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FEATURED COLLECTION INTRODUCTION: CONNECTIVITY OF STREAMS AND WETLANDS TO DOWNSTREAM WATERS[1]

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ABSTRACT: Connectivity is a fundamental but highly dynamic property of watersheds. Variability in the types and degrees of aquatic ecosystem connectivity presents challenges for researchers and managers seeking to accurately quantify its effects on critical hydrologic, biogeochemical, and biological processes. However, protecting natural gradients of connectivity is key to protecting the range of ecosystem services that aquatic ecosystems provide. In this featured collection, we review the available evidence on connections and functions by which streams and wetlands affect the integrity of downstream waters such as large rivers, lakes, reservoirs, and estuaries. The reviews in this collection focus on the types of waters whose protections under the U.S. Clean Water Act have been called into question by U.S. Supreme Court cases. We synthesize 40+ years of research on longitudinal, lateral, and vertical fluxes of energy, material, and biota between aquatic ecosystems included within the Act's frame of reference. Many questions about the roles of streams and wetlands in sustaining downstream water integrity can be answered from currently available literature, and emerging research is rapidly closing data gaps with exciting new insights into aquatic connectivity and function at local, watershed, and regional scales. Synthesis of foundational and emerging research is needed to support science-based efforts to provide safe, reliable sources of fresh water for present and future generations.

(KEY TERMS: ecological integrity; river networks; streams; wetlands; floodplains; riparian areas; watersheds; U.S. Clean Water Act.)

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INTRODUCTION

The principal objective of the U.S. Clean Water Act (CWA) is to "restore and maintain the chemical, physical, and biological integrity of the Nation's waters" (33 U.S.C. § 1362(7)). This objective explicitly establishes the central role of ecological (i.e., chemical, physical, and biological) integrity to the attainment of clean water. Connectivity is a key component of ecological integrity, and has long been a central tenet in aquatic ecosystem research. Concepts and definitions of connectivity have evolved over the past several decades (Taylor et al. 2006) as have metrics for quantifying it (Leibowitz et al. 2018). For the purposes of this featured collection, we define connectivity as follows: *Connectivity is the degree to which components of a watershed are joined and interact by transport mechanisms that function across multiple spatial and temporal scales, and is determined by the characteristics of both the physical landscape and the biota of the specific system.* Here, "physical landscape" refers to abiotic features of the landscape, i.e., the scalable habitat template established by climate, geology, landform, and human activities (Southwood 1988). Within the abiotic template, connections established by exchanges of matter, energy, and living organisms are influenced by the spatial structure and arrangement of habitats and land uses (Turner and Gardner 2015; Leibowitz et al. 2018). This definition of connectivity reflects a systems perspective of watersheds as heterogeneous mosaics of interacting ecosystems in which variations in the duration, magnitude, frequency, timing, and stability of flows form dynamic, spatiotemporal continua of connectivity (Figure 1). These gradients of connectivity, which vary in degree from highly isolated to highly connected, support the wide range of ecosystem functions needed to maintain the chemical, physical, and biological integrity of the nation's waters, and are the focus of this featured collection.

The papers in this featured collection review the results of 40+ years of scientific research on the chemical, physical, and biological connectivity of streams and wetlands to larger, downstream waters, such as rivers, lakes, and coastal waters (hereafter collectively referred to as downstream waters). They synthesize the substantial body of scientific evidence on the ecological effects of source waters — and in particular, small or temporary streams and nontidal wetlands — on the ecological integrity of downstream waters and, as a collection, summarize the state-of-the-science on the interrelatedness of these diverse aquatic ecosystems.

BACKGROUND ON THE FEATURED COLLECTION

The reviews in this collection were originally developed as a report (USEPA 2013, 2015) that provided the scientific basis for a 2015 rulemaking by the U.S. Environmental Protection Agency (EPA) and the U.S. Army Corps of Engineers (Corps) to clarify the definition of "waters of the United States," which determines the scope of CWA jurisdiction. The resulting regulation, titled the *Clean Water Rule* (FR 80 FR 37054; https://www.federalregister.gov/d/2015-13435/page-37054) went into effect in most U.S. states in August 2015, but was stayed nationwide by the U.S. Court of Appeals for the Sixth Circuit in October 2015 pending the outcome of litigation. At the time of this writing, the 2015 regulation is in review by the issuing agencies under direction of an Executive Order, issued in February 2017, to rescind or revise it (FR 82-42, 12532; https://www.whitehouse.gov/presidential-actions/presidential-executive-order-restoring-rule-law-federalism-economic-growth-reviewing-waters-united-states-rule/).

