AFS SPECIAL REPORT

Headwater Streams and Wetlands are Critical for Sustaining Fish, Fisheries, and Ecosystem Services

Photo credit: Peter Turcik

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Headwater streams and wetlands are integral components of watersheds that are critical for biodiversity, fisheries, ecosystem functions, natural resource-based economies, and human society and culture. These and other ecosystem services provided by intact and clean headwater streams and wetlands are critical for a sustainable future. Loss of legal protections for these vulnerable ecosystems would create a cascade of consequences, including reduced water quality, impaired ecosystem functioning, and loss of fish habitat for commercial and recreational fish species. Many fish species currently listed as threatened or endangered would face increased risks, and other taxa would become more vulnerable. In most regions of the USA, increased pollution and other impacts to headwaters would have negative economic consequences. Headwaters and the fishes they sustain have major cultural importance for many segments of U.S. society. Native peoples, in particular, have intimate relationships with fish and the streams that support them. Headwaters ecosystems and the natural, socio-cultural, and economic services they provide are already severely threatened, and would face even more loss under the Waters of the United States (WOTUS) rule recently proposed by the Trump administration.

INTRODUCTION

Headwaters are broadly defined as portions of a river basin that contribute to the development and maintenance of downstream navigable waters including rivers, lakes, and oceans (FEMAT 1993). Headwaters include wetlands outside of floodplains, small stream tributaries with permanent flow, tributaries with intermittent flow (e.g., periodic or seasonal flows supported by groundwater or precipitation), or tributaries or areas of the landscape with ephemeral flows (e.g., short-term flows that occur as a direct result of a rainfall event; USEPA 2013; USGS 2013). Headwater streams comprise the majority of river networks globally (Datry et al. 2014a); in the conterminous United States, headwater streams comprise 79% of river length, and they directly drain just over 70% of the land area (Figure 1). Along with wetlands, these ecosystems are essential for sustaining fish and fisheries in the USA (Nadeau and Rains 2007; Larned et al. 2010; Datry et al. 2014b). When headwaters are polluted, or headwater habitats are destroyed, fish, fisheries, and ecosystem services (i.e., benefits that humans gain from the natural environment and from normally functioning ecosystems) are compromised or completely lost.

With the U.S. Clean Water Act of 1972 (Federal Water Pollution Control Act), Congress recognized the importance of aquatic habitat and ecosystem connectivity in the stated objective of the Act "to restore and maintain the chemical, physical, and biological integrity of the nation's waters." Biological integrity has been defined as "the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of the natural habitat of the region" (Frey 1977; Karr and Dudley 1981). The Act provides authority for the federal government to protect navigable waterways from channelization, pollution, and other forms of impairment by making it unlawful to discharge dredged or fill material into "navigable waters" without a permit, 33 U. S. C. §§1311(a), 1342(a). This authority extends to wetlands that are not navigable but adjacent to navigable-in-fact waterways (*United States v. Riverside Bayview Homes, Inc.*, 474 U.S. 121, 1985). The authority does not extend to waters that lack a "significant nexus" to navigable waters (*Solid Waste Agency of Northern Cook County [SWANCC] v. Army Corps of Engineers*, 531 U. S. 159, 2001). However, federal jurisdiction over non-navigable and their adjacent waters remained unclear.

The 2006 Supreme Court decision *Rapanos v. United States* (547 U.S. 715, 2006) did little to resolve the confusion, with a split decision from the Court regarding the extent of federal jurisdiction. In writing for four justices, Justice Scalia defined "waters of the United States" as only those waters and wetlands that contain "a relatively permanent flow" or that possess "a continuous surface connection" to waters with relatively permanent flow. Scalia's definition excluded intermittent and ephemeral streams, and wetlands that lack a continuous surface connection to other jurisdictional waters (i.e., wetlands outside of floodplains). This definition differs from that posited by Justice Kennedy in an opinion concurring with the plurality judgment to remand the case for further proceedings but not agreeing with the reasoning of the four justices represented by Scalia. In contrast, Kennedy gave deference to Congressional intent to allow the agencies to regulate pollution (dredge and fill) of waters of the United States. Justice Kennedy ruled that wetlands outside of floodplains, and intermittent and ephemeral streams should be included as waters of the United States if they "significantly affect the physical, chemical, and biological integrity" of downstream navigable waters. Therefore, Kennedy's definition of waters of the United States includes headwaters that are not necessarily navigable but are nevertheless connected to some degree with navigable waters downstream.

Following an extensive scientific review of the literature on waterbody connectivity (USEPA 2015), which included a detailed review by a U.S. Environmental Protection Agency

Headwaters in a Nutshell

- Headwater streams comprise 79% of our nation's stream networks; wetlands outside of floodplains comprise 6.59 million ha in the conterminous USA.
- Headwater streams and wetlands strongly influence ecological functions and fisheries not only within headwater regions, but also in downstream rivers, lakes, and coastal areas.
- Headwater ecosystems provide habitat for many endemic and threatened fish species as well as species supporting economically important fisheries.
- Headwaters provide native fish species with refuge from invasive aquatic species and can provide threatened species with critical refuge habitat.
- Commercial and recreational fisheries, which are dependent on headwaters, are vital economic components of local and regional economies.
- Headwater streams and wetlands are culturally important for many segments of U.S. society, with particularly high significance for many native peoples.
- Estimates of headwaters at risk under a narrower rule are likely low, because many of the 33% of streams in the conterminous western USA mapped as perennial were found to be intermittent or ephemeral.
- Headwater ecosystem impairment, loss, or destruction is assured under the revised WOTUS rule proposed, and would have severe and long-lasting negative consequences for fisheries and environmental conditions throughout the USA.

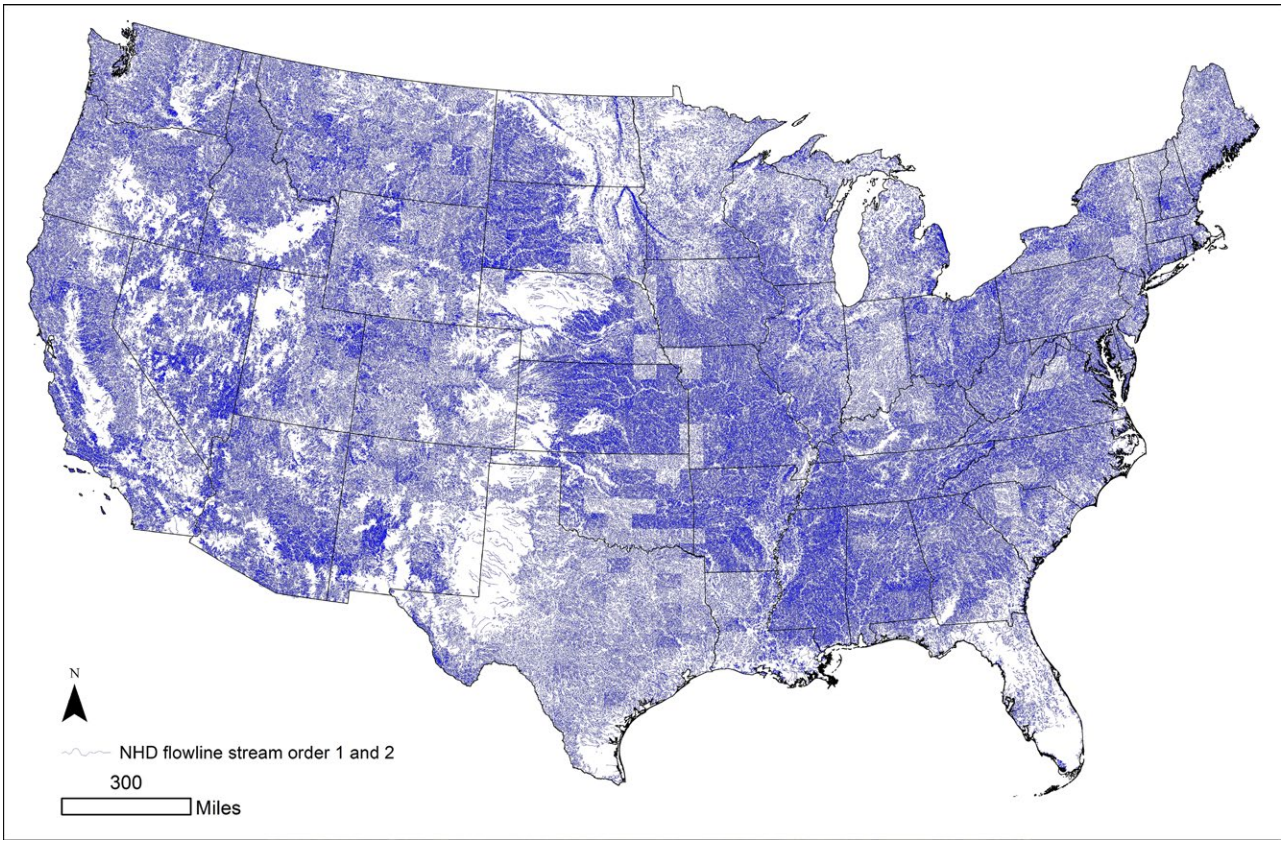

Figure 1. Map of 1st- and 2nd-order tributaries (a stream lacking a tributary and a stream with only first-order tributaries, respectively) comprising river networks of the conterminous United States as characterized by the 1:100,000 scale National Hydrography Dataset Plus Version 2 (NHDPlusV2; USEPA & USGS 2012). However, this is not a full accounting of all 1st- and 2nd-order headwater streams. Currently, it is not possible to comprehensively map all headwater streams because of the sheer number of headwater tributaries that comprise river networks, variability in tributary flow permanence, and the resolution and accuracy of available spatial data necessary to accurately map or model streams and other overland flows (Hughes and Omernik 1981). For example, note the differing stream densities that occur within different regions of the USA (e.g., Indiana versus the Central Plains) or even within states (e.g., varied densities throughout Oklahoma). The differences in density result from state-by-state differences in how streams are mapped or modeled. Despite these limitations, the NHDPlusV2 represents the most comprehensive coverage of tributaries and catchments available for the U.S., allowing us to assess their general prominence of headwaters in U.S. river networks.

(EPA) Science Advisory Board (SAB) of technical experts from the public ("SAB Review;" SAB, 2014 Letter to Gina McCarthy, Review of the Draft EPA Report Connectivity of Streams and Wetlands to Downstream Waters: A Review and Synthesis of Scientific Evidence), the Obama administration issued the Waters of the Unites States (WOTUS) Rule in 2015 that clarified the jurisdiction of the Clean Water Act to include protections for intermittent and ephemeral headwater streams and hydrologically connected wetlands (i.e., with a permanent surface inflow or outflow and directly adjacent to navigable waters), with wetlands outside of the floodplains to be evaluated on a case-by-case basis. The American Fisheries Society (AFS) supports that rule and the science underpinning its development, as documented by review of more than 1,200 peer-reviewed scientific studies by technical experts to determine degrees of connectivity and their ecological consequences between navigable waters, wetlands, and headwater streams (USEPA 2015). On February 28, 2017, the Trump administration issued an executive order directing the EPA and the Department of the Army to review and rescind or revise the 2015 rule. The proposed "Recodification of Pre-Existing Rules" (U.S. Army Corps of Engineers, Department of Defense, USEPA 2018 Revised Definition of "Waters of the United States") establishes a narrower legal definition, implementing the pre-Obama era regulations that provided fewer protections for thousands of miles of headwater streams and millions of acres of wetlands outside of floodplains. Those wetlands are distributed across 6.59 million ha in the conterminous USA as, for example, playa lakes, prairie potholes, Carolina and Delmarva bays, pocosins, and vernal pools; they provide valuable habitat for fish and other organisms and are particularly vulnerable ecosystems (Tiner 2003; Lane and D'Amico 2016; Creed et al. 2017; Figure 2). We refer to headwater streams and wetlands outside of floodplains collectively as "headwaters." However, we also emphasize the inherent complexity of natural systems, and recognize and provide examples of waterbody types that provide similar functions as headwaters such as floodplain wetlands that lack a continuous hydrologic surface connection to a river, low-gradient streams that flow through floodplains, and sloughs and side-channels of navigable rivers.

