect to the river network. It is the relative isolation of these wetlands,
31 combined with their storage capacity, that allows them to store water and reduce peak
32 streamflows and downstream flooding (Novitzki, 1979; Hubbard and Linder, 1986; Vining,
33 2002; Bullock and Acreman, 2003; McEachern et al., 2006; Gleason et al., 2007). For example,
34 depressional wetlands in Florida had an average potential wetland water storage capacity of
35 $1,619 \text{ m}^3 \text{ ha}^{-1}$ (Lane and D'Amico, 2010). These same sink and lag functions will also act on
36 any materials associated with stored water, such as sediments and pollutants. Increased isolation

1 can also decrease the spread of pathogens (e.g., Hess, 1996) and invasive species (e.g., Bodamer
2 and Bossenbroek, 2008), and increase the rate of local adaptation (e.g., Fraser et al., 2011).

3 4 **5.5. WETLANDS: SYNTHESIS AND IMPLICATIONS**

5 **5.5.1. Riparian and Floodplain Wetlands**

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

18 19 **5.5.2. Unidirectional Wetlands**

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

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

31 Based on what is known about how water flows across the landscape (see Chapter 3),
32 hydrologists and ecologists would generally agree that all unidirectional wetlands are
33 interconnected to some degree with each other and with stream networks; this is why the water
34 cycle environment is referred to as the hydrosphere. There also is general agreement among
35 hydrologists and ecologists that some areas are more connected or have a greater influence than

1 others. The purpose of this review is to determine, based on the peer-reviewed literature, the
 2 degree of connectivity and associated effects between different unidirectional wetlands and
 3 downstream waters.

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

Physical Connectivity and Function
<ul style="list-style-type: none"> 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.
<ul style="list-style-type: none"> Riparian connectivity ranges from longitudinal flow and exchange in mountainous headwater streams to increasing lateral flow and exchange in river valleys and coastal terrain.
<ul style="list-style-type: none"> 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.
<ul style="list-style-type: none"> 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.
<ul style="list-style-type: none"> Riparian areas influence stream geomorphology during periodic flooding through release of stored sediments.
<ul style="list-style-type: none"> Forested riparian areas provide woody debris that helps to shape stream morphology.
<ul style="list-style-type: none"> Riparian vegetation shades the stream and influences and regulates stream temperature and stream net primary productivity.
<ul style="list-style-type: none"> Groundwater that flows through riparian areas and into the stream helps moderate stream temperatures.
Chemical Connectivity and Function
<ul style="list-style-type: none"> Riparian areas, acting as buffers, are critical to protecting streamwater quality.
<ul style="list-style-type: none"> The structure of the riparian area (e.g., vegetation, wetlands, redox potential) influences its ability to effectively increase water quality before it reaches the stream.
<ul style="list-style-type: none"> The near-stream portion of a riparian area is often more important in protecting streamwater quality than is the near-field (adjacent to uplands) portion.
<ul style="list-style-type: none"> Allochthonous inputs are generally most important to food webs in small headwater streams, especially in forested areas. As rivers become larger, primary production becomes increasingly important.
<ul style="list-style-type: none"> 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
<ul style="list-style-type: none"> 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.
<ul style="list-style-type: none"> 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.
<ul style="list-style-type: none"> Riparian/floodplain wetlands provide food sources for stream and river invertebrates.
<ul style="list-style-type: none"> 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.

4

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

Physical Connectivity and Function
<ul style="list-style-type: none"> The connections of unidirectional wetlands with downstream waters exist along a spectrum from truly isolated depressional wetlands, to those connected through groundwater, to those connected via intermittent or permanent surface flows.
<ul style="list-style-type: none"> The degree to which outputs (or connections) are dominated by surface water vs. groundwater is controlled in part by soil permeability: Permeable soils favor groundwater outputs, while impermeable soils result in surface water outputs. Other factors, such as topographic setting, can also play a role.
<ul style="list-style-type: none"> Groundwater recharge is common in unidirectional wetlands and can be particularly important sources of water to aquifers during dry periods.
<ul style="list-style-type: none"> Groundwater networks extend from the local to the intermediate and regional scales, and provide a mechanism by which unidirectional wetlands can influence other water bodies over various time frames.
<ul style="list-style-type: none"> Even in cases where unidirectional wetlands lack a connection to other water bodies, they can influence downstream water through water storage and mitigation of peak flows (flood reduction/attenuation).
Chemical Connectivity and Function
<ul style="list-style-type: none"> Insofar as they often act as buffers between sources of pollution and riparian areas, unidirectional wetlands are a first line of defense in protecting streams from polluted waters.
<ul style="list-style-type: none"> Unidirectional wetlands affect nutrient delivery and water quality.
<ul style="list-style-type: none"> Unidirectional wetlands are a principal source for dissolved organic carbon (which supports primary productivity) to some downstream waters; the area of a basin with unidirectional wetlands is directly correlated to the contribution of that basin to dissolved organic carbon in downstream waters.
<ul style="list-style-type: none"> Unidirectional wetlands are sources of mercury: Microbial processes in unidirectional wetlands methylate mercury, which can be translocated through near-surface and surface flows to downstream waters where it can bioaccumulate.
<ul style="list-style-type: none"> Unidirectional wetlands are sinks for sediment, nutrients (including phosphorus, nitrate, and ammonium), metals (for example, nickel and cobalt), and pesticides (for example, atrazine).
<ul style="list-style-type: none"> Unidirectional wetlands can remove, retain, or transform many of the nutrient inputs to which they are exposed.
Biological Connectivity and Function
<ul style="list-style-type: none"> Natural periodic and permanent human-engineered surface water connections can connect biological communities in unidirectional wetlands and the river network; in addition, wind dispersal and overland movement connect these waterbody types with frequency decreasing as a function of distance and/or other landscape barriers.
<ul style="list-style-type: none"> Migratory birds are vectors of plant and invertebrate movement between unidirectional wetlands and the river network, though their influence has not been fully quantified.
<ul style="list-style-type: none"> Unidirectional wetlands promote biological interactions that can be important to the life history requirements of some stream species.
<ul style="list-style-type: none"> Overland (“fill-and-spill”) hydrologic connections can support biologic connections. For example, stream fish found in wetlands that periodically dry down indicate presence of surface flows sufficient for colonization.

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

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

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

30 The literature that we reviewed—which included more than 130 peer-reviewed articles
31 on unidirectional wetlands—does not provide us sufficient information to evaluate the type or
32 degree of connectivity (absolute or relative) or the variability in connectivity for those
33 unidirectional wetlands that lack surface water connections to downstream waters. This lack of
34 information applies to groups of these wetlands within a particular watershed and to comparisons
35 between different types of regional wetlands. For example, the literature does not tell us whether
36 connectivity between vernal pools and downstream waters is greater than connectivity between

1 prairie potholes and downstream waters. We emphasize that this does not mean these wetlands
2 do or do not have connectivity with downstream waters. Rather, it means that the literature we
3 reviewed does not allow us to distinguish connectivity of these wetland types from each other.
4 Literature that was not included in our review, such as reports from local resource agencies,
5 could allow the connectivity of these wetlands to be further evaluated, as could analysis of
6 existing or new data or field evaluation.

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

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

1 wetlands and downstream waters through groundwater connections, occasional spillage, or
2 biological connections. Thus, the term “geographically isolated” should not be used to infer lack
3 of hydrologic, chemical, or biological connectivity. Key conclusions from our literature review
4 on unidirectional wetlands are summarized in Table 5-4.

6 **5.6. CASE STUDY: OXBOW LAKES**

7 **5.6.1. Abstract**

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

15 **5.6.2. Introduction**

16 **5.6.2.1. *Origin and Description***

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

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

30 Oxbow lakes are an integral element in alluvial floodplain valleys of meandering rivers
31 around the world (Winemiller et al., 2000; Glinska-Lewczuk, 2009). Studies of these
32 ecosystems have been conducted in river floodplains in Australia (e.g., Crook and Gillanders,
33 2006), Europe (e.g., Hein et al., 2003), North America (e.g., Winemiller et al., 2000; Zeug et al.,
34 2005), and South America (e.g., da Silva et al., 2010). Due to the common origin, characteristics

1 of, and interactions between oxbow lakes and rivers, evidence from around the world is
2 presented here.

3 **5.6.3. Evidence**

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

9

10 **5.6.3.1. Physical Connections**

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

20 Regional- and local-scale climate and hydrogeologic patterns are important for
21 understanding the dynamics of physical connectivity between oxbow lakes and active river
22 channels. Regional differences influence the predictability of hydrologic connectivity between
23 rivers and oxbow lakes. In temperate rivers (e.g., Brazos River, TX), surface flow connections
24 between the river channel and oxbow lakes are likely to occur at irregular intervals, in response
25 to flow magnitude and lake geomorphology (Humphries et al., 1999; Zeug and Winemiller,
26 2008). Tropical rivers, in contrast, are likely to have more regular inundation patterns associated
27 with seasonal flooding (Junk et al., 1989; da Silva et al., 2010). The predictability of subsurface
28 connections also can vary regionally. An isotope tracer analysis of lakes in the Old Crow Flats,
29 Yukon Territory, Canada, indicated that oxbow lakes receive much of their water input from
30 shallow groundwater flow during the relatively short thaw season (Turner et al., 2010). The
31 regularity of connectivity has important implications for the exchange of chemical and biological
32 material between oxbow lakes and the river (e.g., Junk et al., 1989; Humphries et al., 1999).

33 Local landscape characteristics and position of water bodies in the floodplain influence
34 the relative contribution of surface and subsurface water movement between individual lakes and
35 the active river channel. A study of oxbow lakes on the Loire and Allier Rivers, France,

1 demonstrates this. Water in two oxbow lakes had different geochemical signatures, suggesting a
2 difference between when river water was introduced to the lakes (Negrel et al., 2003). The
3 younger oxbow lake was more connected to the surface network due to its closer proximity to the
4 river channel and a small stream connection, while an older oxbow lake, which was more distant
5 from the river channel, was more dependent on subsurface flow (Negrel et al., 2003).

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

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

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

1 **5.6.3.2. Chemical Connections**

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

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

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

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

1 nutrients in terrestrial runoff before the runoff reaches the river channel (Winemiller et al.,
2 2000).

3

4 **5.6.3.3. Biological Connections**

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

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

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

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

34 Connectivity between oxbow lakes in the floodplain and the active river channel is
35 important for maintaining mollusk populations in oxbow lakes. A comparison of three oxbow
36 lakes with different levels of connectivity (lotic, semilotic, and isolated) showed the highest level

1 of mollusk diversity in the semilotic lake (eight vs. four taxa in each of the other lakes) on the
2 Lyna River, Poland (Obolewski et al., 2009). In this example, the occurrence of taxa was
3 associated with physiochemical characteristics (oxygen, temperature, and phosphorus) of oxbow
4 lakes. These findings support the idea that the degree of oxbow lake-river connectivity
5 influences the abundance and composition of mollusk communities in floodplain water bodies,
6 and these communities support the diversity of mollusk taxa throughout the river system
7 (Reckendorfer et al., 2006).

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

16 Oxbow lakes have food resources and habitat that often support abundant fish
17 populations (Winemiller et al., 2000; Zeug et al., 2005; Zeug and Winemiller, 2008; Zeug et al.,
18 2009). A comparison of fish biomass in oxbow lakes and a river channel showed that fish
19 biomass in oxbow lakes was three times the biomass caught in rivers. Average catch per unit
20 effort in oxbow lakes was 364.3 g per 10-m seine haul and 5,318 g m⁻¹ ha⁻¹ of gillnet sampling,
21 versus 138.1 g per 10-m seine haul and 495 g m⁻¹ ha⁻¹ of gillnet sampling in the river
22 (Winemiller et al., 2000). Additional studies by this research group have found similar patterns
23 for juvenile fish (Zeug and Winemiller, 2008).