The need for rulemaking to clarify CWA scope arose from three Supreme Court cases in 1985, 2001, and 2006 that created uncertainty about the regulatory status of some types of waters. In 1985, the Court's unanimous decision in *United States v. Riverside Bayview Homes* (474 U.S. 12) upheld the agencies' long-standing practice of regulating "adjacent" wetlands, defined as wetlands that are "bordering, contiguous, or neighboring" to a "navigable water." (Note: Regulatory and legal terms are shown in quotation marks to avoid confusion with other usages.) In a 2001 case, *Solid Waste Agency of Northern Cook County (SWANCC) v. U.S. Army Corps of Engineers* (531 U.S. 159), the Court decided 5-4 that use by migratory birds was not, by itself, sufficient for CWA jurisdiction over intrastate, nonnavigable, isolated waters, including the many ponds and wetlands along common flyways and overwintering areas. Most recently, in 2006, the Supreme Court heard *Rapanos v. United States*, 547 U.S. 715, a case challenging the inclusion of nonnavigable tributaries and their "adjacent" wetlands in CWA jurisdiction. The Court's split (4-1-4) ruling in *Rapanos* yielded multiple, conflicting opinions with no majority decision. Justice Scalia and three other Justices argued that the scope of the CWA includes only "*relatively permanent, standing or flowing bodies of water*" and wetlands with a "*continuous surface connection*" to such waters. Justice Kennedy concurred with Scalia et al. that *Rapanos* should be remanded to the lower courts, but disagreed with their standard of relative permanence for

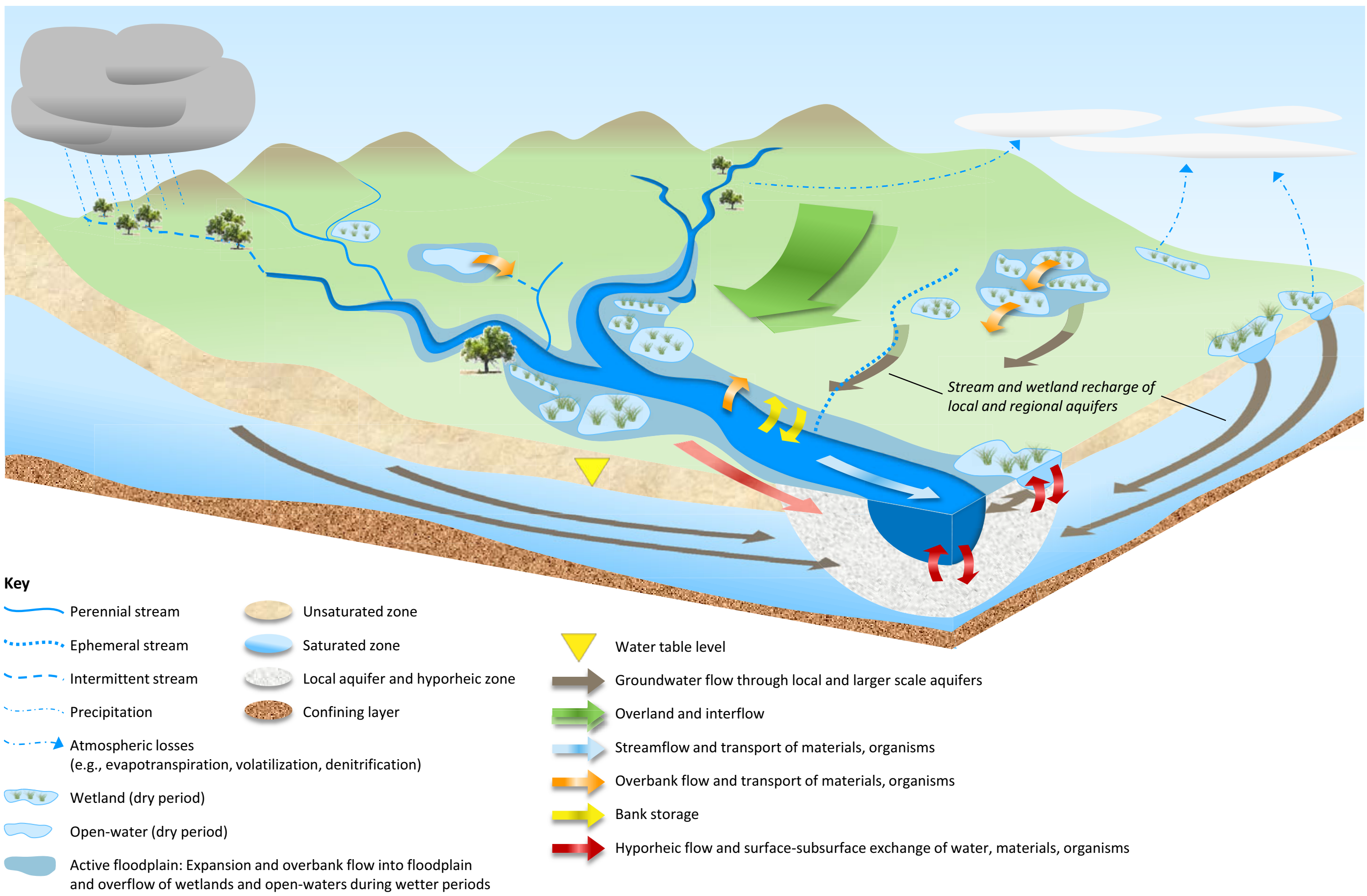

FIGURE 1. Hydrologic flow paths. Arrows are representative of surface water and groundwater flows occurring throughout a watershed. Subsurface flows are shown within the cross section, and by faded arrows outside the cross section. Source: USEPA (2015).