Headwaters provide numerous services that are essential to ecosystems (Peterson et al. 2001; Meyer et al. 2003), including sustaining aquifers and supplying clean water for more than

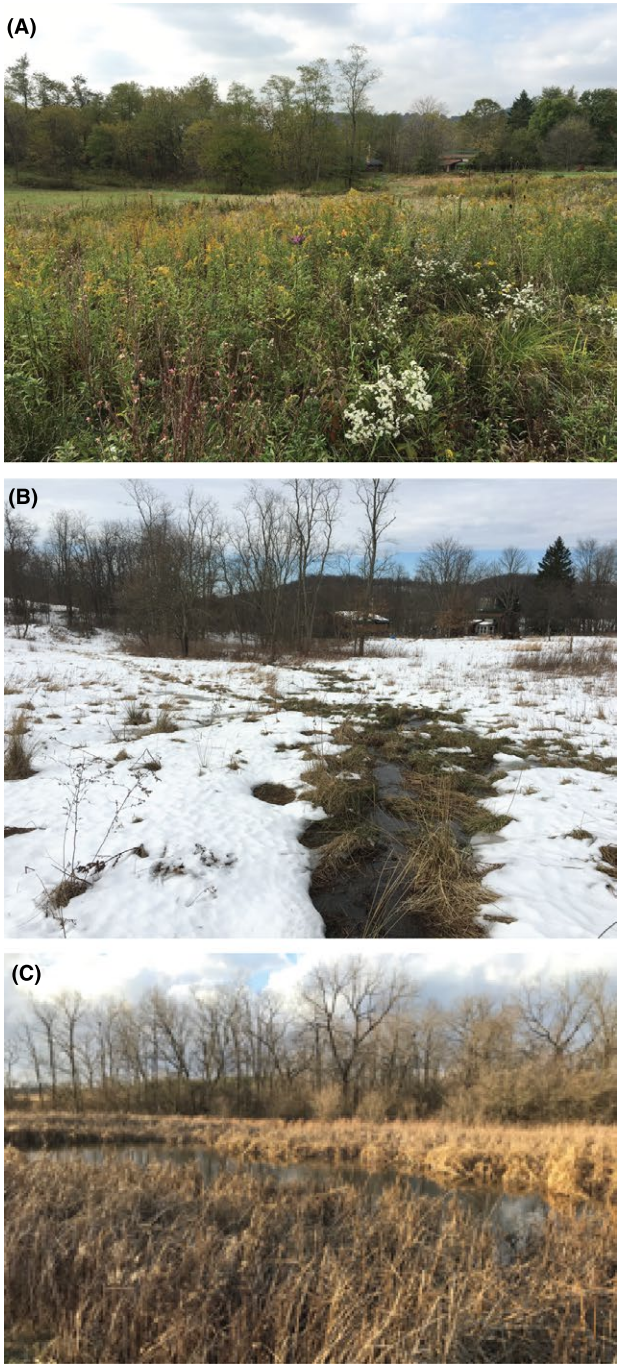

Figure 2. Wetlands outside of floodplains—such as the headwater/source wetland **(A)** in summer and **(B)** winter in Pennsylvania and the **(C)** prairie wetland in Ohio—would be particularly vulnerable to loss of protections. Photo credits: P. D. Shirey: A, B; S. M. P. Sullivan: C.

one-third of the U.S. population (USEPA 2009). At regional scales, headwaters are critical for sustaining aquatic biodiversity (Meyer et al. 2007; Clarke et al. 2008) and for providing vital spawning and rearing habitat for migratory fishes, including commercially fished species (Quinn 2005; Schindler et al. 2010; McClenachan et al. 2015). Headwaters provide dispersal corridors and habitat for fishes and other aquatic and semi-aquatic organisms (e.g., invertebrates, amphibians, and birds), including many endemic and rare species (Steward et al. 2012; Jaeger et al. 2014; Sullivan et al. 2015). Ephemeral headwater streams can support levels of aquatic invertebrate diversity and abundance comparable to, or greater than, those estimated for perennial headwaters, as well as taxa found nowhere else in the watershed (Dieterich and Anderson 2000; Progar and Moldenke 2002; Price et al. 2003).

Headwaters and their ecosystem services are tightly intertwined with the nation's cultural landscape (Boraas and Knott 2018) and are highly vulnerable to a host of human impacts (Creed et al. 2017). Climate change, channel modification, water diversion, and land development (e.g., urbanization, agriculture, mining, deforestation) impair and destroy headwaters by, for example, increasing erosion, sedimentation, and desiccation in both headwaters and downstream reaches of river networks (Walsh et al. 2005; Freeman et al. 2007; Perkin et al. 2017). Pollution of headwaters, including runoff of excess nutrients and other pollutants, degrades water quality affecting downstream ecosystems. Two striking U.S. examples are discharge effluent from mining (Woody et al. 2010; Daniel et al. 2015; Giam et al. 2018) and nutrient loading in the Mississippi River causing the Gulf of Mexico's "dead zone," a vast area of hypoxia that reduces biodiversity and commercial fisheries, with major economic and social costs (Rabalais et al. 1995; Rabotyagov et al. 2014). Similarly, polluted headwaters contribute to harmful algal blooms that result in toxic water, fish kills, domestic animal and human morbidity, and economic damage (Tango 2008; Zimmer 2014; Staletovich 2018). For wetlands outside of floodplains, global estimates indicate continued loss of >30% since 1970 (Dixon et al. 2016).

Discrepancies between actual and estimated stream length and type have long been recognized as problematic and may lead to increased ambiguity in applying a narrower WOTUS rule, especially over time. Headwater stream losses in many regions of the USA are underestimated because drainage networks have not been mapped at sufficiently fine spatial scales (Hughes and Omernik 1981; Meyer and Wallace 2001; Colson et al. 2008), thus posing serious risk to ecological and societal benefits (Creed et al. 2017). Stream type is also often misattributed or changes over time, for example, 207,770 km (33%) of the total length of stream networks in the conterminous western USA mapped as perennial was determined to be non-perennial or not a stream. The map error varied from 55% of stream length in the Southwest to 33% in the western Great Plains to 24% in the western mountains (Stoddard et al. 2005). Changes in estimates from perennial to intermittent or ephemeral streams is a result of mapping errors, climate change, and water withdrawals. Similarly, Perkin et al. (2017) determined a loss of 558 km (21%) of stream length from 1950 to 1980 in the Upper Kansas River Basin, presumably as a result of ground-water pumping accentuated by climate change. These investigators projected a cumulative loss of 844 km (32%) by 2060. In other words, highly vulnerable intermittent and ephemeral streams and rivers are increasingly replacing perennial streams and rivers.

Non-perennial streams and non-floodplain wetlands are integral components of aquatic ecosystems, especially when considered in the aggregate. As supported by the SAB Review (SAB, 2014 Letter to Gina McCarthy, Review of the Draft EPA Report Connectivity of Streams and Wetlands to Downstream Waters: A Review and Synthesis of Scientific Evidence), connectivity between headwaters and downstream waterbodies reflects a gradient in the variability of the frequency, duration, magnitude, predictability, and consequences of physical, chemical, and biological connections. The SAB Review notes

BOX 1. LONGNOSE SUCKERS LINK TRIBUTARY STREAMS AND LAKES

Several fish species migrate from the Laurentian Great Lakes into headwater tributaries to spawn. During spring, Longnose Suckers *Catostomus catostomus* undergo massive spawning runs from Lake Michigan into tributary streams (Figure 3). Egg and larval survival to outmigration appears to be strongly influenced by spring flow and temperature, and this variability can influence stock dynamics (Childress et al. 2016). Egg mortality and excretion by migrating adult suckers contributes significant amounts of nitrogen and phosphorus to stream ecosystems. The millions of larval suckers that may be exported from a single stream to the lake provide a significant nutritional subsidy for a host of recreational fishes that include Walleye *Sander vitreus*, bass, and salmon (Childress and McIntyre 2015). Stream network connectivity has been reduced over large portions of Great Lakes drainage basins, with negative effects on Longnose Suckers, the ecosystem functions they support, and stocks of other fishes that migrate into tributaries for spawning.

that even low levels of connectivity can be important relative to impacts on the chemical, physical, and biological integrity of downstream waters. The SAB Review also highlights the importance of the cumulative effects of streams and wetlands on downstream waters. These relationships also vary spatially and temporally as in some areas, such as arid regions, ephemeral streams comprise the majority of the stream network. Although they flow infrequently during an annual cycle, they are integral to the ecological function of their watersheds, which have evolved with this type of flow network (Meyer et al. 2003). In these and other systems, ephemeral streams and wetlands provide unique and essential habitat for species for which there is no known perennial equivalency (Falke et al. 2010, 2012; Medley and Shirey 2013; Hutson et al. 2018).

Because of the importance of headwaters, any rule that excludes their protection will have far reaching implications for fish, wildlife, and their habitats, as well as economies dependent on those ecosystems. Headwaters are key to the sustainability of fish stocks in both upstream and downstream waters. Threatened and endangered species will be harder to recover, and more species will be at risk of becoming imperiled. Simply put, loss of protections for headwaters would have grave consequences for fish and fisheries. Ultimately, communities across the USA would lose the economic, social, and cultural benefits derived from headwaters. In the following sections, we provide a brief overview of scientific evidence supporting the ecological, social, economic, and cultural importance of headwaters, and highlight some implications of returning to reduced federal protections.

HEADWATERS SUPPORT ECOSYSTEMS

Headwaters perform ecological functions (i.e., biological, geochemical, and physical processes that occur within an ecosystem) that are critical for ecosystem services throughout their drainage basins. Headwaters deliver water, sediments, and organic material to downstream waters; contribute to nutrient cycling and water quality; enhance flood protection and mitigation; and provide recreational opportunities (Gomi et al. 2002; Richardson and Danehy 2007; Hill et al. 2014; Cohen et al. 2016). Headwater ecosystems provide both habitat and food resources for fish and other aquatic and riparian organisms; in turn, fish in headwaters affect food-web dynamics and contribute to the functioning of headwater ecosystems (Richardson and Danehy 2007; Sullivan 2012; Hill et al. 2014). Ecosystem functions in headwaters also maintain aquatic and riparian biodiversity and the sustainability of fish stocks not only in headwater reaches, but also in larger downstream habitats. These and other functions of headwater streams make them economically vital, with recent estimates at $US15.7 trillion/year in ecosystem services for the conterminous USA and Hawai'i (Nadeau and Rains 2007). For wetlands outside of floodplains, ecosystem service estimates are $673 billion/year for the conterminous USA (Lane and D'Amico 2016).

Headwaters receive runoff and groundwater from watersheds and discharge to larger waterbodies downstream. In doing so, they transport sediment and organic material, including large wood from adjacent and upstream riparian systems that are essential for the ecological condition of downstream ecosystems (Gregory et al. 1991; Benda and Dunne 1997). Drifting organic matter (organisms and particulate organic matter) from headwaters provides food for fishes and invertebrates in downstream reaches (Gomi et al. 2002; Wipfli and Gregovich 2002; Wipfli and Baxter 2010). The provisioning of

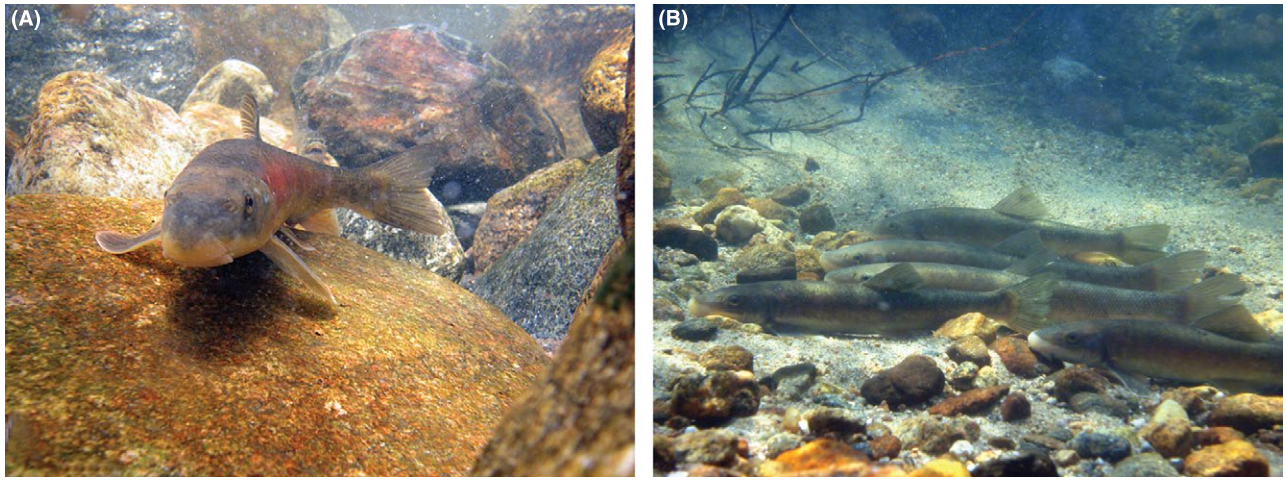

Figure 3. An individual Longnose Sucker **(A)**, and an aggregation **(B)** similar to those that spawn en masse in tributaries of Lake Michigan. Photo credit: Jeremy Monroe, Freshwaters Illustrated.

large wood for habitat development is crucial for aquatic biota, including juvenile salmon and trout (Bilby and Ward 1991; Bilby et al. 2003; Herdrich et al. 2018). Changes in the large-wood recruitment regime resulting from timber harvests have depleted complexity in many mountain streams (Fausch and Young 2004) as well as in streams in other areas of the country (e.g., upper Midwest; Richards 1976; Wohl 2014). Removing wood from streams can also result in reduction of pools and overall habitat complexity as well as fewer and smaller individuals of both coldwater and warmwater fishes (Fausch and Northcote 1992; Dolloff and Warren 2003). Unpolluted headwaters are essential for maintenance of coldwater fish stocks, including Chinook Salmon *Oncorhynchus tshawytscha*, Coho Salmon *O. kisutch*, Steelhead *O. mykiss*, Cutthroat Trout *O. clarkii*, Bull Trout *Salvelinus confluentus*, Apache Trout *O. apache*, Gila Trout *O. gilae*, Golden Trout *O. aguabonita*, Redband Trout *O. mykiss*, Brook Trout *S. fontinalis*, Brown Trout *Salmo trutta*, and Atlantic Salmon *S. salar*.