24 Periodic surface water connections between the river and oxbow lakes facilitate the
25 movement of fish from the river to oxbow lakes, where riverine fish can exploit these relatively
26 productive floodplain water bodies before moving back to the river. Dietary data provide
27 evidence that oxbow lakes are important spawning and nursery habitats for gizzard shad in the
28 Brazos River, TX (Zeug et al., 2009). Isotope analysis showed that gizzard shad in oxbow lakes
29 had different isotopic signatures based on habitat type: oxbow, river, and an oxbow-river mixture
30 (Zeug et al., 2009). Although oxbow lakes clearly provided habitat for both juvenile and adult
31 shad, the authors did not observe oxbow-specific isotopic signatures in shad in the river channel
32 (Zeug et al., 2009). In addition, an analysis of otolith chemical signatures by Crook and
33 Gillanders (2006) indicates that floodplain lakes were an important source of carp recruitment to
34 the Murray-Darling River, where floodplain lakes were estimated to be the source of 98% of the
35 young-of-year carp for areas 140 km downstream of the floodplain lakes. In a third example,
36 floodplain water bodies, with their diverse and productive habitats, were considered nurseries for

1 drifting larvae of migratory fish (Meschiatti et al., 2000). Half of the migratory fish species from
2 the Mogi-Guacu River, Brazil also were observed as juveniles in oxbow lakes along the river (24
3 of the 46 migratory riverine species were observed in 2 oxbow lakes), and most of the migratory
4 fish observed in oxbow lakes were juveniles, rather than larvae or reproductively mature age
5 classes (Meschiatti et al., 2000). This age structure suggests that the oxbow lakes were not the
6 site of reproduction, but were important habitats for juvenile fish.

7 Individual fish species have specific habitat and reproductive requirements and use
8 floodplain habitats in different ways, giving the dynamic hydrologic connectivity of oxbow lakes
9 and the river network added significance. For example, owing to variable flow in the Rio
10 Grande, NM, recruitment success varies between years of high (e.g., Junk et al., 1989) and low
11 flow (e.g., Humphries et al., 1999), which contributes to overall fish diversity in the Rio Grande
12 (Pease et al., 2006). Likewise, in a 5-year study of fish in floodplain lakes, Shoup and Wahl
13 (2009) discuss how individual oxbow lakes had different conditions and thus varied in suitability
14 for different fish species. In their study, interannual variability was present in oxbow lake
15 hydrology (lake-river connectivity ranged from 0 to more than 21 weeks per year) and water
16 chemistry, and in associated differences in fish assemblages (Shoup and Wahl, 2009). Because
17 of the complex relationships observed in their study, Shoup and Wahl (2009) concluded that the
18 entire floodplain should be considered a single functioning unit that supports the overall
19 biological integrity of a river.

21 **5.6.4. Oxbow Lakes: Synthesis and Implications**

22 The key findings of this case study are as follows:

- 23
24 • Evidence indicates the presence of physical, chemical, and biological connections
25 between oxbow lakes and the river channel. These connections are influenced by the
26 specific local and regional characteristics of both the oxbow lakes and the river.
- 27
28 • Some of the best-documented observed functions of oxbow lakes are as sources or
29 sinks for water, sinks for nutrients from upland runoff that might otherwise flow into
rivers, and both sources of food and refuges for riverine biota.
- 30
31 • Human alteration of these connections can be detrimental to the dynamics that
32 balance connectivity and exchange between oxbow lakes and the active river channel.
33 Practices that alter the natural flow regime of the river (e.g., river regulation) or
34 inhibit periodic flooding of oxbow lakes (e.g., levees) affect movement of water and
35 sediment, the use of oxbow lakes by riverine fish, and the regional biological
diversity of floodplain water bodies.
- 36
37 • Interannual variability in oxbow lake hydrology, water chemistry, and fish
assemblages demonstrate complex relationships between rivers and floodplain

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

3
4 Although the incidence of observed connectivity between oxbow lakes and river
5 networks varies according to spatial, temporal, physical, and biological factors, most of the
6 evidence examined indicates that oxbow lakes are important determinants of the physical,
7 chemical, and biological condition and function of rivers.

8 9 **5.7. CASE STUDY: CAROLINA AND DELMARVA BAYS**

10 **5.7.1. Abstract**

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

24 25 **5.7.2. Introduction**

26 **5.7.2.1. *Definition and Geographic Extent***

27 Carolina bays are elliptical, ponded, depressional wetlands that occur along the Atlantic
28 coastal plain from northern Florida to New Jersey (Prouty, 1952; Williams, 1996; Hunsinger and
29 Lannoo, 2005). They have been called geographically isolated wetlands (i.e., wetlands
30 surrounded by uplands; Tiner, 2003c), and range in water levels from permanently inundated to
31 frequently dry (Sharitz, 2003). Carolina bays range in size from greater than 3,600 ha to less
32 than 1 ha and are most abundant in North Carolina and South Carolina (Sharitz and Gibbons,
33 1982; Sharitz, 2003). Carolina bays that are geographically specific to the Delmarva Peninsula
34 are often referred to as Delmarva bays. Delmarva bays frequently have the same elliptical shape

1 and orientation as other Carolina bays (Stolt and Rabenhorst, 1987a), yet some lack the shape or
2 rim (Sharitz, 2003).

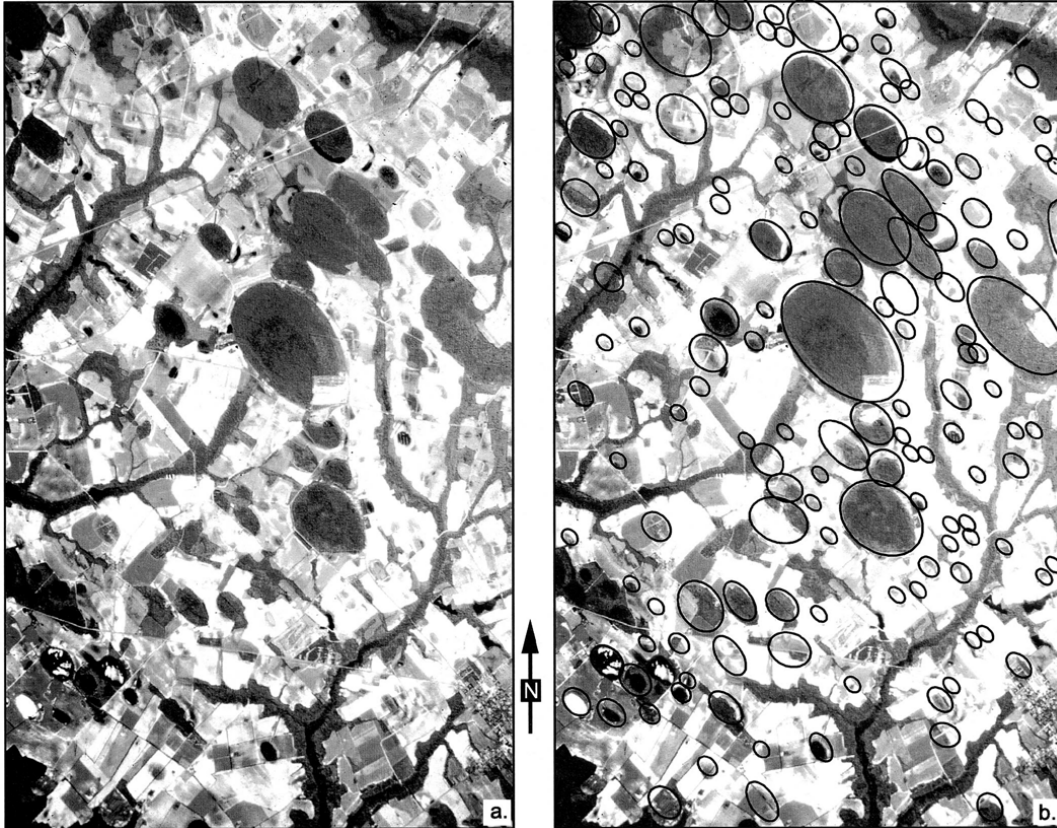
3 The number of Carolina bays was estimated at 500,000 in the 1950s (Prouty, 1952), but
4 only 10,000–20,000 remained by the early 1990s (Richardson and Gibbons, 1993). Carolina and
5 Delmarva bays have been ditched and drained for agricultural purposes (see Figure 5-1; Sharitz,
6 2003). A study of 2,651 Carolina bays in South Carolina found that 97% of bays larger than
7 0.8 ha had been disturbed by agriculture or logging (Bennett and Nelson, 1991). The northern
8 Delmarva Peninsula has an estimated 1,500–2,500 Delmarva bays remaining (Stolt and
9 Rabenhorst, 1987a). The true number of Carolina and Delmarva bays is likely to be
10 underestimated, because many are too small to be mapped. The National Wetlands Inventory
11 maps have mapping units of 0.4–1.2 ha, but the Department of Energy’s Savannah River Site on
12 the upper coastal plain of South Carolina has 371 known Carolina bays with 46% having an area
13 of 1.2 ha or less (Sharitz, 2003).

14 15 **5.7.2.2. Geology**

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

26 27 **5.7.2.3. Hydrology**

28 Carolina and Delmarva bays gain water primarily from precipitation and lose water by
29 evapotranspiration (Sharitz, 2003). Thus, these systems respond to seasonal rainfall, snowmelt,
30 and temperature. The water levels of Carolina and Delmarva bays therefore fluctuate. The water
31 level in a bay can change from 1–2 m above the soil surface to more than 1 m below the surface
32 (Knight et al., 1989; Schalles and Shure, 1989; Lide et al., 1995; Sharitz, 2003). Bays often are
33 wetter in winter and early spring, when evapotranspiration rates are low, and tend to dry down
34



1
2
3 **Figure 5-1. Aerial photograph of Carolina bays within a region of the upper**
4 **Coastal Plain of South Carolina.** (A) Infrared image showing the pattern of
5 intact and disturbed Carolina bays within a region of the upper Coastal Plain of
6 South Carolina (scale: 1 cm = 1.5 km), and (B) the same image with bays (or
7 former bays that have been disturbed by agriculture) outlined.
8

9 Reprinted with permission from Sharitz (2003).
10

11
12 in summer when evapotranspiration rates are high. Recent work by Lang et al. (2012) using
13 highly accurate LiDAR derived stream maps has shown that the proportion of wetlands
14 intersected by stream channels (and thus not geographically isolated) is higher than previously
15 thought. In an analysis of the Tuckahoe Creek watershed in the Delmarva Peninsula, the High
16 Resolution NHD and NHD Plus were found to underestimate the number of wetlands intersected
17 by natural stream channels by 13% and 27% respectively (Lang et al. 2012). Other hydrologic
18 inputs into bays include artesian wells (Wells and Boyce, 1953), shallow groundwater (Phillips
19 and Shedlock, 1993; Lide et al., 1995; Caldwell et al., 2007b), inlet channels (Sharitz, 2003), and
20 some surface runoff during periods of high rainfall. Some bays, particularly those along the
21 coast, can be flooded by high tides and thus are connected to coastal waters (Bliley and Pettry,
22 1979; Sharitz, 2003).

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

6 **5.7.2.4. Water Chemistry**

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

12 Newman and Schalles (1990) reported variable water chemistry in a study of 49 Carolina
13 bays in North Carolina and South Carolina that spanned two transects from inland to the coast.
14 All 49 bays were acidic (median pH = 4.6) and were classified as soft waters (median
15 calcium = 1.69 mg Ca²⁺ L⁻¹). DOC represented 38% of the water anions (median
16 DOC = 17.2 mg L⁻¹). Bays with thick peat layers tended to be low in nutrients, whereas bays
17 with thin peat layers had water quality characteristics similar to local groundwater (Newman and
18 Schalles, 1990). Phillips and Shedlock (1993) also associated bay water chemistry with shallow
19 groundwater; their study found similarities in water chemistry between upland groundwater and
20 the margins of three Delmarva bays. The few studies of nutrient cycling within bays indicate
21 some have the proper wetting and drying cycles to promote denitrification (the conversion of
22 nitrate to nitrogen gas; Groffman et al., 1992; Whigham and Jordan, 2003).