jurisdiction. In a separate opinion, Justice Kennedy wrote that tributaries, wetlands, and open waters must "possess 'significant nexus' to waters that are or were navigable in-fact or that could reasonably be so made." He argued that a water body has "significance nexus" if, "either alone or in combination with similarly situated lands in the region, [it] significantly affect[s] the chemical, physical, and biological integrity of other covered waters more readily understood as 'navigable.'" In a third, dissenting opinion, Justice Stevens and three other Justices agreed with the regulatory agencies that the waters at issue were jurisdictional under the CWA, and that the Corps' decision to assert jurisdiction over the particular wetlands in question was both "reasonable" and "permissible." The dissenting Justices also stated that the multiple standards issued in these Court opinions "can only muddy the jurisdictional waters." For a more complete history of the CWA and legal challenges to its jurisdiction, see Downing et al. (2003), Downing et al. (2007), Nadeau and Rains (2007), and Adler (2013, 2015).

While the uncertainties raised by these court cases cannot be resolved by science alone (Adler 2015; Alexander 2015; Hawkins 2015), the available scientific literature provides a large body of evidence on the connectivity and ecological functions of water bodies in question — primarily, small or temporary streams and nontidal wetlands that can influence the chemical, physical, or biological integrity of large rivers, lakes, and coastal waters. The authors of this introduction and featured collection worked together on a five-year interdisciplinary review of literature on watershed connections that have potential widespread relevance to CWA programs. In September 2013, a draft of the EPA report (USEPA 2013) was released for public comment and independent peer review. The peer review (2013–2014) was conducted by a panel of 27 experts nominated by the public and convened by EPA's Science Advisory Board (SAB). All SAB panel meetings are open to the public, and all SAB documents — including comments, meeting notes, and draft and final reports — are available on the SAB's website. The proceedings of this SAB review, and the panel's final report to EPA's administrator, can be found at https://yosemite.epa.gov/sab/sabproduct.nsf/02ad90b136fc21ef85256eba00436459/7724357376745f48852579e60043e88c!OpenDocument&TableRow=2.3#2. Comments from this SAB panel's report (USEPA 2014) were incorporated into EPA's final report (USEPA 2015) and were further considered while writing the papers in this featured collection.

Collectively, the papers presented here provide a synthesis of evidence pertaining to the interrelatedness of freshwater ecosystems, emphasizing what is known about the watershed-scale functions of streams, wetlands, and open waters whose jurisdictional status under the CWA have been called into question by the three U.S. Supreme Court cases summarized briefly above. While relevant to regulatory decisions under the CWA, these papers are technical reviews of peer-reviewed scientific literature. As such, they do not consider or establish EPA policy and do not consider or propose legal standards for CWA jurisdiction.

Because the original intent of these reviews was to inform the 2015 regulation clarifying the definition of "waters of the United States," the papers in this collection address three charge questions that were developed in 2010 for that effort (Table 1). These questions were formulated through iterative dialogues between scientists in EPA's Office of Research (ORD), attorneys and policy specialists in EPA's Office of Water, and EPA's Office of General Counsel (OGC) to identify the specific nature of the policy needs, and to determine, within that scope, which questions could be informed by a formal review of scientific (ORD) or legal (OGC) knowledge. Policy questions expressed in terms of CWA regulations (which include categories such as "adjacent waters," "traditional navigable waters," and "other waters") were translated into terms that could be used to search the literature (Table 1). For example, "adjacent" waters were translated into "wetlands and open waters in riparian areas and floodplains." The regulatory term "traditional navigable waters" is derived from the statutory term "navigable waters" (Downing et al. 2003) and serves as a reference for many CWA jurisdictional determinations. It includes large streams and rivers, lakes, reservoirs, coastal waters, but is not limited to water bodies that are "navigable-in-fact" (Downing et al. 2003; Adler 2015). For the purposes of these reviews, we use the term "downstream waters" as a flexible surrogate for "traditional navigable waters" (Table 1).

This introductory paper describes the featured collection, briefly reviews the concept of connectivity in freshwater science, and summarizes major conclusions across the papers in the collection. Leibowitz et al. (2018) provide a framework to understand hydrological, chemical, and biological connectivity, focused on the mechanisms by which wetlands and headwater streams connect to and contribute to rivers. Fritz et al. (2018) review evidence of the physical and chemical connections by which streams and associated riparian and floodplain wetlands influence the structure and function of downstream waters (i.e., the fluvial hydrosystem; Figure 1). Lane et al. (2018) review the functions and effects of diverse wetland and open-water systems occurring outside of riparian areas and floodplains on downstream waters (Figure 1). Schofield et al. (2018) review the literature on how movements of aquatic and semiaquatic biota connect freshwater habitats over various temporal and spatial scales (Figure 2). Finally, Goodrich et al. (2018) present a regionally focused case study on the connections and effects of the intermittent and ephemeral streams and rivers that dominate the arid southwestern U.S. Each review also considers biotic and abiotic factors that influence connectivity, and synthesizes information on ecosystem functions

TABLE 1. Translating connectivity-related questions between regulatory policy and science. This table crosswalks regulatory and scientific questions that determined the scope of the reviews in this featured collection. Regulatory and legal terms are shown in quotation marks to avoid confusion with other usages. Modified from USEPA (2015).