When the natural flow regimes of headwater streams are altered, downstream water quality often is impaired. Headwaters mediate the intensity and frequency of downstream floods, and play a significant role in global carbon and nitrogen cycling (Gomi et al. 2002; Bernhardt et al. 2005; Lowe and Likens 2005; Marx et al. 2017). Discharge from headwaters also influences downstream fluxes of dissolved and particulate organic matter and nutrients (Alexander et al. 2007; Lassaletta et al. 2010). The cycling of nutrients—including rates of nitrogen uptake, storage, regeneration, and export—is a critical function of headwaters. For instance, Peterson et al. (2001) reported that the most rapid uptake and transformation of inorganic nitrogen can occur in the smallest streams of a catchment, particularly temporary streams, where tightly coupled water-streambed interactions facilitate in-stream retention of nitrogen. Most nitrogen flowing through a drainage network is estimated to come from headwater streams; in the northeastern USA, headwater tributaries can deliver up to 45% of the nitrogen load flowing downstream (Alexander et al. 2007). Additionally, transfer of nitrogen to the atmosphere occurs in headwater systems through denitrification (Mulholland et al. 2009). Hotspots of nutrient transformations are typically linked to physical and microbial processes in headwaters (e.g., McClain et al. 2003). Channel alterations, excess nutrients and sediments, and losses of flows in headwater streams deteriorate water quality (e.g., eutrophication and hypoxia) in downstream systems throughout the USA (Alexander et al. 2007; USEPA 2016a, 2016b; USEPA 2009). Further loss of headwater systems is expected to have major negative consequences for biogeochemical cycles at local to continental and global scales.

Important ecological functions and ecosystem services are provided even by ephemeral and intermittent headwaters (Steward et al. 2012). In arid and semi-arid regions, dry streambeds are "seed and egg banks" for aquatic biota, and when flowing, function as dispersal corridors and temporal ecotones linking wet and dry phases. During dry phases, ephemeral streams store organic material; when flowing, these streams are hotspots for nutrient cycling and other biogeochemical processes (Fisher et al. 1982; McClain et al. 2003). In some arid regions, up to 96% of streams contain little or no flow during much of the year; however, during monsoons they are critical for conveying runoff (Meyer et al. 2003). Permeable surficial geology and low slopes can reduce flood peaks in headwaters and extend the flow of cool water to downstream reaches, thereby expanding thermal refuges (Gomi et al. 2002). Cool headwaters provide important thermal refuges in regions especially susceptible to climate change, including the desert Southwest and intermountain western United States.

Although fish abundance and diversity generally are lower in headwater systems compared to downstream reaches (Schlosser 1987), species composition can be distinct from the rest of the network (Paller 1994). Further, headwaters often support ecological specialist as well as threatened taxa not found elsewhere within the river network (DeRolph et al. 2015; Liang et al. 2013; Lowe and Likens 2005; also see *The importance of headwaters for imperiled species*). Fish inhabiting wetlands located outside of floodplains may benefit from greater availability of food resources compared to habitats in other aquatic ecosystems (Snodgrass et al. 2001; Baber et al. 2002).

Fish contribute both directly and indirectly to headwater ecosystem processes (e.g., Hanson et al. 2005) that, in turn, affect biodiversity and productivity in the receiving river network (Meyer et al. 2007). Through their spawning and foraging activities, fish influence local biotic communities by modifying substrates (e.g., spawning salmonid redds; Montgomery et al. 1996; Moore et al. 2004) and resuspending detritus and other particulate organic matter into the water column (e.g., benthic feeding by the Ozark Minnow *Notropis nubilis*; Gelwick et al. 1997) where it drifts downstream to support populations of aquatic invertebrates. Furthermore, fish feeding and excretion increase availability of inorganic nutrients and stimulate aquatic primary productivity (McIntyre et al. 2008).

Fish are often the top predators in headwater food webs, and thereby exert top-down control of invertebrate assemblages and indirectly affect ecosystem functions such as aquatic primary and secondary production, the latter including emergent aquatic insects that export biomass from streams to terrestrial food webs (Nakano et al. 1999; Baxter et al. 2004). Fish also link aquatic and terrestrial ecosystems in other, more direct ways. During annual leaf-out periods, insectivorous fishes feed on arthropods that fall from riparian vegetation into streams (Wipfli 1997; Baxter et al. 2005). Fish also provide important nutritional subsidies for terrestrial consumers, such as the American dipper *Cinclus mexicanus*, North America's only aquatic songbird (e.g., Sullivan et al. 2015), and grizzly bear *Ursus arctos* (e.g., Matt and Suring 2018).

Many fish species occupy both headwater and downstream habitats during their life cycles (Fausch et al. 2002). For instance, most anadromous salmonids return to their natal streams after spending most of their lives in the ocean. In doing so, fish transport marine-derived nutrients to headwater streams (Zhang et al. 2003). Marine-derived nutrients from salmon carcasses have been shown to increase production of aquatic basal resources, macroinvertebrates, and resident fish stocks (Zhang et al. 2003; Janetski et al. 2009). Marine-derived nutrients are especially important for oligotrophic streams, which are predominant in the Pacific Northwest and Alaska where even small inputs of certain nutrients and sources of organic matter can significantly augment ecosystem productivity (Bilby et al. 1996). Moreover, fish in headwater streams are an important food source for terrestrial consumers, thereby transferring nutrients and energy from aquatic to terrestrial ecosystems. By linking nutrients, energy, and gene pools across space and time, fish migration has been characterized as a type of ecological "memory" of an ecosystem (Holling and Sanderson 1996). Headwaters, their receiving waters, and their functions already have been severely degraded by multiple human activities, including channel alteration, water diversion, and

land modification by agriculture, livestock grazing, mining, and urbanization (e.g., Hughes et al. 2010, 2014, 2016; Beschta et al. 2013). These land uses and others have eliminated countless headwater streams and wetlands that once served as natural primary, secondary, and tertiary nutrient, sediment, and contaminant treatment systems, thereby leading to untreated runoff from diffuse pollution sources (Karr and Schlosser 1978; Karr 1991; Gammon 2005; Woody et al. 2010; Hughes et al. 2014; Daniel et al. 2015). These stressors have caused biological and environmental degradation to over 70% of stream and river length in the conterminous USA (USEPA 2009; Crawford et al. 2016; USEPA 2016a, 2016b). Wetland loss—including but not limited to wetlands outside of floodplains—across the USA is staggering, with some Midwestern states (e.g., Illinois, Indiana, Ohio, Missouri) having lost >85% of wetland area since the 1780s (Dahl 1990). Given the vulnerability and many important ecosystem functions provided by headwaters, policies that would reduce protections are a serious concern.

HEADWATERS SUPPORT IMPERILED SPECIES

Habitat loss and pollution are the primary causes of extinction of aquatic biota (Miller et al. 1989; Dudgeon et al. 2006; Arthington et al. 2016), and emerging threats exacerbate population decline of rare or range-restricted species (Minckley and Deacon 1991; Reid and Mandrak 2008; Shirey et al. 2018). Many threatened desert fishes, such as pupfishes *Cyprinodon* spp., have geographic distributions limited entirely to one or more isolated spring-fed headwaters (Rogowski et al. 2006; Dzul et al. 2013; Figure 4) but many such isolated waters would likely not be protected under a narrower rule. In the 1950s and 1960s, groundwater pumping in Nevada destroyed springs and associated spring-fed wetlands, resulting in the extinction of Las Vegas Dace *Rhinichthys deaconi* and Ash Meadows Poolfish *Empetrichthys merriami*, and put other species at risk of extinction, including the Devils Hole Pupfish *Cyprinodon diabolis*. By highlighting the plight of the remaining imperiled desert fishes, fisheries professionals increased public awareness of the nexus between groundwater and surface water habitat (Deacon and Williams 1991). This awareness stimulated support for halting groundwater pumping in order to protect the remaining habitat and avert further extinctions, although new threats continue to emerge (Deacon et al. 2007). For instance, up to 31 rare and endangered fish species or subspecies that inhabit headwater streams or springs of Nevada, Utah, and California are threatened by proposed groundwater withdrawals in southern Nevada.

Figure 4. **(A)** Death Valley Pupfish *Cyprinodon salinus* spawn during spring flows in **(B)** Salt Creek, Death Valley National Park, California. **(C)** a boardwalk provides access to view the Death Valley Pupfish during winter and spring flows. **(D)** Salt Creek ceases to flow during the remainder of the year and Death Valley Pupfish take refuge in headwater pools. Photo Credit: A–C, National Park Service; D, Jessica Wilson, Creative Commons.

Again, the primary objective of the Clean Water Act (1972) is to restore and maintain the chemical, physical, and biological integrity of the nation's waters. That objective includes species that have become imperiled and are listed as threatened or endangered federally under the Endangered Species Act or protected by states and other entities (Angermeier and Karr 1994). If headwater impairment threatens a federally listed species residing in navigable waters downstream, then that headwater clearly would merit protection under the Clean Water Act because it meets the "significant nexus" test (after SWANCC 2001), and this would be true whether flows are intermittent or ephemeral.

Cavefish habitat demonstrates the importance of the significant nexus perspective, because ephemeral or intermittent headwaters support habitat for imperiled species living in habitat farther downstream (Figure 5). Aquatic habitats of federally listed Ozark Cavefish *Amblyopsis rosae* (threatened) in Cave Springs Cave, Arkansas (Graening et al. 2010), and Alabama Cavefish *Speoplatyrhinus poulsoni* (endangered) in Key Cave, Alabama (USFWS 2017), are supplied water from streams that flow intermittently above and below the surface at intervals as well as seeps, sink holes, and fractures in karst formations. Headwater streams in this region are not navigable, but they are essential for cavefish habitat, and their discharge contributes to flows in the Illinois (Arkansas; Brown et al. 1998) and Tennessee (USFWS 2017) rivers. Therefore, pollution of a sinkhole impacts both cave habitat and navigable waters downstream. A narrower rule defining waters of the United States that excludes headwaters in karst terrain would allow cavefish habitat to be polluted or destroyed such as by filling of or discharging to sinkholes.

Whereas cavefish are restricted to habitats fed by headwaters, other fishes use headwater streams and wetlands that are intermittent or ephemeral during specific stages of

Figure 5. **(A)** Fed by headwaters in karst topography, Cave Springs Cave discharges groundwater to Osage Creek, a tributary to the navigable Illinois River. The Cave Springs Cave headwater (Photo Credit: Arkansas Natural Heritage Commission) provides habitat for **(B)** the federally threatened Ozark Cavefish *Amblyopsis rosae* (Photo Credit: Jim Rathert, Missouri Department of Conservation). **(C)** The Calapooia River's lowland tributaries provide habitat to several species including the first fish species to be delisted under the Endangered Species Act (Photo Credit: Randall Colvin), **(D)** the Oregon Chub *Oregonichthys crameri* (Photo Credit: USFWS). **(E)** The Arikaree River (Photo Credit: Jeff Falke) is an intermittent plains streams in eastern Colorado that supported 16 native fish species adapted to this harsh habitat, including **(F)** the Orangethroat Darter *Etheostoma spectabile* (Photo Credit: Jeremy Monroe, Freshwaters Illustrated) that is imperiled in Colorado.