23 Several studies have shown that Carolina bays have the proper hydrology, organic matter
24 content, and pH for the methylation of mercury (Snodgrass et al., 2000b; Brant et al., 2002).
25 Mercury pollution enters water bodies from atmospheric deposition, typically in the ionic form
26 of Hg²⁺. Bacteria can convert Hg²⁺ to methylmercury, the bioavailable form of mercury that can
27 accumulate in fish, birds, and other organisms. Periodic drying and flooding of Carolina bays,
28 especially shallow ones, promotes mercury methylation and release (Snodgrass et al., 2000b).
29 Mercury levels did not reach acute doses but pose a chronic risk to fish (Snodgrass et al., 2000b)
30 and birds that feed on these fish (Brant et al., 2002).

31 32 **5.7.2.5. Biological Communities**

33 The wetting and drying cycles of Carolina and Delmarva bays promote a diverse biota,
34 including the presence of numerous rare and endemic species (Sutter and Kral, 1994; Edwards
35 and Weakley, 2001; Sharitz, 2003). Eleven types of vegetation communities have been

1 described in regional surveys of Carolina bays, including species-rich herbaceous communities
2 and cypress ponds (Bennett and Nelson, 1991; Weakley and Schafale, 1991). A seed bank study
3 at the Savannah River Site in South Carolina reported higher diversity than any other reported
4 freshwater wetland habitat (Kirkman and Sharitz, 1994). Researchers estimate that more than
5 one-third of rare plant species in the Southeast occur in nonalluvial wetlands including Carolina
6 bays (Sutter and Kral, 1994; Sharitz, 2003).

7 Carolina and Delmarva bays are highly valuable for providing habitat and food web
8 support for invertebrates and vertebrates (Sharitz, 2003). For example, a Savannah River Site
9 study of zooplankton found 44 species of cladocerans and 7 species of copepods (Mahoney et al.,
10 1990). Another invertebrate study showed that a 1.5-ha Carolina bay contained 115 taxa of
11 aquatic and semiaquatic insects from 29 families and 7 orders; more than 11,600 and
12 8,400 insects emerged from the bay in 1992 and 1993, respectively (Leeper and Taylor, 1998).

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

23 Sharitz and Gibbons (1982) also reported 6 turtle species, 9 lizard species, 19 snake
24 species, and 13 small mammal species in bays. American alligators (*Alligator mississippiensis*)
25 also are indigenous to southern Carolina bays (Sharitz and Gibbons, 1982). Endangered wood
26 storks (*Mycteria americana*) nest in Carolina bays, and birds such as egrets, coots, wood ducks,
27 and other migratory waterfowl also use Carolina and Delmarva bays (Sharitz and Gibbons,
28 1982).

30 **5.7.3. Evidence of Connectivity**

31 **5.7.3.1. Physical Connections**

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

1 A study by Lide et al. (1995) found a groundwater connection to a Carolina bay. The
2 study examined a 7-ha Carolina bay on the Savannah River Site typical of other bays in western
3 South Carolina with loamy-sand substrate and an underlying clay layer (Lide et al., 1995). The
4 2-year study examined data from 38 piezometers, borehole logs, pond stage records, and weather
5 data. They concluded that the Carolina bay was not a perched wetland, but a surface expression
6 of the water table. Although fluctuation of pond stage was largely controlled by precipitation
7 and evapotranspiration, nearly continuous shallow groundwater recharge was present and
8 shallow groundwater discharge occurred periodically.

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

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

23 Caldwell et al. (2007b) also used a model to understand the hydrology of three Carolina
24 bays in North Carolina and inferred groundwater connections. All three bays were larger than
25 100 ha, and their hydrology had not been altered by artificial drainage. Soil types were mineral
26 on the perimeter to mostly organic in the center. The team modeled bay hydrology using
27 climate, vegetation, soils, and hydrology data. They estimated that 10% of water inputs to the
28 bays were surface runoff. Groundwater inflow was the source of 3–26% of water volume into
29 the perimeter of the bays, and groundwater outflow volume (2–21%) was frequent in the center
30 of the bays (Caldwell et al., 2007b).

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

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

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

14 **5.7.3.2. Chemical Connections**

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

22 Carolina and Delmarva bays are frequently connected chemically to downstream waters
23 through ditches. If the bays are sediment and nutrient sinks due to their surficial isolation, ditch
24 connections would make them sources for these materials. For example, Bennet and Nelson
25 (1991) reported that 71% of 2,600 bays were disturbed by agriculture. Whereas the bays might
26 have been a nutrient sink for excess fertilizer that was in surface runoff, these nutrients could
27 now pass through the bays and into the ditches, reaching downstream locations. Additionally,
28 the conditions in Carolina bays have been shown to promote mercury methylation (Snodgrass et
29 al., 2000b). If these bays connect to downstream waters via ditches, some bioavailable mercury
30 would be expected to move to other waters.

32 **5.7.3.3. Biological Connections**

33 Carolina and Delmarva bays are “hotspots” for regional biological diversity and animal
34 use (Sharitz, 2003), which indicates a high potential for movement between bays and other water

1 bodies. The current published evidence for biological connections between bays and other
2 waters is, however, limited or indirect.

3 The presence of fish in Carolina and Delmarva bays indirectly demonstrates that these
4 bays are connected to other waters. For example, fish were found in 21% of 63 Carolina bays on
5 the Savannah River Site, many of which dry out during parts of the year; fish likely colonized
6 these bays through intermittent or permanent surface hydrologic connections (Snodgrass et al.,
7 1996). One Carolina bay in North Carolina, Mattamuskeet Bay, has been colonized by both
8 freshwater and estuarine fishes through four canals connecting the bay to Pamlico Sound
9 (Rulifson and Wall, 2006).

10 Insect emergence from bays can affect nearby waters. Leeper and Taylor (1998) studied
11 insects in a 1.5-ha Carolina bay and recorded 115 taxa representing 29 families. There were
12 39 genera of the family Chironomidae, 16 of which are known to live in both pond and stream
13 environments (Hudson et al., 1990; Leeper and Taylor, 1998). Although Leeper and Taylor
14 (1998) did not directly document movement, these species can hatch in Carolina bays and then
15 become important food sources for fish in nearby streams after adult emergence and aerial
16 dispersal. The total number of chironomids emerging from the aforementioned Carolina bay was
17 moderate compared to other wetlands, but cumulative emergence from thousands of bays across
18 the landscape would create a significant food source for organisms, including fish, in other
19 nearby waters.

20 Carolina and Delmarva bays are immensely productive amphibian breeding habitats, and
21 are critical for persistence of pond-breeding amphibian populations that can move to other water
22 bodies (Sharitz and Gibbons, 1982). Gibbons et al. (2006) documented more than
23 360,000 juvenile amphibians, from 24 species, emigrating from one Carolina bay during a single
24 breeding season. Greater than 95% of the biomass (about 1,330 kg) came from juveniles of the
25 southern leopard frog (*Rana sphenocephala*), which is known to use both stream and wetland
26 habitats (see Table 5-2). Given the finding that 12–19% of Carolina and Delmarva bays were
27 within 100 m of a tributary (Sharitz, 2003), amphibians emigrating from these bays could
28 transfer extremely high levels of energy and organic matter into rivers and streams. For
29 example, a gene flow study of the wood frog (*Rana sylvatica*), also abundant in Carolina bays,
30 determined that these frogs could move distances of more than 1,600 m (Semlitsch, 2000).
31 About 90% of Carolina bays located in the Savannah River Site have a tributary or river within
32 this distance (Sharitz, 2003).

33 34 **5.7.4. Carolina and Delmarva Bays: Synthesis and Implications**

35 The key findings of this case study are as follows:
36

- 1 • Both peat-based and mineral-based bays have been shown to have shallow
2 groundwater inputs and outputs.
- 3 • Some Delmarva bays have surface water connections to the Chesapeake Bay, and the
4 many bays within proximity to each other and to nearby permanent waters can be
5 connected during high precipitation events.
- 6 • Human channeling and ditching of the bays are widespread and create surface
7 connection to other waters.
- 8 • Fish are found in bays that periodically dry out, indirectly showing that a hydrologic
9 connection occurred at some time.
- 10 • Dispersive amphibians and reptiles use bays for breeding or rearing young.
- 11 • The abundant insects in bays could become part of the food chain for downstream
12 fish.

13
14 Although generally supporting the existence of or potential for connectivity between
15 Carolina and Delmarva bays and regional rivers or estuaries, the preponderance of evidence
16 found in the literature we reviewed for this case study is indirect. Furthermore, evidence from
17 this literature review that these connections influence the physical, chemical, and biological
18 conditions and functions of rivers or estuaries is circumstantial. Therefore, the literature that we
19 reviewed does not provide sufficient information to fully evaluate the impact of Carolina and
20 Delmarva bays on rivers and estuaries at this time.

21

22 **5.8. CASE STUDY: PRAIRIE POTHOLE**

23 **5.8.1. Abstract**

24 Prairie potholes are a complex of glacially formed wetlands, usually occurring in
25 depressions that lack permanent natural outlets, that are found in the central United States and
26 Canada. The vast area they occupy is variable in many aspects, including climatically,
27 topographically, geologically, and in terms of land use and alteration, which imparts variation on
28 the potholes themselves. Potholes demonstrate a wide range of hydrologic permanence, from
29 holding permanent standing water to wetting only in years with high precipitation, which in turn
30 influences the diversity and structure of their biological communities. Owing in large part to
31 their spatial and temporal variability, individual prairie potholes span the entire continuum of
32 connectivity to and isolation from the river network and other bodies of water. Potholes
33 generally accumulate and retain water effectively due to the low permeability of their underlying
34 soil, which can modulate flow characteristics of nearby streams and rivers. Potholes also can

1 accumulate chemicals in overland flow, thereby reducing chemical loading to other bodies of
2 water. When potholes are artificially connected to streams and lakes through drainage, isolation
3 is eliminated and they become sources of water and chemicals. Potholes also support a
4 community of highly mobile organisms, from plants to invertebrates to birds, that travel among
5 potholes and that can biologically connect the entire complex to the river network.

6 **5.8.2. Introduction**

7 Prairie potholes are a complex of wetlands and water bodies that cover more than
8 700,000 km² of the north-central United States and southern Canada, in an area referred to as the
9 PPR (Kantrud et al., 1989). Formed by the retreat of Pleistocene glaciers, potholes are shallow
10 depressions underlain by low-permeability, clay-rich glacial tills that allow for the collection and
11 temporary retention of water. Prairie potholes range widely in size from more than 200 ha to less
12 than 0.5 ha in surface area with an average of 1 ha or less (Cowardin et al., 1981; Kahara et al.,
13 2009). Their density across the landscape varies from region to region, from roughly
14 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
15 several factors, including patterns of glacial movement, topography, and climate (van der Valk
16 and Pederson, 2003; Kahara et al., 2009).

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

23 24 **5.8.2.1. Hydrologic Dynamics**

25 Prairie potholes are hydrologically dynamic and heterogeneous, varying both spatially
26 and temporally (Euliss et al., 2004). Water inflows consist largely of precipitation in the form of
27 spring snowmelt runoff or summer rain falling directly into the depressions (Carroll et al., 2005).
28 Some potholes also receive groundwater discharge (Winter and Rosenberry, 1998).
29 Evapotranspiration accounts for most of the water outflow in most potholes (Carroll et al., 2005;
30 van der Kamp and Hayashi, 2009). In some situations, water can leave the basin as overland
31 flow (known as “fill-and-spill”) and shallow or regional groundwater recharge. Potholes with
32 groundwater flow-through or with directional reversal of groundwater flow (discharge under
33 some conditions and recharge under others) have also been identified (Rosenberry and Winter,
34 1997).

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

14 Spatial variation in precipitation affects interannual variation in water level and
15 hydrologic permanence. The east-west gradient across much of the PPR delivers >800 mm of
16 average precipitation to northwestern Iowa each year and <500 mm of average precipitation to
17 most of North Dakota. These dynamics also depend on 20- to 200-year, large-scale climate
18 cycles, including periodic flood and drought conditions (Ashworth, 1999; Leibowitz and Vining,
19 2003). Annual average climate and longer climate cycles profoundly affect individual pothole
20 dynamics as well as interactions both among potholes and between potholes and broader
21 landscape features (Winter and Rosenberry, 1998; Johnson et al., 2004). Hydrologic dynamics
22 can have major effects on the diversity and abundance of biota (e.g., Euliss and Mushet, 2004).