Regulatory question	Review question	Featured papers
What tributaries have a "significant[1] nexus" to "traditional navigable waters"?	What are the connections to and effects of ephemeral, intermittent, and perennial streams on downstream waters?	Leibowitz et al. (2018) Fritz et al. (2018) Schofield et al. (2018) Goodrich et al. (2018)
What "adjacent" waters have a "significant[1] nexus" to "traditional navigable waters"?	What are the connections to and effects of riparian or floodplain wetlands and open waters on downstream waters?	Leibowitz et al. (2018) Fritz et al. (2018) Schofield et al. (2018)
What categories of "other waters" have a "significant[1] nexus" to "traditional navigable waters"?	What are the connections to and effects of wetlands and open waters in nonfloodplain settings on downstream waters?	Leibowitz et al. (2018) Lane et al. (2018) Schofield et al. (2018)

[1]"Significant," as used here, is a policy determination informed by science; it does not refer to statistical significance.

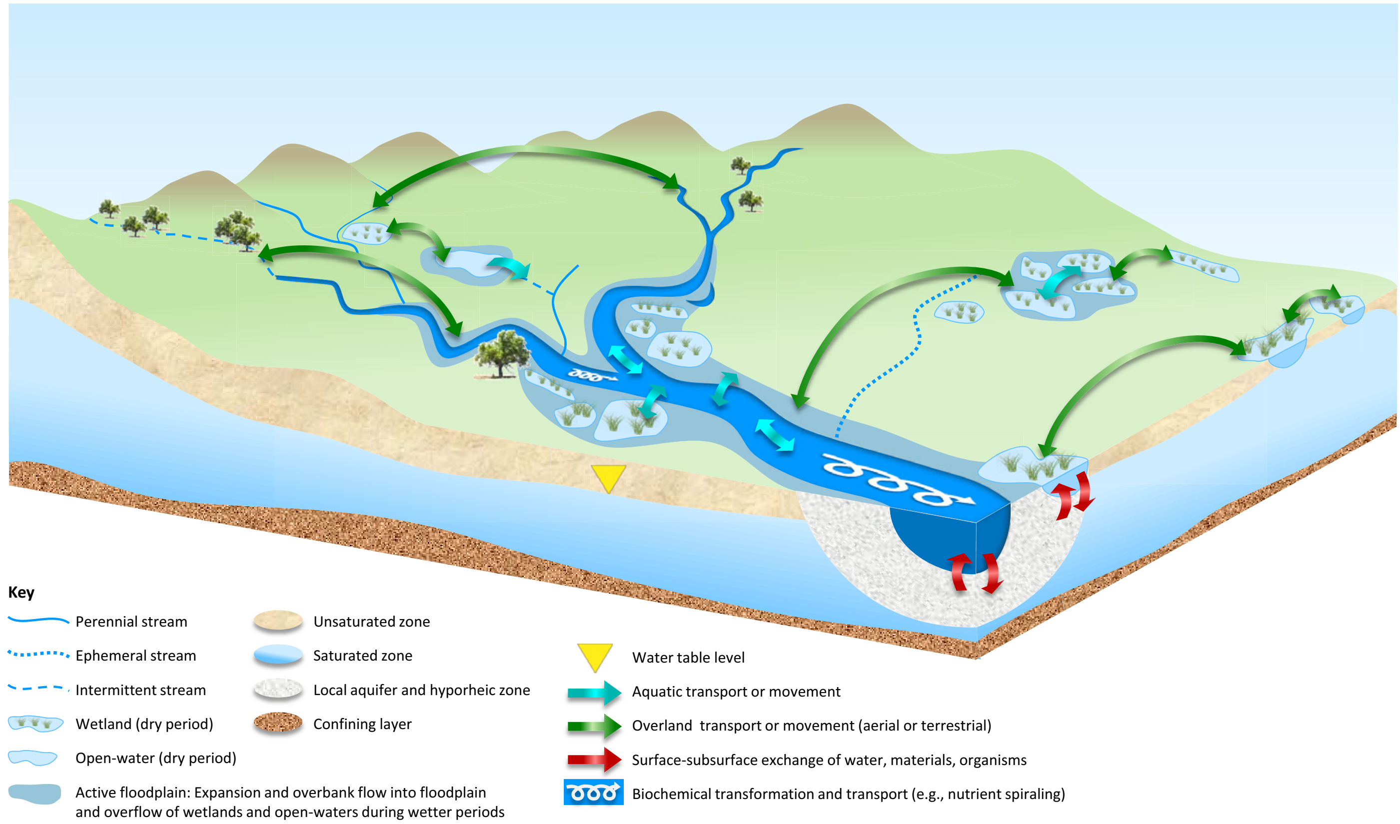

FIGURE 2. Biological pathways. Arrows are representative of biological pathways occurring throughout a watershed. This figure also includes representative biogeochemical pathways occurring in streams and floodplains. Source: USEPA (2015).

associated with different types and degrees of connectivity (Figure 3).