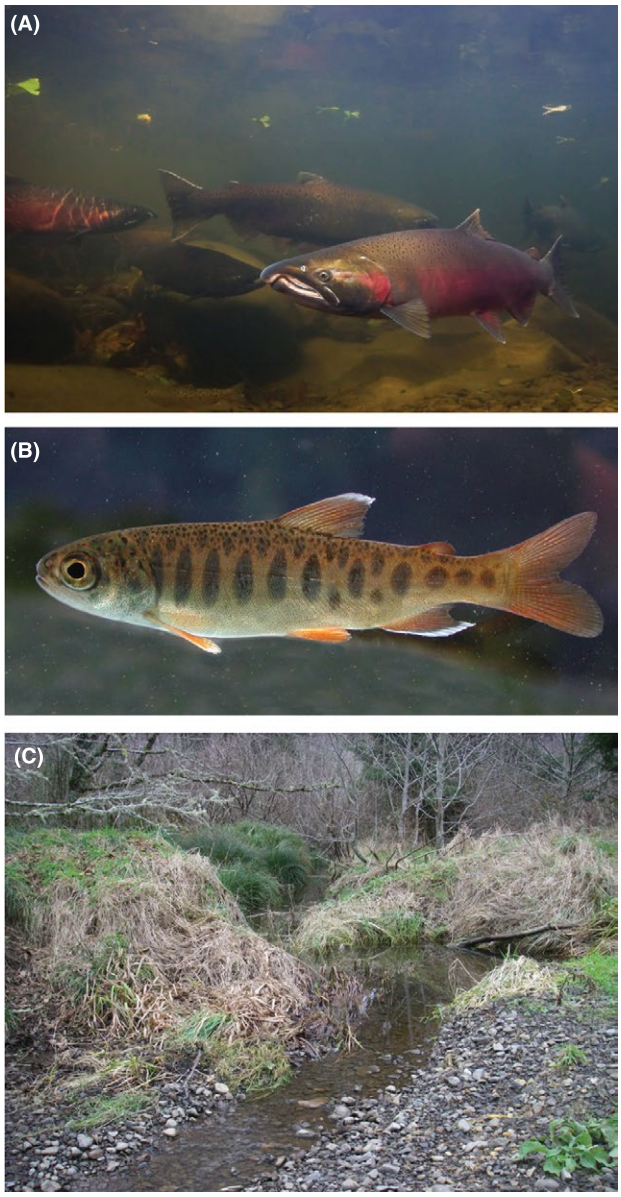

Figure 6. The Oregon Coast Coho Salmon (**A**; Jeremy Monroe, Freshwaters Illustrated) is an evolutionarily significant unit listed as threatened under the Endangered Species Act. Juvenile coho (**B**; Lance Campbell); of several life history types of this species use very small headwater habitats in coastal streams that are wet only in winter, including side-channels and backwaters that are dry during summer like Crowley Creek, Oregon in the Salmon River watershed (**C**; Trevan Cornwell).

their life cycles. Because they may be dry for much of the year, these headwaters might seem unimportant for fishes, and yet they can be essential for the persistence of certain stocks. Intermittent streams are important spawning and refuge habitats for imperiled salmon, trout, darters, minnows, suckers, and other fishes (Figures 5 and 6). Examples include federally listed Coho Salmon and Chinook Salmon, species with juveniles that occupy headwater tributaries and seasonal floodplain wetlands during winter. During the rest of the year, these habitats are either dry or so small that they are not considered suitable salmon habitat (Brown and Hartman 1988; Sommer et al. 2001; Jones et al. 2014; Katz et al. 2017; Woelfle-Erskine et al. 2017). Nonetheless, these intermittent habitats can play a critical role in recruitment. Coho Salmon smolts that inhabit pools in intermittent headwater streams in Oregon are larger than smolts from perennial streams in the same river basin (Wigington et al. 2006). Because larger smolts have higher ocean survival rates, the loss of these intermittent streams could be detrimental to salmon populations in coastal drainages.

Historically, western Oregon's upper Willamette River was bordered by a floodplain forest 2–9 km wide with multiple shaded waterways; winter floods markedly increased its floodplain stream network (Hughes et al. in press). During the past century, agriculture and channelization have altered or eliminated most intermittent water bodies in the valley. However, the remaining temporary streams and ditches still provide critical habitat for a wide diversity of native fish species, such as Cutthroat Trout, Rainbow Trout *O. mykiss*, endangered Chinook Salmon, and the endemic Oregon Chub *Oregonichthyes crameri*. These seasonal habitats provide flood refuge, rearing habitats, and separation from invasive alien fish species, all of which are essential for recovering and maintaining valuable sport and commercial fisheries and endangered species (Colvin et al. 2009; Hughes et al. in press; Figure 5). Collaborations with Willamette Valley landowners have been instrumental in improving Oregon Chub habitat and its delisting, and farmers are pleased to know that their winter-wet waterways offer important habitats for valued salmonids.

Headwater streams also are important for salmon in the eastern USA. In Maine, federally endangered Atlantic Salmon migrate up rivers and streams in early summer to take residence in deep pools with cool, well-oxygenated water prior to their ascent into tributaries for spawning during fall (Baum 1997; NMFS 2009). Atlantic Salmon eggs, larvae, and juveniles require clean gravel and cool, oxygenated water to ensure adequate growth and survival in headwaters until returning to marine habitat to mature (Danie et al. 1984; NMFS 2009). Recovery of Atlantic Salmon stocks may also require reestablishing populations of other diadromous species, such as Alewives *Alosa pseudoharengus*, that also depend on headwaters and that were important prey (Saunders et al. 2006). A narrower rule that excludes intermittent headwaters in the Pacific Northwest and New England would allow pollution and destruction of significant salmon habitat and further risk the extirpation of salmon.

Non-anadromous trout and charr also use headwaters as critical habitats, including for spawning and refuge from harsh conditions. Nearly half of the population of Rainbow Trout in a Sierra Nevada mountain stream spawned in an intermittent tributary that provided refuge from flood disturbance and nonnative Brook Trout (Erman and Hawthorne 1976). In their native range, Brook Trout are highly reliant on cool headwaters (Figure 7) and face declines in much of their native distribution due to impacts from dams, water diversion, channelization, and sedimentation (Curry et al. 1997; Etnier 1997; Hudy et al. 2008). Throughout the western United States, the many subspecies of native Cutthroat Trout persist primarily in small headwater streams above natural or created barriers that create refuges from nonnative species (Shepard et al. 2005; Roberts et al. 2013).

Many headwaters of the western Great Plains and dry valleys of the intermountain western United States are ephemeral, and yet are important habitats for fish during months when they have water (Figures 5 and 8). Several imperiled minnow species use ephemeral or intermittent backwaters in floodplain wetlands adjacent to stream channels for spawning and rearing (e.g., *Hybognathus* spp.; Falke et al. 2010, 2012; Medley

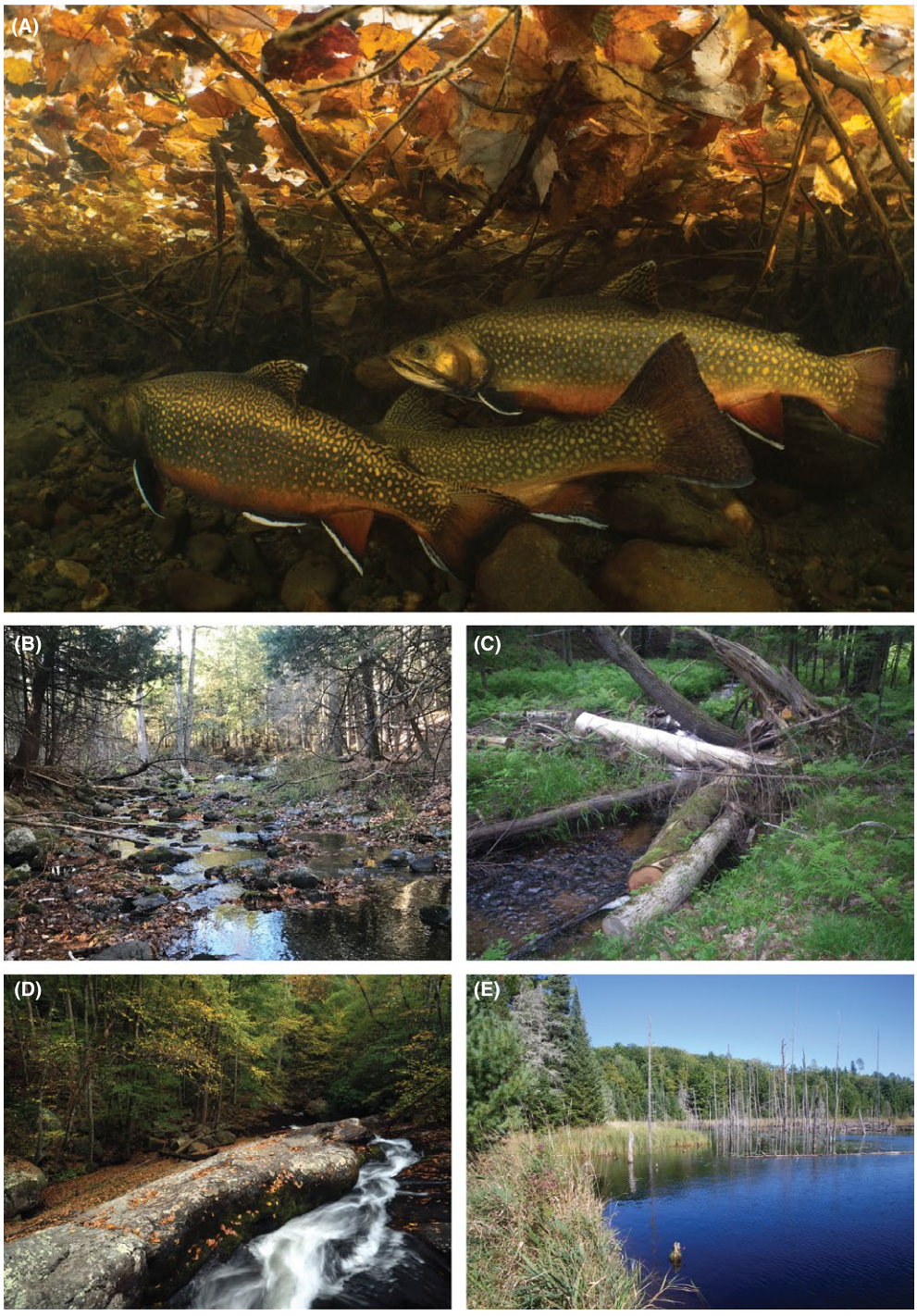

Figure 7. **(A)** Brook Trout *Salvelinus fontinalis* require cold, clear, and well-oxygenated water often found in headwater habitats. Examples of headwater streams inhabited by Brook Trout are shown for **(B)** a stream which becomes intermittent and composed of isolated pools in dry years in Maine (Photo Credit: Susan A.R. Colvin), **(C)** Michigan (Photo Credit: Patrick D. Shirey), and **(D)** an Appalachian headwater stream (Photo Credit: David Herasimtschuk, Freshwaters Illustrated). **(E)** an intermittent stream in Wisconsin impounded by beaver *Castor canadensis* creates diverse headwater habitat and provides ecosystem services of nutrient cycling and floodwater storage (Photo Credit: Patrick D. Shirey).

and Shirey 2013; Hutson et al. 2018). Many minnows, suckers, sunfishes, and darters in arid-land streams disperse between deep pools that retain water by exploiting ephemeral channels when flowing (Fausch and Bramblett 1991; Labbe and Fausch 2000). Though adjacent floodplain wetlands of navigable waters that are defined as wetlands are currently regulated under the Clean Water Act (*United States v. Riverside Bayview 1985*), if the protection of temporary headwaters were to be rescinded, significant amounts of this essential fish habitat would be at risk from changes in headwater source flows or pollution resulting from fill and contaminated discharges.

Headwaters sometimes provide the last refuge for species threatened by loss of habitat elsewhere in the watershed. Examples include the federally endangered Yellowcheek

Figure 8. **(A)** Cottonwood Creek is an intermittent tributary of the Gunnison River (Colorado River basin) in western Colorado that hosts large numbers of **(B)** Bluehead Sucker *Catostomus discobolus*, **(C)** Flannelmouth Sucker *C. latipinnis*, and **(D)** Roundtail Chub *Gila robusta* during spring spawning. Stream discharge varies widely based on snowfall, but these three imperiled species show considerable behavioral plasticity in timing their entry from the main river to this headwater tributary to take advantage of the seasonally available spawning habitat it provides. Fish enter the stream as soon as water depths permit, often in consecutive years. Spawning suckers of both species displayed tributary residency of more than 25 days in years when March or early April flows were adequate **(E** and **F)**, and more than 10,000 individuals used the stream annually (Hooley-Underwood et al., in press). Adults and just-hatched larvae subsequently moved out of the stream **(G)**, and by mid-June **(H)** flow ceased and the streambed dried completely. Intermittent tributaries like these are critical for sustaining populations of these three species, which are the subject of rangewide conservation efforts to prevent listing under the Endangered Species Act.

Darter *Etheostoma moorei* (endemic to the Boston Mountains of Arkansas; Robison and Buchanan 1988; Magoulick and Lynch 2015) and the federally threatened Leopard Darter *Percina pantherina* (endemic to a few headwater streams in the Ouachita Mountains of southeastern Oklahoma and southwestern Arkansas; Zale et al. 1994). The endangered Shortnose Sucker *Chasmistes brevirostris* and Lost River Sucker *Deltistes luxatus* depend on clean gravel in headwater tributaries or springs for spawning as well as adjacent wetlands and nearshore vegetation for juvenile rearing (USFWS 2012b). Wetlands that were replaced by pasture and cropland have contributed to the continued listing of these species. Thermal habitats unique to mountain headwater streams throughout the western Unites States are expected to provide important refuges for native species in the face of climate change, including many of conservation concern, such as Bull Trout and many subspecies of Cutthroat Trout (Wenger et al. 2011; Isaak et al. 2016). For the highly endemic Miller Lake Lamprey *Lampetra minima* and southeastern pygmy sunfishes *Elassoma* spp., headwaters provide refuge from thermal stress, extreme hydrological conditions, and exposure to invasive species (Hayes et al. 1998; Meyer et al. 2007).