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

34

1 **5.8.2.2. Chemical Functions**

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

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

18

19 **5.8.2.3. Ecological Characteristics**

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

30 Perhaps the best known and well studied attribute of prairie potholes is their role as
31 productive feeding and nesting habitat for waterfowl. Of the 34 species of duck that breed in
32 North America, 12 are common in the region, which contributes up to 80% of the continent's
33 waterfowl game (Batt et al., 1989). In addition, a diverse assemblage of microorganisms,
34 invertebrates, amphibians, reptiles, and sometimes fish, obligately or facultatively, use potholes

1 to feed or reproduce. For example, 44 different invertebrate taxa, including nematodes,
2 mollusks, and arthropods, were collected in Iowa potholes (Hentges and Stewart, 2010).

4 **5.8.3. Evidence**

5 **5.8.3.1. Physical Connections**

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

10 One of the most noted hydrologic functions of potholes is water storage. Because most
11 of the water outflow in potholes is via evapotranspiration, potholes can become water sinks,
12 preventing flow to other waters in their river or terminal lake basins. Several studies have
13 quantified the large water storage capacity of prairie pothole complexes. A conservative
14 estimate puts the amount of precipitation that can be retained in prairie potholes on land enrolled
15 in the federal Conservation Reserve Program and Wetland Reserve Program at more than
16 555 million m³ (Gleason et al., 2008). In various subbasins across the PPR, including those that
17 feed Devils Lake and the Red River of the North, both of which have a long history of flooding,
18 potholes have consistently been estimated to hold tens of millions of cubic meters of water
19 (Hubbard and Linder, 1986; Vining, 2002; Gleason et al., 2007).

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

1 numerous, including effects on stream geomorphology, habitat alteration, and ecological effects
2 (reviewed in Blann et al., 2009).

3 Studies in some regions show a lack of association between pothole water storage and
4 aspects of streamflow. For instance, modeling of an Iowa watershed indicated that total pothole
5 outflow and total maximum pothole volume do not impact streamflow characteristics (Du et al.,
6 2005). At the Minnesota watershed within the Red River basin discussed previously, simulated
7 annual and daily streamflow decreased with increased pothole water storage capacity but peak
8 streamflow was not reduced during a simulated flooding event, possibly due to an overwhelmed
9 capacity of wetlands and upland soils to retain additional water (Vining, 2004). In yet another
10 Minnesota watershed, wetland water storage provided no explanatory power in estimating peak
11 streamflows for small streams (Lorenz et al., 2010).

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

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

33 Individual potholes range from isolated to highly connected to other potholes via shallow
34 local and deeper regional groundwater flows. A high water table and soil pocketed with root
35 pores or fractures from wet-dry cycles promote water movement between wetlands via shallow
36 groundwater aquifers. In these cases, water moves most often from topographically high,

1 recharge wetlands to low, discharge wetlands (van der Kamp and Hayashi, 2009), although a
2 single wetland can shift from recharge to discharge in years where the water table is high
3 (Carroll et al., 2005). Other wetlands shift multiple times from recharge to discharge conditions
4 during a single year, which can either facilitate or prevent groundwater connections to adjacent
5 wetlands (Rosenberry and Winter, 1997). Potholes can connect to the river network via
6 groundwater if both are located within the zone of shallow local aquifer flows. One study in
7 North Dakota described prairie wetlands and lakes as water sources to the topographically low
8 James River via shallow groundwater flow (Swanson et al., 1988). Broader, regional movement
9 of groundwater is restricted by very low permeability clay-rich tills that can keep deep
10 groundwater recharge to only millimeters per year on average over a drainage basin (van der
11 Kamp and Hayashi, 1998).

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

25

26 **5.8.3.2. Chemical Connections**

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

1 agricultural runoff they receive to nitrous oxide or nitrogen gas. Denitrification can transform up
2 to 80% of nitrate that runs off into potholes (Crumpton and Goldsborough, 1998 and references
3 therein).

4 On the other hand, potholes that are periodically hydrologically connected to other bodies
5 of water via overland flow can transfer chemicals, such as dissolved ions (Leibowitz and Vining,
6 2003). Potholes modified by ditching or drainage also have increased hydrologic connectivity
7 and, therefore, chemical connectivity to other water bodies (Whigham and Jordan, 2003).

8 Wetlands drained for agriculture can contribute nitrogen, phosphorus, sediment, pesticides, and
9 herbicides to the waters into which they drain (reviewed in Blann et al., 2009). For example, two
10 wetlands in southwestern Minnesota fitted with surface drains that connected to subsurface tiles
11 emptying into the Watonwan River (a tributary of the Minnesota River) were found to be sources
12 of total solids and total phosphorus to the river during periods of high runoff (Ginting et al.,
13 2000).

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

22 23 **5.8.3.3. *Biological Connections***

24 Dispersal capabilities of organisms residing in potholes and features of the landscapes
25 they must traverse help determine the strength of biological connectivity. Although some
26 research has focused on internal seed and egg bank dynamics (e.g., van der Valk and Davis,
27 1978; Gleason et al., 2004), increasing evidence suggests that potholes are not biologically
28 isolated. In fact, the observation that potholes lack an endemic aquatic and semiaquatic flora or
29 fauna suggests that, at least over evolutionary time, potholes have been well connected
30 biologically to communities in other ecosystems (van der Valk and Pederson, 2003).

31 Organisms can move into and out of potholes via wind, water, or land, either by
32 self-propelling or hitchhiking on other mobile organisms. Many species of wetland plants and
33 insects are dispersed on the wind (Keiper et al., 2002; Soons, 2006), including cattail (*Typha*
34 *spp.*) seeds, which can disperse over huge areas (>80 ha; van Digglen, 2006) and have been
35 found to quickly, passively colonize previously drained, restored potholes (Galatowitsch and van
36 der Valk, 1996). Plants and invertebrates also can travel by becoming attached to or consumed

1 and excreted by waterfowl (Amezaga et al., 2002). Seeds of up to half a dozen common pothole
2 plants can be consumed and excreted by ducks in a viable state; because migrating waterfowl fly
3 such long distances, the maximum dispersal distance of these hitchhiking plants is estimated to
4 be 1,400 km (Mueller and van der Valk, 2002). Additionally, fast and efficient recolonization of
5 species in restored potholes, including floating aquatics and emergent perennials, is likely
6 facilitated by waterfowl movement (Aronson and Galatowitsch, 2008). Waterfowl often move
7 between wetlands during the breeding season in search of food and cover, and some species also
8 use habitats within the river network as wetlands dry or freeze (Pattenden and Boag, 1989;
9 Murkin and Caldwell, 2000). Water also can provide a means for biologically connecting
10 potholes. Fish and other organisms or parts of organisms that can be suspended in water (e.g.,
11 floating insect larvae or seeds) have been hypothesized to move between potholes during spillage
12 events (Zimmer et al., 2001; van der Valk and Pederson, 2003; Herwig et al., 2010). Dispersal
13 of waterborne organisms also can occur through manmade waterways (i.e., ditches) that connect
14 potholes to stream networks (Hanson et al., 2005; Hentges and Stewart, 2010; Herwig et al.,
15 2010). Most of these studies cite only anecdotal evidence for dispersal through ditches.
16 Populations of aquatic plants in agricultural ditches in Europe, however, are genetically highly
17 structured along these man-made waterways, suggesting that these watercourses determine
18 dispersal pathways (Gornall et al., 1998).

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

30 Landscape features, including distance, relief, and human alterations, can promote or
31 restrict biological connections between wetlands and larger bodies of water. Distance is a major
32 factor: For a given species, wetlands located closer together will exchange more organisms than
33 wetlands that are farther apart. Therefore, landscapes in which potholes are located in relative
34 proximity to each other and to the river network are likely to be connected more frequently and
35 by more species. For example, restored potholes in pothole-dense areas tend to be recolonized
36 by plants more efficiently (Mulhouse and Galatowitsch, 2003), and high pothole density

1 promotes greater movement of waterfowl (Krapu et al., 1997). Unfortunately, quantification of
2 biological effects of potholes on larger waters is severely limited. In most cases, studies
3 involving biological isolation or connectivity in the PPR have focused on the potholes
4 themselves as sources and recipients of organisms.

6 **5.8.4. Prairie Potholes: Synthesis and Implications**

7 The key findings for this case study are as follows:

- 8
- 9 • The degree to which prairie potholes are connected or have the potential to connect to
10 river networks depends on many factors. These factors include distance to rivers or
11 streams, topography, precipitation, climate cycles (seasonal and on longer time
12 scales), biotic community composition, and artificial drainage. Within the PPR,
13 distance to rivers and streams is strongly influenced by the three major physiographic
14 regions (Red River Valley, Drift Prairie, and Missouri Coteau), which vary in the
15 number of potholes and stream density (e.g., see Figures 3-20A and B).
- 16 • On a watershed scale, unaltered potholes often function as hydrologic sinks,
17 sequestering water and reducing annual streamflow, but can become sources as they
18 spill overland under high precipitation and/or low relief. When artificially drained or
19 ditched, potholes can become sources of water, nutrients, sediment, and pesticides.
20 Their roles as sinks and sources affect river geomorphology and biological
21 communities.
- 22 • Potholes also might have direct biological effects on river networks via connectivity
23 of resident populations, although these effects are less well known and studied.

24

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

33 **5.9. CASE STUDY: VERNAL POOLS**

34 **5.9.1. Abstract**

35 Vernal pools are shallow, seasonal wetlands that accumulate water during colder, wetter
36 months and gradually dry down during warmer, dryer months. Despite differences in geology,
37 climate, and biological communities, some common findings about the hydrologic connectivity

1 of vernal pools in different regions include evidence for temporary or permanent outlets, frequent
2 filling and spilling of higher pools into lower elevation swales and stream channels, and
3 conditions supporting subsurface flows through pools without perched aquifers to nearby
4 streams. Insects and amphibians that can live in streams or permanent pools opportunistically
5 use glaciated vernal pools as alternative breeding habitat, refuge from predators or environmental
6 stressors, hunting or foraging habitat, or stepping-stone corridors for dispersal and migration.
7 Nonglaciated vernal pools in western states are reservoirs of biodiversity and can be connected
8 genetically to other locations and aquatic habitats through wind- and animal-mediated dispersal.
9

10 **5.9.2. Introduction**

11 The term vernal pool is broadly used to describe shallow, fishless pools situated on
12 bedrock or low-permeability soils that lack continuous surface water connection to permanent
13 water bodies but have a seasonal period of inundation on which aquatic species depend for
14 completion of their life cycles (Zedler, 2003). This case study reviews evidence for physical and
15 biological relationships between vernal pools and downstream waters in the western United
16 States (western vernal pools) and glaciated areas of northeastern and midwestern states (northern
17 vernal pools), where vernal pools are particularly abundant (Zedler, 2003).
18

19 **5.9.2.1. Geography and Geology**

20 **5.9.2.1.1. Western vernal pools**

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

29 Historically, vernal pools covered 518 km², or 5–6% of the total land surface in southern
30 California and northern Baja, but losses in that area have been substantial (Bauder and
31 McMillan, 1998). Pools occur on impermeable or slowly permeable soils or bedrock (Smith and
32 Verrill, 1998) that limit percolation and thus produce surficial aquifers that perch above regional
33 groundwater aquifers. Pool-forming soil layers in this region include clay-rich soils,
34 silica-cemented hardpans (duripans), volcanic mudflows, or bedrock (Weitkamp et al., 1996;
35 Hobson and Dahlgren, 1998; Smith and Verrill, 1998; Rains et al., 2006). Because their

1 hydrology and ecology are so tightly coupled with the local and regional geological processes
2 that formed them, western vernal pools typically occur within “vernal pool landscapes” (Smith
3 and Verrill, 1998), or complexes of pools in which swales connect pools to each other and to
4 seasonal streams (Weitkamp et al., 1996; Rains et al., 2008).