The primary pathways of aquatic connectivity considered here are surface water flows, shallow groundwater flows, and movements of aquatic and semiaquatic organisms, all of which connect watersheds in four dimensions (Table 2).

Key considerations in our synthesis of aquatic connectivity are ecosystem functions within watershed components (e.g., streams, wetlands) that alter fluxes of materials or movements of organisms between them (Leibowitz et al. 2018). These functions are broadly categorized into source, sink, refuge, lag, and transformation (Leibowitz et al. 2018).

In this collection, the term "connectivity" — which has many contexts and definitions in the literature — is shorthand for the complex interactions of landscape, climate, and biota that support ecological integrity (Figure 3). Our reviews focus on connections of potential relevance to CWA programs, but draw from the rich history of research (next section) that built the foundation for current understanding of the role of connectivity in maintaining the integrity and resilience of downstream waters (Figure 3).

THE CONCEPT OF CONNECTIVITY IN FRESHWATER SCIENCE

Connectivity has long been central to the study of freshwater ecology, hydrology, biogeochemistry, and geomorphology. The River Continuum Concept (RCC) (Vannote et al. 1980) portrayed the stream network, from the headwaters to the river mouth, as a complex hydrologic gradient with predictable longitudinal patterns of ecological structure and function. The key to the RCC pattern is that downstream communities are organized, in large part, by upstream communities and their processes (Vannote et al. 1980; Battin et al. 2009). The Serial Discontinuity Concept (Ward and Stanford 1983) built on the RCC to further understand how dams and impoundments disrupt the longitudinal patterns of ecological function in flowing waters with predictable downstream effects. The Spiraling Concept (Webster and Patten 1979; Newbold et al. 1981; Elwood et al. 1983) described how river network connectivity can be conceptualized and measured as materials cycle from dissolved forms to transiently stored forms in living organisms, then back to dissolved forms, as they are transported downstream.

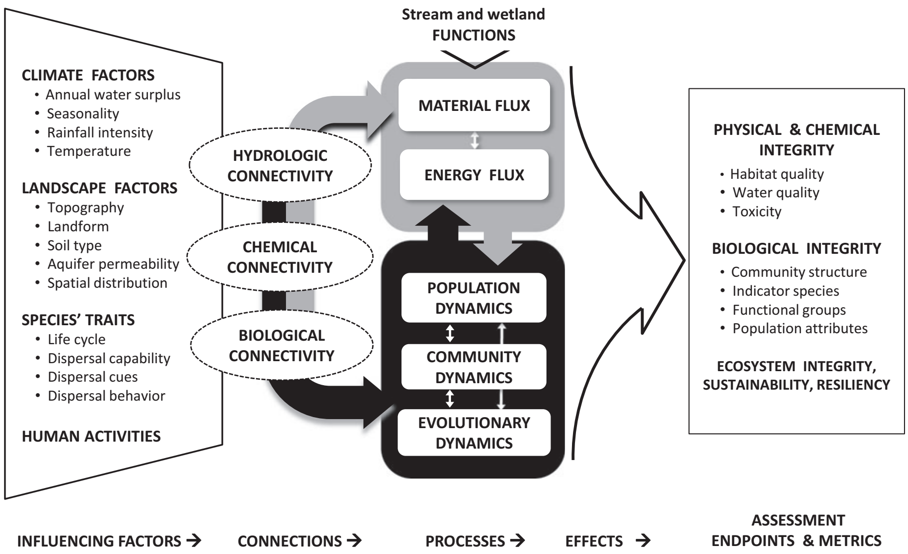

FIGURE 3. The role of connectivity in maintaining the integrity of water. Climate, landscape, species' traits, and human activities (Influencing Factors) interact to form Connections (hydrologic, chemical, and biological) between ecosystems throughout and across watersheds. Fluxes of materials and energy, and movements of living organisms, are enabled, inhibited, or modified by functions within watershed components (e.g., streams, wetlands) that modify the timing of transport and the quantity and quality of resources available to downstream communities (Effects). Monitoring programs have developed metrics for assessing physical habitat, water quality, and biological assemblages as indicators of the ecological (i.e., physical, chemical, and biological) integrity of downstream waters (Assessment Endpoints and Metrics). Source: USEPA (2015).

TABLE 2. Dimensions of watershed connectivity. Modified from USEPA (2015).