Protecting headwater habitats is critical for the recovery and delisting of several endangered fishes. For instance, the recently delisted Modoc Sucker *Catostomus microps* is abundant in intermittent and low-flow headwater streams in northeastern California and southern Oregon (Moyle and Marciochi 1975). Delisting resulted from protecting headwater tributaries and wetlands on public and private lands from threats that included livestock grazing and stream channelization that eliminated refuge pools (Moyle and Marciochi 1975; USFWS 2015). By protecting headwaters, the United States can not only reduce the uncertainty and economic costs that come with an imperiled species being listed under the ESA, but also provide the foundation for successful recovery and delisting of species.

HEADWATERS SUPPORT RECREATIONAL AND COMMERCIAL FISHERIES

Inland and coastal fisheries resources have tremendous economic and social importance. In the USA, commercial and recreational fisheries contributed over $208 billion in economic impact and 1.62 million jobs in 2015 (NMFS 2015). Fishing is a major recreational activity in the USA, with nearly 12 million participants in 2011 and creating 439 thousand jobs and generating more than $63 billion across the United States in 2015 (USFWS 2012a, NMFS 2015). For instance, headwater tributaries in the western USA are visited annually by thousands of anglers for both catch-and-release as well as harvest fishing. Nationally, trout anglers spent $3.5 billion on their pursuits, supported over 100 thousand jobs, and had a $10 billion economic impact, including $1.3 billion in federal and state tax revenues in 2006 (USFWS 2014).

An important consideration for the protection of headwaters is to safeguard recreational and commercial fisheries from point and non-point sources of pollution. Removing those protections will perpetuate current sources of pollution and worsen future impacts to downstream fisheries. In many regions of the USA, past and current pollution continues to degrade fisheries. For example, in the western USA, legacy metal and acid-mine drainage into headwater systems continue to threaten recreational trout fisheries (Woody et al. 2010). In 2015, the Gold King Mine spilled approximately 3 million gallons of untreated acid mine drainage into a headwater stream, instantly changing the color and turbidity of the stream for 2 days, and closing a valuable trout fishery for the entire summer (Rodriguez-Freire et al. 2016). Climate change and the increased frequency of warmer and drier years is predicted to extirpate trout from nearly half their habitat throughout the interior western United States by the 2080s (Wenger et al. 2011), as well as fragment the remaining habitats and reduce trout population sizes and their connectivity (Williams et al. 2015; Isaak et al. 2016). Further erosion of protections for headwaters may reduce or end opportunities to catch trout in these waters and have huge impacts on recreational angling tourism.

Recreational fisheries and headwaters are tightly interconnected. Depending on the state and location, the daily economic value of trout angling was $50–157 per person (USFWS 2012a). For example, blue-ribbon trout streams in two Idaho and Wyoming river basins yielded $12 million and $29 million in county income and 341 and 851 jobs in 2004, respectively (Hughes 2015). The trout fishery in Colorado alone was valued at $1.3 billion in 2011 (Williams et al. 2015). Brook Trout fishing in northern Maine generated over $150 million in 2013 and anglers spent $200 per day on fishing logistics (Fleming 2016). In Pennsylvania, trout anglers spent $45 per day and generated $2 million annually for rural economies (MDNR 2018). North Carolina trout anglers generated $174 million in economic output (NCWRC 2013). Based on travel cost modeling, Georgian trout anglers spent $60–160 per trip, generating $70–200 million annually (Dorison 2012). Recent estimates of freshwater fishing contributions to U.S. Gross Domestic Product total $41.9 billion while providing 526.6 thousand jobs nationwide (Allen et al. 2018). Economic contributions from freshwater fishing is also increasing, growing 11% since 2011 (Allen et al. 2018). It is also critical economic growth when compared to other sectors, collectively the outdoor recreation economy grew 3.8% in 2016 while the overall economy grew 2.8% during the same time period (Allen et al. 2018).

The headwater systems that support these recreational fisheries are typically found at higher elevations, with critical physical habitat requirements (e.g., temperature, flow, and dissolved oxygen) for prized trout species. Species-specific habitat requirements are uniquely provided by these streams and driven by annual snow accumulation (and snowmelt). Recreational anglers avidly pursue several target fishes (Cutthroat Trout, Rainbow Trout, Bull Trout, Brook Trout, Brown Trout, and Arctic Grayling *Thymallus arcticus*) found in these higher-elevation streams. Although they represent a small proportion of recreational angling nationally, these stocks sustain a huge market for fly-fishing anglers from throughout the USA and other nations.

Trout are not the only prized fishery that depends on headwaters. The Alligator Gar *Atractosteus spatula*, one of the largest and most primitive fishes in North America, is a popular target for anglers and archers in the southeastern USA. This fishery has created a booming market for gar-fishing guides that charge $750 per day (Benning 2009). Alligator Gar stocks have declined throughout their native ranges, including apparent extirpations in many regions. During late spring and summer high flows, adult gar move from rivers into small floodplain tributaries (and ditches) to spawn in flooded ephemeral wetlands and fields containing submerged vegetation (Solomon et al. 2013; Kluender et al. 2016). Recruitment success of juvenile gar is correlated with large, long-duration

summer floods and spawning habitat availability (Buckmeier et al. 2017; Robertson et al. 2018). This connectivity allows for gar dispersal between rivers and ephemeral floodplain headwaters, which is critical for sustaining this species (Robertson et al. 2018).

Commercial fisheries are affected by headwaters both directly and indirectly. Among the most valuable commercial fisheries dependent on headwaters are the salmon fisheries of Alaska and the Pacific Northwest. From 2012 to 2015, salmon commercial and recreational fisheries were valued at $3.4 million in economic output and produced $1.2 million in wages and 27 thousand full-time jobs annually (Gislason et al. 2017). The world's most valuable wild salmon fishery in Bristol Bay, Alaska, where headwaters remain relatively pristine, generates $1.5 billion in annual economic activity and 20 thousand full-time jobs (BBNC 2017). As mentioned previously, spawning Pacific Salmon *Oncorhynchus* spp. import marine-derived nutrients into nutrient-poor headwaters, thereby augmenting production of basal resources in aquatic food webs. In the northeastern United States, a burgeoning commercial fishery has developed for juvenile American Eel *Anguilla rostrata* to supply Asian markets. American Eel catches in Maine were valued at more than $10 million annually from 2015 to 2017 (ASMFC 2017b), and the fishery provided well over $20 million in 2018 (Whittle 2018). Some estimates suggest American Eel stocks along the eastern coast of North America have declined dramatically in the last several decades (Busch et al. 1998). However, conclusions from recent assessments on stock status are variable, ranging from "threatened" and "endangered" to "not threatened or endangered" (Jessop and Lee 2016). More clearly, headwaters are important rearing habitats for American Eel, and stream restoration has been recommended as an important strategy for recovery where depleted (Machut et al. 2007).

Protections currently afforded to headwaters through the 2015 WOTUS rule help maintain and contribute to the stability of commercial and recreational fisheries and the rural economies that they support. In rural areas, nature tourism also contributes to sustainable economic growth where visitors spend recreational dollars to see rare fish up close (Figure 4). For example, the Ash Meadows National Wildlife Refuge is home to the highest concentration of endemic species in the USA and draws nearly 70 thousand visitors annually that contribute over $3 million to the local economy (unpublished data from Ash Meadows National Wildlife Refuge, Visitor Service Staff).

HEADWATERS ARE CULTURALLY SIGNIFICANT

Cultural values of headwaters and the downstream rivers they support are diverse, and clearly expressed in nature-based tourism, aesthetic values, recreational fishing, and other activities (Beier et al. 2017). Human–natural resource relationships have evolved in the context of intricate interactions among cultures, communities, and water (e.g., its quality, access, use, and associated resources) for both native and other peoples (Johnston 2013). Wild salmon, for example, hold central roles in the creation and migration narratives of native peoples, and continue to be present in prayers and visions in addition to diets (Stumpff 2001). Fly fishing for trout can be a religious, transformative experience for many. This pursuit strengthens ties with nature, shapes local-to-regional economies, and has a complex history with environmental stewardship (Hemingway 1973; Maclean 1976; Brown 2012, 2015). However, impairment of headwaters has strongly altered the interactions between people and nature, with the ecosystem services provided by rivers to society declining over time (Gilvear et al. 2013; Lynn et al. 2013; Marttila et al. 2016).

The spiritual and socio-cultural values of fish and healthy ecosystems—which are dependent on clean, free-flowing headwaters—are intangible and extend well beyond any economic measures (Boraas and Knott 2018). Pacific Salmon fisheries are a major source of subsistence and income for many native peoples in Alaska and the western USA (e.g., Boraas and Knott 2018). Salmon are also a traditional "first food," honored in many tribal traditions and strongly linked to cultural identities (e.g., CRITFC 2018; NPT 2018). For example, the Nimiipuu (Nez Perce) view salmon as economic and spiritual keystones, with the survival of the tribe and the salmon being interdependent (Colombi 2012).

Similar to Pacific Salmon, Bull Trout inhabiting western streams are culturally important to many groups, including the Confederated Salish and Kootenai Tribes. Bull Trout are part of the history, oral traditions, culture, and identity that are passed down among generations (CSKT 2011). The Confederated Tribes of western Montana credit the abundance of Bull Trout for preventing starvation during harsh winters (Laughlin and Gibson 2011). Even though Bull Trout are not currently harvested for subsistence and economic purposes, Rich Janssen, the natural resource manager for the Confederated Salish and Kootenai Tribes, highlights their interrelationship as follows: "It's part of who you are. It's part of your culture. It's part of your history. You don't want to lose who you are. You don't want to lose that connection" (Laughlin and Gibson 2011).

The importance of headwaters to indigenous cultures extends beyond the well-established examples from Alaska, the Pacific Northwest, and intermountain western USA. For instance, the Ash Meadows National Wildlife Refuge is also culturally important to the Timbisha Shoshone and Southern Paiute peoples because of its life-giving pools fed by headwater springs (Shirey et al. 2018). The Rio Grande and Colorado River flow from headwaters in the Rocky Mountains through traditional lands of the largest concentrations of indigenous peoples within the conterminous USA (Navajo, Apache, Pueblo, and others) and intersect the ranges of Apache Trout and Gila Trout. These headwater ecosystems and the services they provide are central to traditional place-based lifestyles of indigenous tribes (Johnston 2013). Eastern North Carolina Cherokee highly value headwater streams for their cultural significance (extending back thousands of years) as well as for fishery-based tourism (Balster 2018). For the Passamoquoddy of present-day Maine, water and fish are sacred and inextricably linked to their history, culture, traditional beliefs, lore, and spirituality (Bassett 2015). Caloric-rich Alewife and Blueback Herring *A. aestivalis* migrate from the ocean to spawn in the headwaters of the St. Croix River, Maine, where they were a key resource with cultural importance for the Passamoquoddy for thousands of years before European colonization and habitat impairment from pollution, dams, overfishing, and stocking of alien species. In 2013, in cooperation with the Bureau of Indian Affairs, U.S. Fish and Wildlife Service, NOAA and others, the Passamoquoddy began restoring the St. Croix Watershed and returning these species to the ecosystem and the Passamoquoddy people. Traditional ecological knowledge provides an important line of evidence supporting protection and restoration of headwaters. For example, Maine Sea Grant and the National Marine Fisheries Service (NMFS) collaborated to document and disseminate harvesters' knowledge of

BOX 2. ALEWIVES IN MAINE

Alewives *Alosa pseudoharengus*, ascend freshwater rivers and tributaries in early summer to access lakes and headwater ponds where they spawn; in the fall, juvenile Alewives migrate from headwaters to the marine environment (Saunders et al. 2006; Figure 9). Alewife recovery resulting from dam removals and improved access has provided an additional food resource for endangered Atlantic Salmon and terrestrial piscivores, such as the bald eagle *Haliaeetus leucocephalus*. Restored Alewife stocks also have enhanced local economies by diversifiying fisheries, including creation of a major fishery for bait to supply the lobster fishery (Saunders et al. 2006; McClenachan et al. 2015). Lakes with restored alewife populations also have shown improvements in water quality and clarity because out-migrating juveniles remove phosphorus from these systems (McClenachan et al. 2015). Despite some recent population recoveries of Alewife in Maine, coastwide populations of river herring, including both Alewives and Blueback Herring *A. aestivalis,* are depleted and near historic lows (ASMFC 2017a).