5 **5.9.2.1.2. Northern vernal pools**

6 The geological formations underlying northern vernal pool landscapes were formed by
7 the movement of glaciers across the northeastern and north-central states approximately
8 12,000 years ago. Retreating glaciers scoured basins in rock ledges and mountaintops, or left
9 behind large pieces of ice that later collapsed to form topographic depressions containing
10 deposits of gravel, sand, or mud (Colburn, 2004). Although not all vernal pools in these areas
11 were formed by glaciers, the soils, geology, and evolutionary history of plants and animals in
12 northern vernal pools have been profoundly affected by glacial events. Like western vernal
13 pools, northern vernal pools are significantly grouped or clustered (Brooks, 2005). Grant (2005)
14 found that pools in Massachusetts are more likely to occur in more porous substrates (alluvial,
15 fine grained, or sand/gravel soils) than glacial till or impermeable bedrock, increasing their
16 hydrologic connection to shallow groundwater.

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

21

22 **5.9.2.2. Temporal Dynamics**

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

26

27

28 • Wetting or newly flooded phase: Rainwater, snow, runoff, or snowmelt infiltrate
29 upper layers of permeable soil and, when topsoils are saturated, collect in pool basins
30 formed by impervious rock, clay, or till layers (aquitards or aquicludes; Rains et al.,
31 2008). In early spring, perennial plants sprout and stored seeds germinate in wet
32 soils. Aquatic invertebrate communities develop from resting eggs and seed banks
33 (Colburn, 2004).

34 • Aquatic phase: Soils are saturated and pools hold standing water, in many locations
35 filled to capacity. In some western vernal pools, surface and subsurface flows from
36 upland pools through swales feed downgradient pools, connecting pools at a site and

1 extending the aquatic phase of the pool complex (Weitkamp et al., 1996; Hanes and
2 Stromberg, 1998). Pools are colonized by dispersing insects and breeding
3 amphibians.

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

9
10 In the western United States, vernal complexes saturate and begin to pool during winter
11 rains, reach maximum depth by early spring, and lose all standing water by late spring (Zedler,
12 1987). The timing of filling and drying of northern vernal pools vary, depending on pool type.
13 Colburn (2004) proposed five hydrologic classes for northern vernal pools, based on time of
14 filling and average duration of flooding: (1) short-cycle, spring-filling pools that stay wet for
15 3–4 months; (2) long-cycle, spring-filling pools that stay wet for 5–8 months; (3) short-cycle,
16 fall-filling pools that stay wet for 7–9 months; (4) long-cycle, fall-filling pools that stay wet for
17 9–11 months; and (5) semipermanent pools that stay wet for 36–120 months. Many northern
18 vernal pools do not dry down completely, but retain areas of saturated sediment or standing
19 water in part of the basin. Such pools are considered “incompletely dry,” to differentiate them
20 from pools that are “continuously flooded” or “dry.”

21 22 **5.9.2.3. Ecology**

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

1 (including streams or lakes) use inundated pools periodically for refuge, reproduction, or feeding
2 (King et al., 1996; Williams, 1996; Colburn, 2004).

4 **5.9.3. Evidence**

5 **5.9.3.1. *Physical Connections***

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

13 **5.9.3.1.1. *Western vernal pools***

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

25 Results showed that high and low pools were connected via surface flows 10–60% of the
26 time; surface water flowed through swales connecting low-elevation pools to streams during
27 60% of the inundation period (see Table 5-5). Underlying geology and soil type influenced
28 ponding rates and inundation periods: in water year 2003, pools in clay-rich soils accumulated
29 water at the onset of rainfall and held water longer than pools in hardpan soils, which have
30 higher soil infiltration rates (see Table 5-5; Rains et al., 2008). Horizontal subsurface flows
31 reduced the number and volume of higher-elevation surface flows into hardpan pools, relative to
32 the clay-rich pools. Most water discharging from the swale to the seasonal stream at the hardpan
33 site was perched groundwater that had flowed around, rather than through, the pool basins. In
34 both soil types, however, vernal pool basins, swales, and seasonal streams were shown to be part

1 of a single surface water and shallow groundwater system connected to the river network when
 2 precipitation exceeds storage capacity of the system (Rains et al., 2006; Rains et al., 2008).

3
 4

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

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

^aOctober 1 2002–September 30, 2003.

5
 6

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

18

19 **5.9.3.1.2. Northern vernal pools**

20 Northern vernal pools include both perched and groundwater-connected aquifers (Brooks,
 21 2004; Boone et al., 2006). As in western vernal pools, rainfall or snowmelt in excess of pool
 22 capacity is lost to surface runoff or subsurface flows into shallow, adjacent groundwater (Brooks,
 23 2005). Studies of surface and subsurface inflows and outflows were not found in the literature.

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

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

14 **5.9.3.2. *Biological Connections***

15 Dispersal of vernal pool organisms can be active or passive and occurs at multiple scales:
16 local scale (among adjacent pools), neighborhood scale (among pools in a geographic cluster or
17 complex), or regional (outside of the complex, to other ecosystem types; Compton et al., 2007).
18 Examples of active regional dispersal include insect flight or juvenile dispersal by amphibians.
19 Passive transport is of particular interest for regional-scale dispersal, as it allows plants and
20 low-vagility animals such as microcrustaceans to move over long distances. Examples of
21 passive transport to and from unidirectional wetlands and pools include water-mediated dispersal
22 of larvae (e.g., Hulsmans et al., 2007); transport of diapausing (dormant) eggs by waterbirds
23 (e.g., Figuerola et al., 2005; Frisch et al., 2007) or flying insects (e.g., Van De Meutter et al.,
24 2007); and wind-mediated dispersal of dormant eggs, larvae, and adult zooplankton from dry
25 rock pools (Vanschoenwinkel et al., 2009).

26 Western vernal pools are highly productive ecosystems that have evolved in what Zedler
27 (2003) describes as a “balance between isolation and connectedness.” Pacific vernal pool
28 landscapes are tightly coupled with variable climate, soils, and geological formations in the
29 western United States, producing diverse habitats for organisms with different life-history
30 strategies (Bauder and McMillan, 1998). Seasonal wetlands in this region might have served as
31 evolutionary refuges since Mesozoic times (King et al., 1996). As a result, present-day vernal
32 pool communities have a large proportion of passively dispersing, endemic (i.e., restricted to
33 small geographic area) species in genera that are widely distributed across continents and aquatic
34 systems (King et al., 1996; Keeley and Zedler, 1998; Zedler, 2003). This apparent paradox is
35 explained by the fact that individuals transported passively over long distances have colonized,
36 and through time become locally adapted to, different vernal pool landscapes, creating new

1 endemic species from the root stock of ancient lineages. As a result, Pacific vernal pools are
2 now rich reservoirs of genetic and species diversity connected to other locations and aquatic
3 habitats through continuing dispersal. The existence and connectivity of such reserves are
4 especially important at a time when changing climatic conditions are likely to increase
5 intermittency of stream flows and decrease duration of wetland inundations in other areas.

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

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

30 **5.9.4. Vernal Pools: Synthesis and Implications**

31 The key findings from this case study are as follows:

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

- 1 • Documented evidence of surface flows connecting western vernal pool complexes to
2 the river network via swales and seasonal streams is available in the literature.
- 3 • Indirect evidence indicates that surface and subsurface flows connect northern pools
4 without perched aquifers to shallow groundwater and thus to nearby streams.
- 5 • Many insects and amphibians that can live in streams or more permanent pools
6 opportunistically use northern vernal pools as alternative breeding habitat, refuge
7 from predators or environmental stressors, hunting or foraging habitat, or
8 stepping-stone corridors for dispersal and migration.
- 9 • Nonglaciaded vernal pools in western states have achieved a long-term “balance
10 between isolation and connectedness” and have functioned as refuges for plant and
11 animal diversity since the Mesozoic era. They are current reservoirs of biodiversity
12 connected genetically to other locations and aquatic habitats through continuing
13 dispersal.

14
15 Direct evidence supports the existence of seasonal hydrologic connections and indirect
16 evidence supports the movement of organisms between western vernal pool complexes and
17 streams. Indirect evidence supports the existence of hydrologic and biological connections
18 between northern vernal pools and river networks, with potential for storing water during the wet
19 season, and providing alternative breeding habitat or food resources for stream biota.

6. CONCLUSIONS AND DISCUSSION

6.1. MAJOR CONCLUSIONS

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

1. The scientific literature demonstrates that streams, individually or cumulatively, exert a strong influence on the character and functioning of downstream waters. All tributary streams, including perennial, intermittent, and ephemeral streams, are physically, chemically, and biologically connected to downstream rivers via channels and associated alluvial deposits where water and other materials are concentrated, mixed, transformed, and transported. Headwater streams (headwaters) are the most abundant stream type in most river networks, and supply most of the water in rivers. In addition to water, streams transport sediment, wood, organic matter, nutrients, chemical contaminants, and many of the organisms found in rivers. Streams are biologically connected to downstream waters by the dispersal and migration of aquatic and semiaquatic organisms, including fish, amphibians, plants, microorganisms, and invertebrates, that use both up- and downstream habitats during one or more stages of their life cycles, or provide food resources to downstream communities. Physical, chemical, and biological connections between streams and downstream waters interact via processes such as nutrient spiraling, in which stream communities assimilate and chemically transform large quantities of nitrogen and other nutrients that would otherwise increase nutrient loading downstream.
2. Wetlands and open-waters in landscape settings that have bidirectional hydrologic exchanges with streams or rivers (e.g., wetlands and open-waters in riparian areas and floodplains) are physically, chemically, and biologically connected with rivers via the export of channel-forming sediment and woody debris, temporary storage of local groundwater that supports baseflow in rivers, and transport of stored organic matter. They remove and transform excess nutrients such as nitrogen and phosphorus. They provide nursery habitat for breeding fish, colonization opportunities for stream invertebrates, and maturation habitat for stream insects. Moreover, wetlands in this landscape setting serve an important role in the integrity of downstream waters because they also act as sinks by retaining floodwaters, sediment, nutrients, and contaminants that could otherwise negatively impact the condition or function of downstream waters.
3. Wetlands in landscape settings that lack bidirectional hydrologic exchanges with downstream waters (e.g., many prairie potholes, vernal pools, and playa lakes) provide numerous functions that can benefit downstream water quality and integrity. These functions include storage of floodwater; retention and transformation of nutrients, metals, and pesticides; and recharge of groundwater sources of river baseflow. The functions and effects of this diverse group of wetlands, which we refer to as “unidirectional wetlands,” affect the condition of downstream waters if there is a surface or shallow subsurface water connection to the river network. In

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

16
17 **6.2. DISCUSSION**

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

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

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

26 Connectivity has long been a central tenet for the study of water. The River Continuum
27 Concept (Vannote et al., 1980) viewed the entire length of rivers, from source to mouth, as a
28 complex hydrologic gradient with predictable longitudinal patterns of ecological structure and
29 function, in which downstream communities are structured, in part, by upstream communities
30 and processes (Vannote et al., 1980; Battin et al., 2009). The Serial Discontinuity Concept
31 (Ward and Stanford, 1983) built upon the River Continuum Concept to better understand how
32 dams and impoundments disrupt the longitudinal patterns of flowing waters with predictable
33 effects downstream. The Spiraling Concept (Webster and Patten, 1979; Newbold et al., 1981;
34 Elwood et al., 1983) described how the connectivity in river networks can be evaluated and
35 quantified as materials cycle from dissolved forms to transiently stored forms taken up by living
36 organisms and then released back to the water (see Figure 3-14). While these previous

1 frameworks focused on the longitudinal connections of river ecosystems, the subsequent Flood
2 Pulse Concept (Junk et al., 1989) examined the importance of lateral connectivity to adjacent
3 floodplains, including wetlands and open-waters, through seasonal expansion and contraction of
4 flood waters. Ward (1989) summarized the importance of connectivity to lotic ecosystems along
5 longitudinal, lateral, vertical (surface-subsurface), and temporal dimensions, and concluded that
6 running water ecosystems are open systems that greatly interact both with contiguous habitats
7 and other ecosystems in the surrounding landscape.