Dimension	Examples and pathways
Longitudinal (Alexander et al. 2007; Freeman et al. 2007)	• Streamflow and downstream transport of materials, organisms (Figure 1) • Hyporheic flow (Figure 1) • Groundwater flow through local and large-scale aquifers (Figure 1) • Aquatic or overland movement of organisms in or along stream channels (Figure 2) • Biogeochemical transport and transformation (Figure 2)
Lateral (Ward 1989; Stanford and Ward 1993)	• Overbank flow and transport from channels into banks, floodplains, and riparian areas (Figure 1) • Spillage and transport from wetlands and open waters into streams (Figure 1) • Overland flow and interflow (Figure 1) • Groundwater recharge from streams and wetlands (Figure 1) • Bank storage (Figure 1) • Transport or movement of organisms between streams and wetlands or open waters (Figure 2)
Vertical (Amoros and Bornette 2002; Banks et al. 2011)	• Surface-subsurface exchange of water, materials, organisms (Figures 2 and 3) • Groundwater recharge from streams and wetlands (2) • Atmospheric exchanges (Figure 1)
Temporal (Hewlett and Hibbert 1967; Bohonak and Jenkins 2003; Zedler 2003)	• Variable source area (Figure 1) • Seasonal cycles of wetland inundation and outflow to streams (Figure 1) • Migration by aquatic organisms (Figure 2) • Dormancy of aquatic organisms (Figure 2)

These conceptual frameworks focused on the longitudinal connections of river ecosystems, whereas the subsequent Flood Pulse Concept (Junk et al. 1989) examined the importance of lateral connectivity between river channels and floodplains, including wetlands and open waters, through seasonal expansion and contraction of river networks. Ward (1989) summarized the significance of connectivity to lotic ecosystems across four dimensions: longitudinal, lateral, vertical (surface–subsurface), and temporal connections; he concluded that running water ecosystems are open systems because they are highly interactive with both contiguous habitats and other ecosystems in the surrounding landscape (Figure 1). Stanford et al. (2005) related the flows of water and materials through channels and into floodplains to dynamic and interconnected habitats (shifting habitat mosaics) that enable diverse assemblages of aquatic species to coexist (Figures 1 and 2). As these conceptual frameworks illustrate, scientists have long recognized the dynamic hydrologic connectivity that the physical structure of river networks represents.

More recently, scientists have incorporated this network structure into conceptual frameworks describing ecological patterns in river ecosystems and the processes linking them to other watershed components, including wetlands and open waters (Power and Dietrich 2002; Benda et al. 2004; Nadeau and Rains 2007; Rodriguez-Iturbe et al. 2009). The network dynamic hypothesis (Benda et al. 2004) is a physically-based framework for predicting patterns of habitat heterogeneity along rivers, based on dynamics that generate potential biological “hotspots” at tributary confluences. It reflects a more realistic river network perspective through remixing the earlier, more linearly driven frameworks with frameworks describing the patchy and stochastic nature of lotic ecosystems (e.g., Resh et al. 1988; Townsend 1989; Rice et al. 2001). Bunn and Arthington (2002) identified natural flow variability and associated lateral and longitudinal connectivity of stream channels and floodplains as two principal mechanisms linking hydrology to aquatic biodiversity of riverine species (also Leigh et al. 2010). In their review of integrative research on river corridors, Harvey and Gooseff (2015) highlight quantification of connectivity from river-reach to regional scales in terms of “hydrologic exchange flows” that bring downstream flows into contact with hyporheic, riparian, and floodplain environments, where many biogeochemical reactions and contaminant filtration occur.

In addition, application of metapopulation theory and population genetic theory to natural populations has greatly improved our understanding of the role of dispersal and migration in the demographic persistence, community assembly, and evolution of aquatic species (Figure 2) (Hastings and Harrison 1994; Pannell and Charlesworth 2000; Fagan 2002; Bohonak and Jenkins 2003; Waples 2010; Bauer and Hoye 2014). Sheaves (2009) emphasized the key ecological connections — which include process-based connections that maintain habitat function (e.g., nutrient dynamics, trophic function) and movements of individual organisms — throughout a complex of interlinked freshwater, tidal wetland, and estuarine habitats as critical to the persistence of aquatic species, populations, and communities over the full range of time scales.

OVERVIEW OF MAJOR CONCLUSIONS

Based on the review and synthesis of more than four decades of scientific research into aquatic ecosystem connectivity, the papers in this collection found strong evidence supporting the critical role of chemical, physical, and biological connectivity of streams, wetlands, and open waters in maintaining the structure, function, and overall ecological (chemical, physical, and biological) integrity of downstream waters (e.g., rivers, lakes, estuaries, and oceans) (Figure 3). Watersheds are integrated at multiple spatial and temporal scales by flows of surface water and groundwater, transport and transformation of physical and chemical materials, and movements of organisms, which establish varying degrees of connection and isolation among freshwater habitats in space and time.