Alewife, Blueback Herring, and American Eel, all of which are returning to headwater streams following recent dam removals (Hitt et al. 2012; Hogg et al. 2015). Similarly, the Yurok and Karuk people of the Klamath region in northern California, who have deep cultural and subsistence ties with Pacific Lamprey *L. tridentata*, provided important information that improved understanding of lamprey population crashes in the Klamath Basin (Lewis 2009).

The strong interrelationships between native peoples, fish, and fluvial systems also implicate environmental justice issues, particularly as related to chemical contaminants and traditional food systems that include fish (Kuhnlein and Chan 2000). Contaminants affect not only human health, but also broader issues of food security and social and cultural wellbeing (Jewett and Duffy 2007). Impairment of headwaters and water quality extends to many other groups as well, and can lead to greater environmental inequality (e.g., Elkind 2006). Moving forward, heightened respect for and recognition of the rights and values of culturally diverse peoples in the use of river systems, including headwaters and associated resources, warrants additional and thoughtful consideration when legislating and implementing protections (Johnston 2013).

Figure 9. Juvenile Alewife *Alosa pseudoharengus* from Unity Pond, Maine. Photo Credit: Susan A. R. Colvin.

HEADWATERS NEED CONTINUED PROTECTION

The repeal and replacement of the 2015 Clean Water Rule would roll back Clean Water Act protections for a majority of the nation's streams and wetlands, including thousands of miles of headwater streams and millions of acres of wetlands that provide invaluable ecosystem services and habitat for many species of fish. The recently proposed rule, which excludes wetlands outside of floodplains (or those that lack a continuous surface connection to other jurisdictional waters), ephemeral streams, and likely some intermittent streams, would threaten fish and the headwater ecosystems on which they rely, result in severe economic losses, and cause irreparable cultural and social damage. To recap, some examples of headwaters that would not meet Scalia's definition and could lose protection under the new rule include the karst features, critically important to threatened and endangered cavefish (Figure 5); intermittent streams used by imperiled fish for spawning and early rearing (Figure 8); and intermittent side channels and floodplains that provide critical habitat for juvenile salmon (Figure 6). Justice Scalia's definition, which largely aligns with the proposed rule, ignored the intent of Congress in passing and updating the Clean Water Act, failed to give deference to the agencies that implement the law, and issued a decision not grounded in science. In contrast, Justice Kennedy's definition deferred to Congressional intent and federal agency experts and relied on the available scientific evidence. The science of waterbody connectivity has advanced markedly in the time since the *Rapanos* case, and the 2015 Clean Water Rule was based on the demonstrated importance of physical, chemical, and biological connections of headwaters to the ecological condition of navigable waters and their biota (Leibowitz et al. 2018).

Headwaters are critically important for many ecosystem functions, including sustaining fish stocks, with influences extending from small tributary streams and wetlands to navigable waterbodies downstream. The recently proposed rule offers protection only to a narrower subset of headwaters and will have far-reaching implications for fish, wildlife, and humans that depend on freshwater ecosystems. Species already at risk of extinction would be more difficult to recover, and it is highly likely that many fishes and other aquatic taxa would face greater imperilment. It is clear that communities across the USA would lose significant economic, spiritual, and socio-cultural benefits that are derived from headwaters under the proposed rule. Therefore, we recommend that the EPA follow the approach in its National Aquatic Resource Surveys and conduct a formal ecological and economic risk assessment to quantify the potential effects of changing the current WOTUS rule.

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AUTHORS' CONTRIBUTIONS

S.A.R.C. and S.M.P.S. conceived the original structure of the manuscript. S.A.R.C. served as overall lead author and

led the writing of the Introduction. S.M.P.S led the Ecosystem Function and Cultural Significance sections. P.D.S. led the Endangered Species section, with contributions from K.D.F. R.W.C. led the section on Commercial and Recreational Fishing. These authors wrote the manuscript with contributions from all authors. R.M.H., K.O.W., and K.D.F. provided important editorial suggestions.

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REFERENCES

Alexander, R. B., E. W. Boyer, R. A. Smith, G. E. Schwarz, and R. B. Moore. 2007. The role of headwater streams in downstream water quality. Journal of the American Water Resources Association 43(1):41–59.

Allen, T., E. Olds, R. Southwick, B. Scuderi, L. Caputo, and D. Howlett. 2018. Sportfishing in America: an economic force for conservation. Produced for the American Sportfishing Association via Multistate Grant #F17AP00082 awarded by the Wildlife and Sport Fish Restoration Programs of the U.S. Fish and Wildlife Service.

Angermeier, P. L., and J. R. Karr. 1994. Biological integrity versus biological diversity as policy directives. BioScience 44:690–697.

Arthington, A. H., N. K. Dulvy, W. Gladstone, and I. J. Winfield. 2016. Fish conservation in freshwater and marine realms: status, threats and management. Aquatic Conservation: Marine and Freshwater Ecosystems 26:838–857.

ASMFC (Atlantic States Marine Fisheries Commission). 2017a. Stock assessment overview: River Herring. Arlington, Virginia.

ASMFC (Atlantic States Marine Fisheries Commission). 2017b. American Eel Stock Assessment Update. Arlington, Virginia.

Baber, M. J., D. L. Childers, K. J. Babbitt, and D. H. Anderson. 2002. Controls on fish distribution and abundance in temporary wetlands. Canadian Journal of Fisheries and Aquatic Sciences 59:1441–1450.

Balster, L. 2018. Eastern Band of Cherokee uses environmental monitoring to preserve reservation waters and uphold culture dating back thousands of years. Environmental Monitor. Available: https://www.fondriest.com/news/eastern-band-cherokee-uses-environmental-monitoring-preserve-reservation-waters-uphold-culture-dating-back-thousands-years.htm (November 2018)

Bassett, E. 2015. Cultural importance of River Herring to the Passamaquoddy People. Pages 1–25 *in* Sipayik Environmental Department, Pleasant Point Reservation, Passamaquoddy Tribe.

Baum, E. T. 1997. Maine Atlantic Salmon: a National Treasure, 1st edition. Atlantic Salmon Unlimited, Hermon, Maine.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology 85:2656–2663.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201–220.

BBNC (Bristol Bay Native Corporation). 2017. Economic value of Bristol Bay: a national treasure. Available: https://www.bbnc.net/wp-content/uploads/2017/05/BBNC-Pebble-Mine-Economic-Value-of-Bristol-Bay.pdf. (November 2018).

Beier, C. M., J. Caputo, G. B. Lawrence, and T. J. Sullivan. 2017. Loss of ecosystem services due to chronic pollution of forests and surface waters in the Adirondack region (USA). Journal of Environmental Management 191:19–27.

Benda, L., and T. Dunne. 1997. Stochastic forcing of sediment supply to channel networks from landsliding and debris flow. Water Resources Research 33:2849–2863.

Benning, T. 2009. The alligator gar is one ugly fish, with few friends but new fans. The Wall Street Journal. Available: https://www.wsj.com/articles/SB124631318638370373. (November 2018).

Bernhardt, E. S., G. E. Likens, R. O. Hall Jr., D. C. Buso, S. G. Fisher, T. M. Burton, J. L. Meyer, W. H. McDowell, M. S. Mayer, and W. B. Bowden. 2005. Can't see the forest for the stream? In-stream processing and terrestrial nitrogen exports. BioScience 55:219–230.

Beschta, R. L., D. L. Donahue, D. A. DellaSala, J. J. Rhodes, J. R. Karr, M. H. O'Brien, T. L. Fleischner, and C. D. Williams. 2013. Adapting to climate change on western public lands: addressing the ecological effects of domestic, wild, and feral ungulates. Environmental Management 51:474–491.

Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Canadian Journal of Fisheries and Aquatic Sciences 53:164–173.

Bilby, R. E., G. H. Reeves, and C. A. Dolloff. 2003. Sources and variability in aquatic ecosystems; factors controlling biotic production and diversity. Pages 129–146 *in* R. C. Wissmar and P. A. Bisson, editors. Strategies for restoring river ecosystems: sources of variability and uncertainty in natural and managed systems. American Fisheries Society, Bethesda, Maryland.

Bilby, R. E., and J. W. Ward. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and 2nd-growth forests in southwestern Washington. Canadian Journal of Fisheries and Aquatic Sciences 48:2499–2508.

Boraas, A. S., and C. H. Knott. 2018. The indigenous salmon cultures of the Bristol Bay watershed. Pages 3–28 *in* C. A. Woody, editor. Bristol Bay, Alaska: natural resources of the aquatic and terrestrial ecosystems. J. Ross Publishing, Plantation, Florida.

Brown, A. V., G. O. Graening, and P. Vendrell. 1998. Monitoring cavefish population and environmental quality in Cave Springs Cave, Arkansas. A final report submitted to the Arkansas Natural Heritage Commission. Arkansas Water Resources Center Publication No. MSC-214. University of Arkansas, Fayetteville.

Brown, J. C. 2012. Trout culture: an environmental history of fishing in the Rocky Mountain West. Dissertation. Washington State University, Seattle.

Brown, J. C. 2015. Trout culture: how fly fishing forever changed the Rocky Mountain West. University of Washington Press, Seattle.

Brown, T. G., and G. F. Hartman. 1988. Contribution of seasonally flooded lands and minor tributaries to the production of Coho Salmon in Carnation Creek, British Columbia. Transactions of the American Fisheries Society 117:546–551.

Buckmeier, D. L., N. G. Smith, D. J. Daugherty, and D. L. Bennett. 2017. Reproductive ecology of alligator gar: identification of environmental drivers of recruitment success. Journal of the Southeastern Association of Fish and Wildlife Agencies 4:8–17.

Busch, W. D. N., S. J. Lary, C. M. Castilione, and R. P. McDonald. 1998. Pages 98–2 *in* Distribution and availability of Atlantic coast freshwater habitats for American eel (Anguilla rostrata) Amherst. U.S. Fish and Wildlife Service, Administrative Report, New York.

Childress, E. S., and P. B. McIntyre. 2015. Multiple nutrient subsidy pathways form a spawning migration of iteroparous fish. Freshwater Biology 60:490–499.

Childress, E. S., R. Papke, and P. B. McIntyre. 2016. Spawning success and early life history of longnose suckers in Great Lakes tributaries. Ecology of Freshwater Fish 25:393–404.

Clarke, A., R. MacNally, N. Bond, and P. S. Lake. 2008. Macroinvertebrate diversity in headwater streams: a review. Freshwater Biology 53:1707–1721.

Cohen, M. J., I. F. Creed, L. Alexander, N. B. Basu, A. J. K. Calhoun, C. Craft, E. D'Amico, E. DeKeyser, L. Fowler, H. E. Golden, J. W. Jawitz, P. Kalla, L. K. Kirkman, C. R. Lane, M. Lang, S. G. Leibowitz, D. B. Lewis, J. Marton, D. L. McLaughlin, D. M. Mushet, H. Raanan-Kiperwas, M. C. Rains, L. Smith, and S. C. Walls. 2016. Do geographically isolated wetlands influence landscape functions? Proceedings of the National Academy of Sciences 113:1978–1986.

Colombi, B. J. 2012. Salmon and the adaptive capacity of Nimiipuu (Nez Perce) culture to cope with change. American Indian Quarterly 36:75–97.

Colson, T., J. Gregory, J. Dorney, and P. Russell. 2008. Topographic and soil maps do not accurately depict headwater stream networks. National Wetlands Newsletter 30:25–28.

Colvin, R., G. R. Giannico, J. Li, K. L. Boyer, and W. J. Gerth. 2009. Fish use of intermittent watercourses draining agricultural lands in the Upper Willamette River Valley, Oregon. Transactions of the American Fisheries Society 138:1302–1313.

Crawford, S., G. Whelan, D. M. Infante, K. Blackhart, W. M. Daniel, P. L. Fuller, T. Birdsong, D. J. Wieferich, R. McClees–Funinan, S. M. Stedman, K. Herreman, and P. Ruhl. 2016. Through a fish's eye: the status of fish habitats in the United States 2015. National Fish Habitat Partnership. Available: http://assessment.fishhabitat.org/ (November 2018).

Creed, I. F., C. R. Lane, J. N. Serran, L. C. Alexander, N. B. Basu, A. J. K. Calhoun, J. R. Christensen, M. J. Cohen, C. Craft, E. D'Amico, E. DeKeyser, L. Fowler, H. E. Golden, J. W. Jawitz, P. Kalla, L. K. Kirkman, M. Lang, S. G. Leibowitz, D. B. Lewis, J. Marton, D. L. McLaughlin, H. Raanan-Kiperwas, M. C. Rains, K. C. Rains, and L. Smith. 2017. Enhancing protection for vulnerable waters. Nature Geoscience 10:809–815.

CRITFC (Columbia Inter-Tribal Fish Commission). 2018. Salmon culture: Salmon culture of Pacific Northwest Tribes. Available: https://www.critfc.org/salmon-culture/tribal-salmon-culture/ (November 2018).

CSKT (Confederated Tribes of the Kootenai). 2011. Bull Trout's gift: a Salish story of the value of reciprocity. Explore the river. Bull Trout, tribal people, and the Jocko River. University of Nebraska Press, Lincoln.