8 While scientists long focused on the hydrologic connectivity represented by the physical
9 structure of river networks, more recently they have incorporated the network structure explicitly
10 in conceptual frameworks to describe ecological patterns in river ecosystems, and the processes
11 linking them to other watershed components, including wetlands and open-waters (Power and
12 Dietrich, 2002; Benda et al., 2004; Nadeau and Rains, 2007a; Rodriguez-Iturbe et al., 2009).
13 Application of metapopulation theory and population genetic theory to natural populations has
14 greatly improved our understanding of the role of dispersal and migration in the demographic
15 persistence, community assembly, and evolution of aquatic species (Hastings and Harrison,
16 1994; Moilanen and Hanski, 1998; Hanski, 1999; Pannell and Charlesworth, 2000; Fagan, 2002;
17 Bohonak and Jenkins, 2003; Waples, 2010; Fronhofer et al., 2012). Network Dynamic
18 Hypothesis (Benda et al., 2004) reexamines the earlier, linearly driven concepts within context of
19 the patchy and stochastic nature of lotic ecosystems described by others (e.g., Resh et al., 1988;
20 Townsend, 1989; Rice et al., 2001). The Network Dynamic Hypothesis was a physically based
21 framework for predicting heterogeneity patterns seen along a river attributed to confluence
22 effects of tributaries, reflecting a more realistic river network perspective (Benda et al., 2004).
23 Bunn and Arthington (2002) identified natural variability of flows and associated lateral and
24 longitudinal connectivity of stream channels and floodplains as two of the four principle
25 mechanisms linking hydrology to aquatic biodiversity of riverine species (see also Leigh et al.,
26 2010). In a novel study of an ecosystem complex of interlinked estuarine, tidal wetland, and
27 freshwater habitats, Sheaves (2009) focused on the ecology of the key connections among the
28 different habitat types, rather the ecology of each habitat type by itself. This case study
29 emphasized the importance of ecological connectivity—which includes process-based
30 connections that maintain habitat function (e.g., nutrient dynamics, trophic function) as well as
31 movements of individuals—in the persistence of aquatic organisms, populations, communities,
32 and species, over the full range of conceptual time scales.

33 The processes and effects of interest here are those relevant to concepts of “chemical,
34 physical, and biological integrity,” the objective of Clean Water Act programs and basis for the
35 assessment endpoints and metrics used in local, state, and national biomonitoring programs.
36 Figure 6-1 is a simplified conceptual diagram relating hydrologic, chemical, and biological

1 connectivity of freshwater systems to metrics and indicators used in EPA’s national assessments
2 of streams, rivers, lakes, wetlands, and coastal waters. Monitoring programs emphasize
3 integrative, biological measures of water resource structure and function to detect impairments,
4 identify probable causes, and take corrective action. Biological communities are essential
5 components of sustainable, highly functioning aquatic ecosystems. Additionally, biological
6 organisms and communities integrate the effects of transitory and chronic stressors present in the
7 environment and have been used for decades to successfully track changes in the condition of
8 water resources at local, regional, and national scales (Karr, 1991; Barbour et al., 1995; Stoddard
9 et al., 2006; Paulsen et al., 2008). Altered connectivity produces a suite of stressors by
10 modifying the natural biological processes, material fluxes, and energy fluxes that link watershed
11 components (see Figure 6-1) with measurable effects on downstream ecosystems. Relating
12 observed effects to probable causes requires not only reliable measures of candidate stressors and
13 observed effects, but also a clear understanding of the intermediate processes that link them
14 mechanistically (US EPA, 2010). Multiple indicators and measures have been proposed for
15 detecting and quantifying altered connectivity (With et al., 1997; Tischendorf and Fahring, 2000;
16 Moilanen and Nieminen, 2002; Calabrese and Fagan, 2004; Martin and Soranno, 2006; Fullerton
17 et al., 2010; Hermoso et al., 2012). In some cases, the impairment results from structural
18 alteration of landscape attributes (e.g., dam construction, channel incision, loss of overland
19 dispersal corridors). These impairments are relatively easier to detect and quantify than
20 impairment of functional processes (e.g., altered nutrient dynamics, reduced gene flow), but both
21 have important consequences for the short- and long-term integrity of freshwater ecosystems.
22 Palmer and Febria (2012) propose that a combination of structural and functional metrics will
23 perform better than either type individually to monitor condition and identify causes of
24 impairment for restoration. This approach is appropriate for detecting and assessing altered
25 connectivity, which has both structural and functional definitions and is an integral component of
26 both aspects of aquatic ecosystem integrity. To this end, systematic approaches that are rooted in
27 landscape analysis and which incorporate hydroecological dynamics present in streams and in
28 wetland complexes are more likely to be successful in providing information useful for inferring
29 when and where altered connectivity is a cause of impairment to national water resources.
30
31

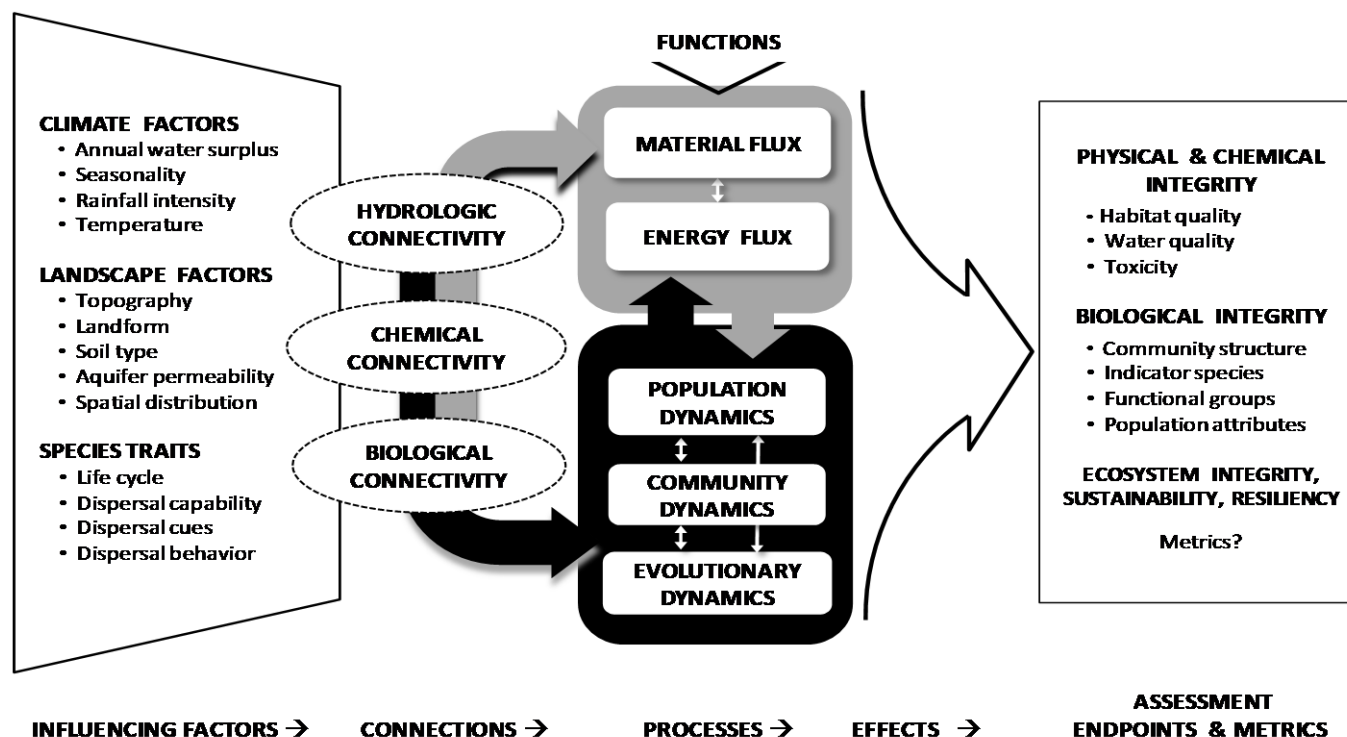


Figure 6-1. The role of connectivity in maintaining the physical, chemical and biological integrity of water. Climate, landscape, and species’ traits (Influencing Factors) interact to form hydrologic, chemical, and biological connections that alter the material and energy fluxes, and biological dynamics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

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

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30

1 **APPENDIX A. GLOSSARY**

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

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

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

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

12 **Alluvial Deposits**—*See* Alluvium.

13 **Alluvial Groundwater**—Groundwater occurring in an alluvial aquifer.

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

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

20 **Anoxic Conditions**—Without detectable dissolved oxygen; anaerobic.

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

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

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

- 1 **Assimilatory Processes**—The incorporation or transformation of simple compounds into more
2 complex compounds.
- 3 **Autochthonous**—Describing organic matter that originates from production within streams,
4 rivers, wetlands, or lakes (e.g., periphyton, macrophytes, phytoplankton).
- 5 **Bank Storage**—Storage of water that flows from a stream to an alluvial aquifer during a flood or
6 period of high streamflow. The volume of water is stored and released after the high-water event
7 over days to weeks. The volume of water stored and the timing of release depends on the
8 hydraulic properties of the alluvial aquifer.
- 9 **Baseflow**—Sustained flow of a stream (or river) in the absence of stormflow (direct runoff).
10 Natural baseflow is sustained by groundwater discharge in the stream network. Baseflow also
11 can be sustained by human sources (e.g., irrigation recharges to groundwater).
- 12 **Basin**—*See* Drainage Basin.
- 13 **Bedrock**—Solid rock underlying loose deposits such as soil or alluvium.
- 14 **Bidirectional Wetland**—A wetland that occurs in a bidirectional wetland setting. *See*
15 Bidirectional Wetland Setting.
- 16 **Bidirectional Wetland Setting**—A landscape setting (e.g., floodplains and most riparian areas)
17 that is subject to bidirectional hydrologic flows between wetlands and the river network through
18 surface water or groundwater. *See* Unidirectional Wetland Setting.
- 19 **Bifurcation**—The branching of a stream or river network.
- 20 **Bifurcation Ratio**—For a stream or river network, the ratio of the number of stream segments of
21 a given stream order to the number of stream segments of the next higher order. This ratio
22 provides a measure of the degree of branching within networks.
- 23 **Bog**—A peat-accumulating wetland that is generally nutrient poor.
- 24 **Braided Channel**—A multithreaded channel where the channels (distributaries) branch and
25 rejoin farther downstream and the channels are separated by mobile, transient bars (poorly
26 vegetated) that are small relative to the size of the channels.

- 1 **Carolina Bays**—Elliptical, ponded, depressional wetlands that range along the Atlantic coastal
2 plain from northern Florida to New Jersey. *See* Delmarva Bays.
- 3 **Catchment**—The area drained by a stream, river, or other water body; typically defined by the
4 topographic divides between one water body and another. *Synonymous with Watershed and*
5 *Drainage Basin.*
- 6 **Channel**—A natural or constructed passageway or depression of perceptible linear extent that
7 conveys water and associated material downgradient.
- 8 **Channelization**—A type of artificial drainage in which complex channels are straightened to
9 increase the rate of water flow from an area.
- 10 **Channelized Flow**—Flow that occurs in a natural or artificial channel.
- 11 **Condition**—General health or quality of an ecosystem, typically assessed using one or more
12 indicators.
- 13 **Confined Aquifer**—An aquifer bounded above and below by confining units of distinctly lower
14 permeability than that of the aquifer itself.
- 15 **Confluence**—The point at which two stream channels intersect to form a single channel.
- 16 **Connectivity**—The degree to which components of a river system are joined, or connected, by
17 various transport mechanisms; connectivity is determined by the characteristics of both the
18 physical landscape and the biota of the specific system.
- 19 **Contributing Area**—Location within a watershed/river network that serves as a source of
20 streamflow or material flux.
- 21 **Contaminants**—Any material that might be harmful to humans or other biological organisms
22 when released to the environment.
- 23 **Deep Groundwater**—Groundwater flow systems having the deepest and longest flowpaths; also
24 referred to as regional groundwater flow systems, they can occur underneath local and
25 intermediate groundwater flow systems. *See* Local Groundwater, Regional Groundwater.
- 26 **Deep Percolation**—Drainage of soil water downward by gravity below the maximum effective

- 1 depth of the root zone toward storage in subsurface strata.
- 2 **Delmarva Bays**—Carolina bays that are geographically specific to the Delmarva Peninsula.
3 These wetlands frequently have the same elliptical shape and orientation as Carolina bays, but
4 can lack the shape or rim. *See* Carolina Bays.
- 5 **Dendritic Stream Network**—A stream network pattern of branching tributaries (see
6 Figure 3-19B).
- 7 **Depressional Wetland**—A wetland occupying a topographic low point that allows the
8 accumulation of surface water. Depressional wetlands can have any combination of inlets and
9 outlets or lack them completely. Examples include kettles, prairie potholes, and Carolina bays.
10 This category also includes slope wetlands (wetlands associated with surface discharge of
11 groundwater or saturated overflow with no channel formation).
- 12 **Diadromous**—Migratory between fresh and salt waters.
- 13 **Direct Runoff**—Runoff that occurs in direct response to precipitation. *See* Stormflow.
- 14 **Discharge**—The volume of water (surface water or groundwater) that passes a given location
15 over a given period of time; the rate of runoff. Often expressed as $\text{ft}^3 \text{s}^{-1}$ or $\text{m}^3 \text{s}^{-1}$.
- 16 **Discontinuous Flow**—Refers to stream or river reaches that have flow in one part of the reach
17 but not another part of the reach. *See* Reach.
- 18 **Dispersal**—Movement by organisms or reproductive materials (e.g., seeds, eggs, genes) away
19 from an existing population or parent organism.
- 20 **Drainage Area**—The spatial extent of a drainage basin. Typically expressed in mi^2 or km^2 .
- 21 **Drainage Basin**—The area drained by a stream, river, or other water body; typically defined by
22 the topographic divides between one water body and another. *Synonymous with* Catchment *and*
23 Watershed.
- 24 **Drainage Density**—The total length of stream channels per unit area (e.g., per mi^2 , km^2).
- 25 **Endorheic Basins**—A closed basin with no outflows to other water bodies.