The literature unequivocally demonstrates that perennial, intermittent, and ephemeral streams, individually or cumulatively, exert a strong influence on the integrity of downstream waters (Fritz et al. 2018; Goodrich et al. 2018) (Figure 1). The existence of a continuous bed and bank structure in river networks is strong geomorphologic evidence for longitudinal connectivity; lateral connections maintain the structure of floodplains and riparian areas via recurrent inundation and deposition of materials during peak and recession flows (Fritz et al. 2018). Perennial, intermittent, and ephemeral headwaters make up the majority of stream channels in most river networks and cumulatively supply most of the water in rivers (Fritz et al. 2018). Flows from ephemeral streams are a major driver of the dynamic hydrology, geomorphology, and biogeochemistry of southwestern rivers, where approximately 80% or more of streams by southwestern state are ephemeral or intermittent (Goodrich et al. 2018). Intervening channels connect headwaters structurally and functionally to large inland or coastal waters via channels, wetlands, and alluvial deposits where water and other materials are concentrated, mixed, transformed, and stored or transported (Fritz et al. 2018).

Wetlands located outside of floodplains and riparian areas (hereafter, nonfloodplain wetlands) are abundant in some regions and perform many of the same functions as wetlands in floodplains and riparian areas. These functions include recharge of groundwater that sustains river baseflows; retention and transformation of nutrients, metals, sediment, and pesticides; export of organisms or propagules to downstream waters; storage and subsequent release of floodwaters; and provision of protective habitats for stream species (Lane et al. 2018). However, the mechanisms by which nonfloodplain wetlands are hydrologically connected to downstream waters differ fundamentally from those for riparian and floodplain wetlands, and their effects on downstream waters can be more challenging to detect and quantify (Lane et al. 2018). Nonfloodplain wetlands can — and typically do — remain chemically and biologically connected, even in the absence of hydrologic connections, by overland or aerial movements of aquatic and semiaquatic organisms and the materials that they transport (Lane et al. 2018; Schofield et al. 2018) (Figures 1 and 2).

There is robust evidence that the movement of organisms between streams, wetlands, open waters, and downstream waters is an integral component of the river food webs that support aquatic life. Streams and wetlands serve numerous functions for downstream waters and their populations, by acting as sources of colonists, food, and genetic diversity; as refuges from adverse abiotic and biotic conditions; and as complementary or obligate habitats for the maturation and reproduction of fish, amphibians, and invertebrates (Schofield et al. 2018). Because many aquatic species are capable of moving overland (e.g., by active flight, walking, wind dispersal), biological connections can be more widespread, complex, and variable than hydrologic connections, and habitats that seem to be hydrologically isolated are often highly connected by movements of aquatic biota (Figure 2). For practical reasons, research into biological connectivity is often conducted in single systems, for example, looking at individual species, assemblages, or ecosystem types. In reality, biological connectivity is best assessed as the cumulative effects of multiple species moving, via multiple pathways and across multiple habitat types, to make use of the full range of resources found in spatially and temporally variable wetlands, streams, rivers, lakes, ponds, and other freshwater habitats found throughout watersheds (Schofield et al. 2018).

Natural variation in degrees of connectivity arises from differences in local and regional climate, landscape, and biotic factors (i.e., connectivity gradients), and is needed to support the range of functions by which streams and wetlands maintain downstream water integrity (Figure 3). For example, whereas large stream channels are highly efficient transport mechanisms for water and other materials, smaller tributaries and riparian or floodplain wetlands provide optimal environments for functions associated with water storage and material transformation (e.g., flood control, denitrification) (Fritz et al. 2018). Therefore, variation in the types and degrees of connectivity enables different ecosystem functions, and its quantification is central to our understanding of how streams and wetlands influence the integrity of downstream waters. In addition, the incremental effects of individual streams and wetlands accumulate throughout (and across) watersheds and must be evaluated in context with other streams and wetlands, as downstream water quality reflects the combined effects of the functions (e.g., of biogeochemical cycling) and connections (e.g., transport of nutrients) of all watershed components (Fritz et al. 2018; Goodrich et al. 2018; Lane et al. 2018; Leibowitz et al. 2018).

Due to the variable functions and aggregate effects of tributaries and wetlands, the size, number, and spatial distribution of streams and wetlands in a watershed are important factors governing the integrity of downstream waters (Fritz et al. 2018; Lane et al. 2018; Schofield et al. 2018). For example, while the probability of a large-magnitude transfer of sediment or organisms from any given headwater stream in a given year might be low (i.e., a low-frequency connection when each stream is considered individually), headwater streams are the most abundant type of stream in most watersheds. The actual probability of a large-magnitude transfer in a given year is therefore much higher when the cumulative contributions are considered. Similarly, nonfloodplain wetlands can store large proportions of snowmelt runoff (30%–60%) and precipitation (11%–20%) received by a watershed, and that storage could be increased by wetland restoration (Lane et al. 2018). Similarly, cumulative export of invertebrates from headwater to downstream waters can be substantial, especially in intermittent and ephemeral streams, as terrestrial invertebrates accumulate in these channels during dry periods and are then transported downstream in wet periods (Schofield et al. 2018).