Curry, R. A., C. Brady, D. L. G. Noakes, and R. G. Danzmann. 1997. Use of small streams by young brook trout spawned in a lake. Transactions of the American Fisheries Society 126:77–83.

Dahl, T. E. 1990. Wetland losses in the United States 1780s to 1980s. US Department of the Interior, Fish and Wildlife Service, Washington, D.C..

Danie, D. S., J. G. Trial, and J. G. Stanley. 1984. Species profiles: life histories and environmental requirements of coastal fish and invertebrates (North Atlantic) Atlantic Salmon. U.S. Fish and Wildlife Service, FWS/OBS-82/11.22.

Daniel, W. M., D. M. Infante, R. M. Hughes, Y. P. Tsang, P. C. Esselman, D. Wieferich, K. Herreman, A. R. Cooper, L. Wang, and W. W. Taylor. 2015. Characterizing coal and mineral mines as a regional source of stress to stream fish assemblages. Ecological Indicators 50:50–61.

Datry, T., S. T. Larned, K. M. Fritz, M. T. Bogan, P. J. Wood, E. I. Meyer, and A. N. Santos. 2014b. Broad-scale patterns of invertebrate richness and community composition in temporary rivers: effects of flow intermittence. Ecography 37:94–104.

Datry, T., S. T. Larned, and K. Tockner. 2014a. Intermittent rivers: a challenge for freshwater ecology. BioScience 64:229–235.

Deacon, J. E., and C. D. Williams. 1991. Ash Meadows and the legacy of the Devils Hole Pupfish. Pages 69–87 *in* W. L. Minckley and J. E. Deacon, editors. Battle against extinction—native fish management in the American West. University of Arizona Press, Tucson.

Deacon, J. E., A. E. Williams, C. D. Williams, and J. E. Williams. 2007. Fueling population growth in Las Vegas: how large-scale groundwater withdrawal could burn regional biodiversity. BioScience 57:688–698.

DeRolph, C. R., S. A. C. Nelson, T. J. Kwak, and E. F. Hain. 2015. Predicting fine-scale distributions of peripheral aquatic species in headwater streams. Ecology and Evolution 5:152–163.

Dieterich, M., and N. H. Anderson. 2000. The invertebrate fauna of summer-dry streams in western Oregon. Archiv für Hydrobiologie 147:273–295.

Dixon, M. J. R., J. Loh, N. C. Davidson, C. Beltrame, R. Freeman, and M. Walpole. 2016. Tracking global change in ecosystem area: the Wetland Extent Trends index. Biological Conservation 193:27–35.

Dolloff, C. A., and M. L. Warren. 2003. Fish relationships with large wood in small streams. American Fisheries Society Symposium 37:179–193.

Dorison, A. M. 2012. Estimating the economic value of trout angling in Georgia: a travel cost model approach. Master's thesis. University of Georgia, Athens.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Leveque, R. J. Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81:163–182.

Dzul, M. C., M. C. Quist, S. J. Dinsmore, D. B. Gaines, and M. R. Bower. 2013. Coarse-scale movement patterns of a small-bodied fish inhabiting a desert stream. Journal of Freshwater Ecology 28(1):27–38.

Elkind, S. S. 2006. Environmental inequality and the urbanization of west coast watersheds. Pacific Historical Review 75(1):53–61.

Erman, D. C., and V. M. Hawthorne. 1976. The quantitative importance of an intermittent stream in the spawning of Rainbow Trout. Transactions of the American Fisheries Society 105:675–681.

Etnier, D. A. 1997. Jeopardized southeastern freshwater fishes: a search for causes. Pages 87–104 *in* G. W. Benz and D. E. Collins, editors. Aquatic fauna in peril: the southeastern perspective, Southeast Aquatic Research Institute Special Publication 1. Lenz Design and Communications, Decatur, Georgia.

Falke, J. A., L. L. Bailey, K. D. Fausch, and K. R. Bestgen. 2012. Colonization and extinction in dynamic habitats: an occupancy approach for a Great Plains stream fish assemblage. Ecology 93:858–867.

Falke, J. A., K. R. Bestgen, and K. D. Fausch. 2010. Streamflow reductions and habitat drying affect growth, survival, and recruitment of brassy minnow across a Great Plains riverscape. Transactions of the American Fisheries Society 139:1566–1583.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52:483–498.

Fausch, K. D., and R. G. Bramblett. 1991. Disturbance and fish communities in intermittent tributaries of a western Great Plains river. Copeia 1991:659–674.

Fausch, K. D., and T. G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 49:682–693.

Fausch, K. D., and M. K. Young. 2004. Interactions between forests and fish in the Rocky Mountains of the USA. Pages 463–484 *in* T. G. Northcote and G. F. Hartman, editors. Fishes and forestry: worldwide watershed interactions and management. Blackwell Science, Oxford, UK.

FEMAT (Forest Ecosystem Management Assessment Team). 1993. Forest ecosystem management: an ecological, economic and social assessment. 1993-793-071. U.S. Government Printing Office, Washington, D.C.

Fisher, S. G., L. J. Gray, N. B. Grimm, and D. E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. Ecological Monographs 52(1):93–110.

Fleming, D. 2016. Brook trout make Maine world-class fishing destination. Available: https://www.pressherald.com/2016/04/18/brook-trout-mystique-a-boost-for-maine/. (November 2018).

Freeman, M. C., C. M. Pringle, and C. R. Jackson. 2007. Hydrologic connectivity and the contribution of stream headwaters to ecological integrity at regional scales. Journal of the American Water Resources Association 43:5–14.

Frey, D.G. 1977. Biological integrity of water—an historical approach. Pages 127–140 *in* R. K. Ballentine, and L. J. Guarraia, editors. The integrity of water. Office of Water & Hazardous Materials. U.S. Environmental Protection Agency, Washington, D.C.

Gammon, J. R. 2005. Wabash River fishes from 1800 to 2000. American Fisheries Society Symposium 45:365–381.

Gelwick, F. P., M. S. Stock, and W. J. Matthews. 1997. Effects of fish, water depth, and predation risk on patch dynamics in a north-temperate river ecosystem. Oikos 80:382–398.

Giam, X., D. Simberloff, and J. D. Olden. 2018. Impact of coal mining on stream biodiversity in the US and its regulatory implications. Nature Sustainability 1:176–183.

Gilvear, D. J., C. J. Spray, and R. Casas-Mulet. 2013. River rehabilitation for the delivery of multiple ecosystem services at the river network scale. Journal of Environmental Management 126:30–43.

Gislason, G., E. Lam, G. Knapp, and M. Guettabi. 2017. Economic impacts of Pacific salmon fisheries. Pacific Salmon Commission, Vancouver, British Columbia, Canada.

Gomi, T., R. C. Sidle, and J. S. Richardson. 2002. Understanding processes and downstream linkages of headwater systems. BioScience 52:905–916.

Graening, G. O., D. B. Fenolio, M. L. Niemiller, A. V. Brown, and J. B. Beard. 2010. The 30-year recovery effort for the Ozark cavefish (*Amblyopsis rosae*): analysis of current distribution, population trends, and conservation status of this threatened species. Environmental Biology of Fish 87:55–88.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience 41:540–552.

Hanson, M. A., K. D. Zimmer, M. G. Butler, B. A. Tangen, B. R. Herwig, and N. H. Euliss. 2005. Biotic interactions as determinants of ecosystem structure in prairie wetlands: an example using fish. Wetlands 25:764–775.

Hayes, D. B., W. W. Taylor, M. T. Drake, S. M. Marod, and G. E. Whelan. 1998. The value of headwaters to Brook Trout (*Salvelinus fontinalis*) in the Ford River, Michigan, USA. Pages 175–185 *in* M. J. Haigh, J. Krecek, G. S. Rajwar and M. P. Kilmartin, editors. Headwaters: water resources and soil conservation. A. A. Balkema, Roterdam, Netherlands.

Hemingway, E. 1973. Big Two-Hearted River. Bantam Books, New York.
Herdrich, A. T., D. L. Winkleman, M. P. Venarsky, D. M. Walters, and E. Wohl. 2018. The loss of large wood affects Rocky Mountain trout populations. Ecology of Freshwater Fish 27:1023–1036.
Hill, B. H., R. K. Kolka, F. H. McCormick, and M. A. Starry. 2014. A synoptic survey of ecosystem services from headwater catchments in the United States. Ecosystem Services 7:106–115.
Hitt, N. P., S. Eyler, and J. E. B. Wofford. 2012. Dam removal increases American Eel abundance in distant headwater streams. Transactions of the American Fisheries Society 141:1171–1179.
Hogg, R. S., S. M. Coghlan, J. Zydlewski, and C. Gardner. 2015. Fish community response to a small-stream dam removal in a Maine coastal river tributary. Transactions of the American Fisheries Society 144:467–479.
Holling, C. S., and S. Sanderson. 1996. Dynamics of (dis)harmony in ecological and social systems. Pages 57–85 *in* S. F. Hanna, C. Folke and K.-G. Mäler, editors. Rights to nature: ecological economic, cultural and political principles of Institutions for the environment. Island Press, Washington, D.C.
Hudy, M., T. M. Thieling, N. Gillespie, and E. P. Smith. 2008. Distribution, status, and land use characteristics of subwatersheds within the native range of Brook Trout in the Eastern United States. North American Journal of Fisheries Management 28:1069–1085.
Hughes, R. M. 2015. Recreational fisheries in the USA: economics, management strategies, and ecological threats. Fisheries Science 81:1–9.
Hughes, R. M., F. Amezcua, D. M. Chambers, W. M. Daniel, J. S. Franks, W. Franzin, D. MacDonald, E. Merriam, G. Neall, P. dos Santos Pompeu, and L. Reynolds. 2016. AFS position paper and policy on mining and fossil fuel extraction. Fisheries 41(1):12–15.
Hughes, R. M., B. L. Bangs, S. V. Gregory, P. D. Scheerer, R. C. Wildman, and J. S. Ziller. In Press. Recovery of Willamette River fish assemblages: successes & remaining threats. *In* C. Krueger, W. Taylor, and S.-J. Youn, editors. From catastrophe to recovery: stories of fish management success. American Fisheries Society, Bethesda, Maryland.
Hughes, R. M., S. Dunham, K. G. Maas-Hebner, J. A. Yeakley, C. Schreck, M. Harte, N. Molina, C. C. Shock, V. W. Kaczynski, and J. Schaeffer. 2014. A review of urban water body challenges and approaches: (1) rehabilitation and remediation. Fisheries 39(1):18–29.
Hughes, R. M., A. T. Herlihy, and P. R. Kaufmann. 2010. An evaluation of qualitative indexes of physical habitat applied to agricultural streams in ten US states. Journal of the American Water Resources Association 46:792–806.
Hughes, R. M., and J. M. Omernik. 1981. Use and misuse of the terms, watershed and stream order. Pages 320–326 *in* L. A. Krumholz, editor. The warmwater streams symposium. Southern Division American Fisheries Society, Bethesda, Maryland.
Hutson, A. M., L. A. Toya, and D. Tave. 2018. Determining preferred spawning habitat of the endangered Rio Grande silvery minnow by hydrological manipulation of a conservation aquaculture facility and the implications for management. Ecohydrology 11:e1964.
Isaak, D. J., M. K. Young, C. H. Luce, S. W. Hostetler, S. J. Wenger, E. E. Peterson, J. M. Ver Hoef, M. C. Groce, D. L. Horan, and D. E. Nagel. 2016. Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. Proceedings of the National Academy of Sciences of the United States of America 113:4374–4379.
Jaeger, K. L., J. D. Olden, and N. A. Pelland. 2014. Climate change poised to threaten hydrologic connectivity and endemic fishes in dryland streams. Proceedings of the National Academy of Sciences United States of America 111:13894–13899.
Janetski, D. J., D. T. Chaloner, S. D. Tiegs, and G. A. Lamberti. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. Oecologia 159:583–595.
Jessop, B. M., and L. M. Lee. 2016. American Eel *Anguilla rostrata* stock status in Canada and the United States. Pages 251–273 *in* T. Arai, editor. Biology and ecology of anguillid eels. CRC Press, Taylor and Francis Group, Boca Raton, Florida.
Jewett, S. C., and L. K. Duffy. 2007. Mercury in fishes of Alaska, with emphasis on subsistence species. Science of the Total Environment 387(1–3):3–27.
Johnston, B. R. 2013. Human needs and environmental rights to water: a biocultural systems approach to hydro development and management. Ecosphere 4(3):1–15.
Jones, K. K., T. J. Cornwell, D. L. Bottom, L. A. Campbell, and S. Stein. 2014. The contribution of estuary-resident life histories to the return of adult *Oncorhynchus kisutch*. Journal of Fish Biology 85:52–80.
Karr, J. R. 1991. Biological integrity: a long-neglected aspect of water resource management. Ecological Applications 1(1):66–84.
Karr, J. R., and D. R. Dudley. 1981. Ecological perspective on water quality goals. Environmental Management 5:55–68.
Karr, J. R., and I. J. Schlosser. 1978. Water resources and the land-water interface. Science 201:229–234.
Katz, J. V., C. Jeffres, J. L. Conrad, T. R. Sommer, J. Martinex, S. Brumbaugh, N. J. Corline, and P. B. Moyle. 2017. Floodplain farm fields provide novel rearing habitat for Chinook salmon. PLoS ONE 12(6):e0177409.
Kluender, E. R., R. Adams, and L. Lewis. 2016. Seasonal habitat use of alligator gar in a river–floodplain ecosystem at multiple spatial scales. Ecology of Freshwater Fish 26:233–246.
Kuhnlein, H. V., and H. M. Chan. 2000. Environment and contaminants in traditional food systems of northern indigenous peoples. Annual Review of Nutrition 20:595–626.
Labbe, T. R., and K. D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. Ecological Applications 10:1774–1791.
Lane, C. R., and E. D'Amico. 2016. Identification of putative geographically isolated wetlands of the conterminous United States. Journal of the American Water Resources Association (JAWRA) 52:705–722.
Larned, S. T., T. Datry, D. B. Arscott, and K. Tockner. 2010. Emerging concepts in temporary-river ecology. Freshwater Biology 55:717–738.
Lassaletta, L., H. Garcia-Gomez, B. S. Gimeno, and J. V. Rovira. 2010. Headwater streams: neglected ecosystems in the EU Water Framework Directive. Implications for nitrogen pollution control. Environmental Science & Policy 13:423–433.
Laughlin, B., and M. Gibson. 2011. The edge of extinction. Montana Native News Project. University of Montana. Available: http://native-news.jour.umt.edu/2011/flathead.html. (November 2018).
Leibowitz, S. G., P. J. Wigington Jr., K. A. Schofield, L. C. Alexander, M. K. Vanderhoof, and H. E. Golden. 2018. Connectivity of Streams and Wetlands to Downstream Waters: An Integrated Systems Framework. Journal of the American Water Resources Association 54:298–322.
Lewis, R. S. P. 2009. Yurok and Karuk traditional ecological knowledge: insights into Pacific Lamprey populations of the lower Klamath basin. Biology, Management, and Conservation of Lampreys in North America 72:1–39.
Liang, L., S. Fei, J. B. Ripy, B. L. Blandford, and T. Grossardt. 2013. Stream habitat modelling for conserving a threatened headwater fish in the upper Cumberland River, Kentucky. River Research and Applications 29:1207–1214.
Lowe, W. H., and G. E. Likens. 2005. Moving headwaters streams to the head of the class. BioScience 55:196–197.
Lynn, K., J. Daigle, J. Hoffman, F. Lake, N. Michelle, D. Ranco, C. Viles, G. Voggesser, and P. Williams. 2013. The impacts of climate change on tribal traditional foods. Climatic Change 120:545–556.
Machut, L., K. E. Limburg, R. E. Schmidt, D. Dittman. 2007. Anthropogenic impacts on American Eel demographics in Hudson River Tributaries, New York. Transactions of the American Fisheries Society 136(6):1699–1713.
Maclean, N. 1976. A river runs through it and other stories. University of Chicago Press, Chicago.
Magoulick, D. D., and D. T. Lynch. 2015. Occupancy and abundance modeling of the endangered Yellowcheek Darter in Arkansas. Copeia 103:433–439.
Marttila, M., K. Kyllonen, and T. P. Karjalainen. 2016. Social success of in-stream habitat improvement: from fisheries enhancement to the delivery of multiple ecosystem services. Ecology and Society 21(1):9.
Marx, A., J. Dusek, J. Jankovec, M. Sanda, T. Vogel, R. Van Geldern, J. Hartmann, and J. A. C. Barth. 2017. A review of CO_2 and associated carbon dynamics in headwater streams: a global perspective. Reviews of Geophysics 55:560–585.
Matt, C. A., and L. H. Suring. 2018. Brown bears. Pages 109–120 *in* C. A. Woody, editor. Bristol Bay, Alaska: natural resources of the aquatic and terrestrial ecosystems. J. Ross Publishing, Plantation, Florida.
McClain, M. E., E. W. Boyer, C. L. Dent, S. E. Gergel, N. B. Grimm, P. M. Groffman, S. C. Hart, J. W. Harvey, C. A. Johnston, E. Mayorga, and W. H. McDowell. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems 6:301–312.
McClenachan, L., S. Lowell, and C. Keaveney. 2015. Social benefits of restoring historical ecosystems and fisheries: alewives in Maine. Ecology and Society 20:31.