- 1 **Ephemeral Stream**—A stream or river that flows briefly in direct response to precipitation;
2 these channels are above the water table at all times.
- 3 **Eutrophication**—Natural or artificial enrichment of a water body by nutrients, typically
4 phosphates and nitrates. If enrichment leads to impairment (e.g., toxic algal blooms),
5 eutrophication is a form of pollution.
- 6 **Evapotranspiration**—The loss of water to the atmosphere that is the combination of
7 evaporation and transpiration losses. Transpiration is the loss of water vapor to air by plants.
- 8 **Fen**—A peat-accumulating wetland characterized by mineral-rich water inputs.
- 9 **Flood**—The occurrence of stream or river flow of such magnitude that it overtops the natural or
10 artificial banks in a reach of the stream or river; where a floodplain exists, a flood is any flow
11 that spreads over or inundates the floodplain. Floods can also result from rising stages in lakes
12 and other water bodies.
- 13 **Flood (100-year)**—Flood level (stage or discharge) with a 1% probability of being equaled or
14 exceeded in a given year.
- 15 **Flood Flows**—Discharge or flow of sufficient magnitude (or greater) to cause a flood.
- 16 **Flood Stage**—The stage at which streams or rivers overtop their natural or artificial banks.
- 17 **Floodwater**—Water associated with a flood event.
- 18 **Floodplain**—A level area bordering a stream or river channel that was built by sediment
19 deposition from the stream or river under present climatic conditions and is inundated during
20 moderate to high flow events. Floodplains formed under historic or prehistoric climatic
21 conditions can be abandoned by rivers and form terraces.
- 22 **Floodplain Wetland**—A wetland that occurs in a floodplain.
- 23 **Flow**—Water movement above ground or below ground.
- 24 **Flow Duration Class**—A classification that assigns streamflow duration to ephemeral,
25 intermittent, or perennial classes.

- 1 **Flow Regime**—The timing of streamflow.
- 2 **Flowpath**—*See* Hydrologic Flowpath.
- 3 **Flux**—Flow of materials between system components per unit time.
- 4 **Gaining Stream or Wetland**—A wetland, stream or river reach that experiences a net gain of
5 water from groundwater (see Figure 3-5). In this situation, the water table elevation in the
6 vicinity of the stream or wetland is higher than the stream or wetland water surface. Conditions
7 conducive to losing or gaining streams and wetlands can change over short distances within river
8 networks and river basins. *See* Losing Stream or Wetland.
- 9 **Geographically Isolated Wetland**—A wetland that is completely surrounded by uplands; for
10 example, hydrophytic plant communities surrounded by terrestrial plant communities or
11 undrained hydric soils surrounded by nonhydric soils. This term is often misunderstood to mean
12 hydrologically isolated. Geographically isolated wetlands vary in their degree of hydrologic and
13 biotic connectivity.
- 14 **Groundwater**—Any water that occurs and flows in the saturated zone. *See* Saturated Zone.
- 15 **Groundwater Discharge** —The flow of groundwater to surface waters; discharge areas occur
16 where the water tables intersect land surfaces. *See* Seep, Spring.
- 17 **Groundwater Discharge Wetland**—A wetland that receives groundwater discharge.
- 18 **Groundwater Flow**—Flow of water in the subsurface saturated zone.
- 19 **Groundwater Flow-through Wetland**—A wetland that has both groundwater inputs and
20 outputs. Groundwater enters the wetland through the upgradient direction and exits the wetland
21 downgradient.
- 22 **Groundwater Recharge**—The process by which groundwater is replenished; a recharge area
23 occurs where precipitation water infiltrates a water surface and is transmitted downward to the
24 saturated zone (aquifer).
- 25 **Groundwater Recharge Wetland**—A wetland that recharges groundwater.
- 26 **Groundwater Reservoir**—A saturated body of groundwater having loosely definable spatial

- 1 limits.
- 2 **Groundwater System**—Reference to the groundwater and geologic materials comprising the
3 saturated zone; the groundwater system as a whole is a three-dimensional flow field.
- 4 **Groundwater-Surface Water Interactions**—Movement of water between surface water bodies
5 and groundwater systems. Flows can occur in either direction.
- 6 **Groundwater Withdrawal**—Pumping of water from aquifers for human uses.
- 7 **Habitat**—Environment (place and conditions) in which organisms reside.
- 8 **Headwater**—Areas from which water originates within a river or stream network. This term
9 typically refers to stream channels but can also describe wetlands or open waters, such as ponds.
- 10 **Headwater Stream**—Headwater streams are first- to third-order streams. Headwater streams
11 can be ephemeral, intermittent, or perennial. *See* Stream Order, Flow Duration Class.
- 12 **Hillslope**—A sloping segment of land surface.
- 13 **Hydraulic Conductivity**—A measure of the permeability of a porous media. For a given
14 hydraulic gradient, water moves more rapidly through media with high hydraulic conductivity
15 than low hydraulic conductivity.
- 16 **Hydraulic Gradient**—Slope of the water table.
- 17 **Hydraulic Head**—The height above a standard datum of the surface of a column of water that
18 can be supported by the static pressure at a given point; for a well, the hydraulic head is the
19 height of the water level in the well compared to a datum elevation.
- 20 **Hydraulics**—The physics of water in its liquid state.
- 21 **Hydrograph**—A graph of stream or river discharge over time. Stage or water table elevation
22 also can be plotted.
- 23 **Hydrograph Falling Limb**—The portion of an event hydrograph in which streamflow is
24 decreasing.
- 25 **Hydrograph Rising Limb**—The portion of an event hydrograph in which streamflow is

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- 1 increasing.
- 2 **Hydrologic Event**—An increase in streamflow resulting from precipitation or snowmelt.
- 3 **Hydrologic Flowpath**—The pathway that water follows as it moves over the watershed surface
4 or through the subsurface environment.
- 5 **Hydrology**—The study of the properties, distribution, and effects of water as a liquid, solid, and
6 gas on Earth’s surface, in the soils and underlying rocks, and in the atmosphere.
- 7 **Hydrologic Landscape**—A landscape with a combination of geology, soils, topography, and
8 climate that has characteristic influences on surface water and groundwater.
- 9 **Hydrologic Permanence**—The frequency and duration of streamflow in channels or the
10 frequency and duration of standing water in wetlands.
- 11 **Hyporheic Flow**—Water from a stream or river channel that enters subsurface materials of the
12 streambed and bank and then returns to the stream or river.
- 13 **Hyporheic Exchange**—Water and solutes exchanged between a surface channel and the shallow
14 subsurface. *See* Hyporheic Flow.
- 15 **Hyporheic Zone**—The area adjacent to and underneath a stream or river in which hyporheic
16 flow occurs. The dimensions of the hyporheic zone are controlled by the distribution and
17 characteristics of alluvium and hydraulic gradients between streams and local groundwater.
- 18 **Infiltration**—The downward entry of water from the land surface into the subsurface.
- 19 **Infiltration Capacity**—The maximum rate at which infiltration can occur at a given location.

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

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

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

9 **Inundation**—To cover dry land with floodwaters.

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

12 **Isotopic Tracer**—*See* Stable Isotope Tracer.

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

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

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

18 **Levee (Artificial)**—An engineered structure built adjacent to a stream or river from various
19 materials to prevent flooding of surrounding areas. The levee raises the elevation of the channel

1 height to convey greater discharge of water without flooding.

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

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

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

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

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

- 1 **Materials**—Any physical, chemical, or biological entity, including but not limited to water, heat
2 energy, sediment, wood, organic matter, nutrients, chemical contaminants, and organisms.
- 3 **Meltwater**—Liquid water that results from the melting of snow, snowpacks, ice, or glaciers.
- 4 **Migration**—Long-distance movements undertaken by organisms on a seasonal basis.
- 5 **Nutrients (In Aquatic Systems)**—Elemental forms of nitrogen, phosphorus, and trace elements,
6 including sulfur, potassium, calcium, and magnesium, that are essential for the growth of
7 organisms but can be contaminants when present in high concentrations.
- 8 **Nutrient Spiraling**—Longitudinal cycles (“spirals”) of nutrient uptake and release along the
9 river continuum. The spirals are created as aquatic organisms consume, transform, and
10 regenerate nutrients, altering the rates of nutrient transport to downstream waters.
- 11 **Open Channel Flow**—Water flowing within natural or artificial channels.
- 12 **Open-waters**—Nontidal lentic water bodies such as lakes and oxbow lakes that are frequently
13 small or shallow.
- 14 **Overbank Flow**—Streamflow that overtops a stream or river channel.
- 15 **Overland Flow**—The portion of streamflow derived from net precipitation that fails to infiltrate
16 in the land surface and runs over the surface to the nearest stream channel without infiltrating at
17 any point.
- 18 **Oxbow Lakes**—Water bodies that originate from the cutoff meanders of rivers and are common
19 in floodplains of large rivers around the world.

- 1 **Peatland**—A wetland that accumulates partially decayed organic matter. Fens and bogs are
2 common examples.
- 3 **Perched Groundwater**—Unconfined groundwater separated from an underlying body of
4 groundwater by an unsaturated zone; perched groundwater is supported by a perching layer (bed)
5 whose permeability is so low that water percolating downward to the underlying unsaturated
6 zone is restricted.
- 7 **Perching Layers**—*See* Perched Groundwater.
- 8 **Percolation**—The downward movement of water through soil or rock formations.
- 9 **Perennial**—This term can be applied to other surface water bodies and groundwater flow or
10 level. *See* Perennial Stream.
- 11 **Perennial Stream**—A stream or portion of a stream that flows year-round and is maintained by
12 local, intermediate, or regional groundwater discharge or flow from higher in the river network.
- 13 **Permanent Waters**—Water bodies that contain water year-round; perennial.
- 14 **Permeability**—Property of a porous medium that allows it to transmit fluids under a hydraulic
15 gradient. For a given hydraulic gradient, water will move more rapidly with high permeability
16 materials than low permeability materials.
- 17 **Phreatophyte**—Plants that use water from the saturated zone.
- 18 **Potentiometric Surface**—The surface representing the level to which groundwater will rise in a
19 well penetrating a confined aquifer.

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

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

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

7 **Primary Production/Productivity**—The fixation of inorganic carbon into organic carbon (e.g.,
8 plant and algae biomass) through the process of photosynthesis. Primary production is the first
9 level of the stream food web, and provides most of the autochthonous carbon produced in
10 streams. It is referred to as Gross Primary Productivity (GPP) or Net Primary Productivity
11 (NPP), where NPP is equal to GPP minus respiration. *See* Respiration, Secondary
12 Production/Productivity.