Assessments of the functional, watershed-scale effects of nonfloodplain wetlands on downstream waters can be especially challenging, as temporal and spatial gradients of connectivity of this diverse group of wetlands (e.g., many prairie potholes, vernal pools, playa lakes) are particularly dynamic (Lane et al. 2018; Leibowitz et al. 2018). Recent research has quantified the connectivity and cumulative effects of many individual nonfloodplain wetlands within watersheds. For example, landscape-scale analysis of inundation from satellite imagery and watershed modeling of groundwater flow paths have shown that apparently "isolated" wetlands can be hydrologically connected seasonally, cyclically, or continuously over long (>30 km) distances, via surface water and groundwater flows that contribute to river baseflow (Lane et al. 2018; Leibowitz et al. 2018). Data from these and other studies provide strong evidence that functions of these wetlands act at multiple spatial and temporal scales to affect hydrologic and chemical fluxes or transfers of water and materials to downstream waters.

SYNTHESIS AND IMPLICATIONS

The overall objective of the U.S. CWA — to restore and maintain the chemical, physical, and biological integrity of the nation's waters — acknowledges the critical role of ecological processes in the attainment of clean water. Interim goals of the CWA related to water quality, populations of shellfish, fish and wildlife, and societal needs (e.g., water for human consumption and recreational uses) recognize the need for advancing the scientific understanding of aquatic ecosystems with authorizations to fund "basic research into the structure and function of fresh water aquatic ecosystems, and to improve understanding of the ecological characteristics necessary to the maintenance of the chemical, physical, and biological integrity of fresh-water aquatic ecosystems" (33 U.S.C. § 1254). The ultimate and interim goals of the CWA are inextricably interconnected. Societal needs for safe drinking water, for example, are highly dependent on surface water ecosystem integrity. In an analysis of water use in the U.S. in 2005, the U.S. Geological Survey found that 77% of the total freshwater used — and 67% of the public drinking water used — came from surface waters (U.S. Geological Survey, Surface Water Use in the United States, 2005. Accessed June 30, 2017, https://water.usgs.gov/edu/wusw.html). In addition, an analysis by EPA in 2009 found that intermittent, ephemeral and perennial-headwater streams are major sources of water for public water supplies (U.S. Environmental Protection Agency, Section 404 of the Clean Water Act. Accessed July 21, 2017, https://www.epa.gov/cwa-404/geographic-information-systems-analysis-surface-drinking-water-provided-intermittent). This study found that a total of 357,404 miles (575,186 km) of streams in the continental U.S. are located within "source protection areas" of public drinking water intakes that have been identified by state and local governments. Of these stream miles, the majority (58%) are intermittent, ephemeral, or perennial headwaters (207,476 miles or 333,900 km). In the year of that study (2009), approximately one-third of the U.S. population (~117,000,000 people) received their drinking water from public sources that are supplied entirely or in part by freshwater intermittent, ephemeral, or perennial headwater streams (U.S. Environmental Protection Agency, Section 404 of the Clean Water Act. Accessed July 21, 2017, https://www.epa.gov/cwa-404/geographic-information-systems-analysis-surface-drinking-water-provided-intermittent). These estimates are conservative, due to the underrepresentation of small streams in the nationally available hydrographic maps (Fritz et al. 2018) used in these analyses.

As demands on surface water sources continue to grow, the need for up-to-date scientific information on natural and anthropogenic controls of freshwater ecosystem integrity is even greater than it was when the CWA was enacted in 1972. The literature reviews in this collection provide a unique synthesis of evidence from the rich history of foundational research into connectivity, much of which was motivated by CWA objectives, and from exciting, new studies that have advanced our scientific understanding of ecological connectivity in terms of scale, precision, and complexity. Current research is closing data gaps identified in this collection and showing promise for near-term improvements in our ability to assess connectivity and integrity. Examples include network-based methods for multiscale, multispecies, and multilevel assessments of ecological networks (Brása et al. 2013; Malvadkar et al. 2015; Engelhard et al. 2016; Rayfield et al. 2016; Pilosof et al. 2017); empirical observations of spatial and temporal surface wetland-stream hydrodynamics at field (Brooks et al. 2018) and landscape scales (Vanderhoof et al. 2016); models that integrate observational data into mechanistic simulations of hydrologic function (Evenson et al. 2016; Ameli and Creed 2017; Golden et al. 2017) or integrate those data with network-based geostatistical analysis (McGuire et al. 2014); and biological connectivity (Bauer and Klaassen 2013). Many questions about the effects of streams and wetlands on downstream water integrity can be answered from the literature reviewed in this featured collection. Emerging research is rapidly closing existing data gaps with new insights into aquatic ecosystem connectivity and function at local, watershed, and regional scales. The syntheses of foundational and emerging research in this collection provide a resource for science-based efforts to restore and maintain safe, reliable sources of fresh water for present and future generations.

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DISCLOSURE

Former JAWRA editor Kenneth J. Lanfear served as acting editor in chief for all articles in this featured collection. Parker J. Wigington, Jr., an author on some of the collection papers and who was JAWRA editor in chief at the time the collection was submitted, had no role in the review or editorial decisions for any part of the collection.

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