13 **Propagule**—Any part of an organism that can give rise to a new individual organism. Seeds,
14 eggs, and spores are propagules.

15 **Reach**—A length of stream channel with relatively uniform discharge, depth, area, and slope.

16 **Recharge Area**—An area in which water infiltrates the surface and reaches the zone of
17 saturation.

18 **Refuge Function**—The protective function of a stream or wetland that allows a material to avoid
19 mortality or loss in a nearby sink area, thereby preventing the net decrease in material flux that
20 would otherwise have occurred (exports = imports). This term typically refers to biological

1 materials. *See* Sink Function.

2 **Regional Groundwater**—Groundwater with a deep, regional-scale flow system; also referred to
3 as deep groundwater. These flow systems can occur beneath local and intermediate groundwater
4 flow systems. *See* Local Groundwater, Deep Groundwater.

5 **Respiration**—The chemical process by which organisms break down organic matter and
6 produce energy for growth, movement, and other biological processes. Aerobic respiration uses
7 oxygen and produces carbon dioxide.

8 **Return Flow**—Water that infiltrates into a land surface and moves to the saturated zone and
9 then returns to the land surface (or displaces water that returns to the soil surface).

10 **Riparian Areas**—Transition areas or zones between terrestrial and aquatic ecosystems that are
11 distinguished by gradients in biophysical conditions, ecological processes, and biota. They are
12 areas through which surface and subsurface hydrology connect water bodies with their adjacent
13 uplands. They include those portions of terrestrial ecosystems that significantly influence
14 exchanges of energy and matter with aquatic ecosystems. Riparian areas are adjacent to
15 perennial, intermittent, and ephemeral streams, lakes, and estuarine-marine shorelines. *See*
16 Upland.

17 **Riparian Wetland**—Portions of riparian areas that meet the Cowardin et al. (1979)
18 three-attribute definition of a wetland (i.e., having wetland hydrology, hydrophytic vegetation, or
19 hydric soils). *See* Wetland.

1 **River**—A relatively large volume of flowing water within a visible channel, including
2 subsurface water moving in the same direction as the surface water, and lateral flows exchanged
3 with associated floodplain and riparian areas. *See* Stream.

4 **River Network**—A hierarchical, interconnected population of channels or swales that drain
5 water to a river. Flow through these channels can be perennial, intermittent, or ephemeral.

6 **River Network Expansion/Contraction**—The extent of flowing water in a river network
7 increases during wet seasons and large precipitation events and decreases during dry periods.
8 *See* Variable Source Area.

9 **River System**—A river and its entire drainage basin (i.e., its watershed), including its river
10 network, associated riparian areas, floodplains, alluvial aquifers, regional aquifers, connected
11 water bodies, geographically isolated water, and terrestrial ecosystems.

12 **Runoff**—The part of precipitation, snowmelt, or other flow contributions (e.g., irrigation water)
13 that appears in surface streams at the outlet of a drainage basin; it can originate from both above
14 land surface (e.g., overland flow) and below land surface sources (e.g., groundwater). Units of
15 runoff are depth of water (similar to precipitation units e.g., mm). This measurement is the depth
16 of water if it were spread across the entire drainage basin.

17 **Saturated Zone**—Water beneath the land surface occurs in two principal zones, the unsaturated
18 zone and the saturated zone. In the unsaturated zone, the voids in soil and geologic material
19 contain both air and water. The upper part of the unsaturated zone is the soil-water zone. The
20 voids in the saturated zone are completely filled with water. Water in the saturated zone is
21 referred to as groundwater. The upper surface of the saturated zone is referred to as the water
22 table. *See* Groundwater.

- 1 **Saturation Overland Flow**—Water that falls onto a saturated land surface and moves overland
2 to the nearest stream or river.
- 3 **Seasonality**—Refers to the seasonal distribution of water surplus of a river system. *See* Water
4 Surplus.
- 5 **Secondary Production/Productivity**—The generation of biomass of consumer organisms that
6 feed on organic material from primary producers (algae, microbes, aquatic and terrestrial plants),
7 and biomass of predators that feed on consumer organisms. *See* Primary
8 Production/Productivity.
- 9 **Seep**—A small area where water slowly flows from the subsurface to the surface. A seep can
10 also refer to a wetland formed by a seep; such a wetland is referred to as a groundwater slope
11 wetland.
- 12 **Seepage**—Water that flows from a seep.
- 13 **Shallow Groundwater**—Groundwater with shallow hydrologic flowpaths. *See* Local
14 Groundwater.
- 15 **Sink Function**—Any function within a stream or wetland that causes a net decrease in a material
16 flux (imports exceed exports).
- 17 **Snowpack**—Accumulation of snow during the winter season; an important source of water for
18 streams and rivers in the western United States.
- 19 **Snowmelt**—The complete or partial melting and release of liquid water from seasonal

- 1 snowpacks.
- 2 **Soil Water**—*See* Saturated Zone.
- 3 **Solute**—A substance that is dissolved in water.
- 4 **Source Area**—The originating location of water or other materials that move through a river
5 system.
- 6 **Source Function**—Any function within a stream or wetland that causes a net increase in a
7 material flux (exports exceed imports).
- 8 **Spillage**—Overflow of water from a depressional wetland to a swale or channel.
- 9 **Spring**—A surface water body formed when the side of a hill, a valley bottom, or other
10 excavation intersects a flowing body of groundwater at or below the local water table.
- 11 **Stable Isotope Tracer**—Certain elements such as oxygen, hydrogen, carbon, and nitrogen have
12 multiple isotopes that occur in nature. These isotopes can be used to track the source and
13 movement of water and other substances.
- 14 **Stage**—The elevation of the top of a water surface.
- 15 **Stream**—A relatively small volume of flowing water within a visible channel, including
16 subsurface water moving in the same direction as the surface water, and lateral flows exchanged
17 with associated floodplain and riparian areas. *See* River.
- 18 **Stream Power**—An index of the erosive capacity of flowing water in stream channels and has

- 1 the mathematical form of: $\omega_a = \tau_o V$, where τ_o is the shear stress at the bed (N/m^2) and V is
2 velocity in m/s. N is metric normal temperature and pressure.
- 3 **Stream Reach**—*See* Reach.
- 4 **Storm**—A precipitation event that produces an increase in streamflow.
- 5 **Stormflow**—The part of flow through a channel that occurs in direct response to precipitation; it
6 includes surface and subsurface sources of flow. *See* Direct Runoff.
- 7 **Stormflow Recession**—Decrease in stormflow following a hydrologic event.
- 8 **Stream Order (Strahler)**—A method for stream classification based on relative position within
9 a river network, where streams lacking upstream tributaries (i.e., headwater streams) are
10 first-order streams and the junction of two streams of the same order results in an increase in
11 stream order (i.e., two first-order streams join to form a second-order stream, two second-order
12 streams join to form a third-order stream, and so on). Where streams of different order join, the
13 larger stream's order is retained. Stream order classifications may differ, depending upon the
14 map scale used to determine order.
- 15 **Streamflow**—Flow of water through a stream or river channel. *See* Discharge.
- 16 **Subsurface Stormflow**—Water that infiltrates into the land surface and moves rapidly (or
17 displaces water that moves rapidly) to streams or rivers during a hydrologic event; term does not
18 specify a specific hydrologic flowpath.
- 19 **Subsurface Water**—All water that occurs below the land surface.

- 1 **Surface Runoff**—*See* Overland Flow.
- 2 **Surface Water**—Water that occurs on Earth’s surface (e.g., springs, streams, rivers, lakes,
3 wetlands, estuaries, oceans).
- 4 **Surface Water Bodies**—Types of water bodies that comprise surface water. *See* Surface Water.
- 5 **Swale**—A nonchannelized, shallow troughlike depression that carries water mainly during
6 rainstorms or snow melt. A swale may or may not be considered a wetland depending on
7 whether it meets the Cowardin et al. (1979) three-attribute wetland criteria. *See* Wetland.
- 8 **Symmetry Ratio**—The size ratio of a minor tributary ($T2$) to a major tributary ($T1$) at a
9 confluence. Discharge ($Q2/Q1$), drainage area ($A2/A1$), or channel width ($W2/W1$) can be used
10 to characterize the ratio of tributary size.
- 11 **Terminal Source Stream**—A first-order stream that intersects another first-order stream.
- 12 **Terrace**—A historic or prehistoric floodplain that has been abandoned by its river and is not
13 currently in the active floodplain. *See* Floodplain.
- 14 **Terrene Wetlands**—“Wetlands surrounded or nearly so by uplands and lacking a channelized
15 outlet stream; a stream may enter or exit this type of wetland but it does not flow through it as a
16 channel; includes a variety of wetlands and natural and human-made ponds” (Tiner, 2011).
- 17 **Tracer**—A substance that can be used to track the source and movement of water and other
18 substances.
- 19 **Transformation Function**—Any function within a stream or wetland that converts a material

1 into a different form; the amount of the base material is unchanged (base exports equal base
2 imports), but the mass of the different forms can vary.

3 **Transmission Loss**—The loss of runoff water by infiltration into stream and river channel beds
4 as water moves downstream; this process is common in arid and semiarid environments.

5 **Tributary**—A stream or river that flows into a higher-order stream or river.

6 **Tributary Junction**—Where a tributary joins a higher-order stream or river.

7 **Turnover length**—The ratio of the downstream flux of organic carbon to ecosystem respiration
8 per length of stream. It approximates the average distance that organic carbon is expected to
9 travel before being consumed and mineralized by aquatic biota.

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

12 **Unidirectional Wetland**—A wetland that occurs in a unidirectional wetland setting. *See*
13 Unidirectional Wetland Setting.

14 **Unidirectional Wetland Setting**—A landscape setting where there is a potential for
15 unidirectional hydrologic flows from wetlands to the river network through surface water or
16 groundwater. *See* Bidirectional Wetland Setting.

17 **Unsaturated Zone**—*See* Saturated Zone.

18 **Uplands**—(1) Higher elevation lands surrounding streams and their floodplains. (2) Within the
19 wetland literature, specifically refers to any area that is not a water body and does not meet the

- 1 Cowardin et al. (1979) three-attribute wetland definition. *See* Wetland.
- 2 **Valley**—A depression of Earth’s surface that drains water between two adjacent uplands.
- 3 **Variable Source Area**—Neither stormflow nor baseflow is uniformly produced from the entire
4 surface or subsurface area of a basin. Instead, the flow of water in a stream at any given moment
5 is under the influence of dynamic, expanding or shrinking source areas, normally representing
6 only a few percent of the total basin areas. The source area is highly variable during stormflow.
7 During large rainfall or snowmelt events, the flowing portions of the river network, and
8 associated source areas, expand. As the event ends, the network and source areas contract.
- 9 **Vernal Pool**—Shallow seasonal wetlands that generally accumulate water during colder, wetter
10 months and gradually dry-down during warmer, dryer months.
- 11 **Water Balance**—The accounting of the volume of water entering, leaving, and being stored in a
12 hydrologic unit or area, typically a drainage basin or aquifer, during a specified period of time.
- 13 **Water Body**—Any sizable accumulation of water on the land surface, including but not limited
14 to streams, rivers, lakes, and wetlands.
- 15 **Water Surplus**—Water that is available for streamflow or recharge of groundwater;
16 precipitation minus evapotranspiration.
- 17 **Water Table**—The top of the zone of saturation of an unconfined aquifer.
- 18 **Watershed**—The area drained by a stream, river, or other water body; typically defined by the
19 topographic divides between one water body and another. *Synonymous with Catchment and*
20 *Drainage Basin.*

- 1 **Wet Channel**—Channel with flowing or standing water.

- 2 **Wetland**—An area that generally exhibits at least one of the following three attributes
- 3 (Cowardin et al., 1979): (1) is inundated or saturated at a frequency sufficient to support, at least
- 4 periodically, plants adapted to a wet environment; (2) contains undrained hydric soil; or
- 5 (3) contains nonsoil saturated by shallow water for part of the growing season.

- 6 **Wetland Storage**—The capacity of a wetland to detain or retain water from various sources.