McIntyre, P. B., A. S. Flecker, M. J. Vanni, J. M. Hood, B. W. Taylor, and S. A. Thomas. 2008. Fish distributions and nutrient cycling in streams: can fish create biogeochemical hotspots? Ecology 89:2335–2346.

MDNR (Maryland Department of Natural Resources). 2018. Maryland Brook Trout. Available: http://dnr.maryland.gov/fisheries/Pages/brook-trout/index.aspx. (November 2018).

Medley, C. N., and P. D. Shirey. 2013. Review and reinterpretation of Rio Grande silvery minnow reproductive ecology using egg biology, life history, hydrology and geomorphology information. Ecohydrology 6:491–505.

Meyer, J. L., L. A. Kaplan, J. D. Newbold, D. L. Strayer, C. J. Woltemade, J. B. Zedler, R. Beilfuss, Q. Carpenter, R. Semlitsch, M. C. Watzin, and P. H. Zedler. 2003. Where rivers are born: the scientific imperative for defending small streams and wetlands. Sierra Club and American Rivers, Washington, D.C.

Meyer, J. L., D. L. Strayer, J. B. Wallace, S. L. Eggert, G. S. Helfman, and N. E. Leonard. 2007. The contribution of headwater streams to biodiversity in river networks. Journal of the American Water Resources Association 43:86–103.

Meyer, J. L., and J. B. Wallace. 2001. Lost linkages and lotic ecology: rediscovering small streams. Pages 295–317 *in* M. C. Press, N. J. Huntly and S. Levin, editors. Ecology: achievement and challenge. Blackwell Science, Oxford, UK.

Miller, R. R., J. D. Williams, and J. E. Williams. 1989. Extinctions of North American fishes during the past century. Fisheries 14(6):22–38.

Minckley, W. L., and J. E. Deacon. 1991. Battle against extinction: native fish management in the American West. University of Arizona Press, Tucson.

Montgomery, D. R., J. M. Buffington, N. P. Peterson, D. Schuett Hames, and T. P. Quinn. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. Canadian Journal of Fisheries and Aquatic Sciences 53:1061–1070.

Moore, J. W., D. E. Schindler, and M. D. Scheuerell. 2004. Disturbance of freshwater habitats by anadromous salmon in Alaska. Oecologia 139:298–308.

Moyle, P. B., and A. Marciochi. 1975. Biology of the Modoc Sucker, *Catostomus microps*, in northeastern California. Copeia 1975:556–560.

Mulholland, P. J., R. O. Hall Jr., D. J. Sobota, W. K. Dodds, S. E. Findlay, N. B. Grimm, S. K. Hamilton, W. H. McDowell, J. M. O'Brien, J. L. Tank, and L. R. Ashkenas. 2009. Nitrate removal in stream ecosystems measured by N-15 addition experiments: denitrification. Limnology and Oceanography 54:666–680.

Nadeau, T. L., and M. C. Rains. 2007. Hydrological connectivity between headwater streams and downstream waters: how science can inform policy. Journal of the American Water Resources Association 43:118–133.

Nakano, S., H. Miyasaka, and N. Kuhura. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435–2441.

NCWRC (North Carolina Wildlife Resources Commission). 2013. North Carolina trout resources management plan. Available: https://www.ncwildlife.org/Portals/0/Fishing/documents/TroutManagementPlan.pdf. Accessed (November 2018).

NMFS (National Marine Fisheries Service). 2009. Biological valuation of Atlantic salmon habitat within the Gulf of Maine Distinct Population Segment. Northeast Region, Gloucester, Massachusetts.

NMFS (National Marine Fisheries Service). 2015. Fisheries economics of the United States, 2015. Government Printing Office, Washington, D.C..

NPT (Nez Perce Tribe). 2018. Nez Perce tribal salmon culture. Nez Perce Tribe, Department of Fisheries Resources Management. Available: http://www.nptfisheries.org/Resources/SalmonCulture.aspx. (November 2018).

Paller, M. H. 1994. Relationships between fish assemblage structure and stream order in South Carolina Coastal Plain streams. Transactions of the American Fisheries Society 123:150–161.

Perkin, J. S., K. B. Gido, J. A. Falke, K. D. Fausch, H. Crockett, E. R. Johnson, and J. Sanderson. 2017. Groundwater declines are linked to changes in Great Plains stream fish assemblages. Proceedings of the National Academy of Sciences of the United States of America 114:7373–7378.

Peterson, B. J., W. M. Wollheim, P. J. Mulholland, J. R. Webster, J. L. Meyer, J. L. Tank, E. Martí, W. B. Bowden, H. M. Valett, A. E. Hershey, W. H. McDowell, W. K. Dodds, S. K. Hamilton, S. Gregory, and D. D. Morrall. 2001. Control of nitrogen export from watersheds by headwater streams. Science 292:86–90.

Price, K., A. Suski, J. McGarvie, B. Beasley, and J. S. Richardson. 2003. Communities of aquatic insects of old-growth and clearcut coastal headwater streams of varying flow persistence. Canadian Journal of Forestry Research 33:416–1432.

Progar, R. A., and A. R. Moldenke. 2002. Insect production from temporary and perennially flowing headwater streams in western Oregon. Journal of Freshwater Ecology 17:391–407.

Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle.

Rabalais, N. N., F. R. Burditt, L. D. Coen, B. E. Cole, C. Eleuterius, K. L. Heck, T. A. McTigue, S. G. Morgan, H. M. Perry, F. M. Truesdale, R. K. Zimmerfaust, and R. J. Zimmerman. 1995. Settlement of *Callinectes sapidus* Megalopae on artificial collectors in four Gulf of Mexico estuaries. Bulletin of Marine Science 57:855–876.

Rabotyagov, S. S., C. L. Kling, P. W. Gassman, N. N. Rabalais, and R. E. Turner. 2014. The economics of dead zones: causes, impacts, policy challenges, and a model of the Gulf of Mexico hypoxic zone. Review of Environmental Economics and Policy 8(1):58–79.

Reid, S. M., and N. E. Mandrak. 2008. Historical changes in the distribution of threatened Channel Darter (Percina copelandi) in Lake Erie with general observations on the beach fish assemblage. Journal of Great Lakes Research 34(2):324–334.

Richards, J. S. 1976. Changes in fish species composition in the Au Sable River, Michigan from the 1920's to 1972. Transactions of the American Fisheries Society 105(1):32–40.

Richardson, J. S., and R. J. Danehy. 2007. A synthesis of the ecology of headwater streams and their riparian zones in temperate forests. Forest Science 53:131–147.

Roberts, J. J., K. D. Fausch, D. P. Peterson, and M. B. Hooten. 2013. Fragmentation and thermal risks from climate change interact to affect persistence of native trout in the Colorado River basin. Global Change Biology 19:1383–1398.

Robertson, C. R., K. Aziz, D. L. Buckmeier, N. G. Smith, and N. Raphelt. 2018. Development of a flow-specific floodplain inundation model to assess alligator gar recruitment success. Transactions of the American Fisheries Society 147:674–686.

Robison, H. W., and T. M. Buchanan. 1988. Fishes of Arkansas. The University of Arkansas Press, Fayetteville.

Rodriguez-Freire, L., S. Avasarala, A. S. Ali, D. Agnew, J. H. Hoover, K. Artyushkova, D. E. Latta, E. J. Peterson, J. Lewis, L. J. Crossey, A. J. Brearley, and J. M. Cerrato. 2016. Investigation of the Gold King mine spill impact in water and sediments downstream of the Animas river. Environmental Science and Technology 50:11539–11548.

Rogowski, D. L., H. Reiser, and C. A. Stockwell. 2006. Fish habitat associations in a spatially variable desert stream. Journal of Fish Biology 68:1473–1483.

Saunders, R., M. A. Hachey, and C. W. Fay. 2006. Maine's diadromous fish community: past, present, and implications for Atlantic Salmon recovery. Fisheries 31:527–547.

Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature 465:609–U102.

Schlosser, I. J. 1987. A conceptual framework for fish communities in small warmwater streams. Pages 17–34 *in* W. J. Matthews, and D. C. Heins, editor. Community and evolutionary ecology of North American stream fishes. Oklahoma University Press, Oklahoma City.

Shepard, B. B., B. E. May, and W. Urie. 2005. Status and conservation of Westslope Cutthroat Trout within the western United States. North American Journal of Fisheries Management 25:1426–1440.

Shirey, P. D., L. H. Roulson, and T. Bigford. 2018. Imperiled species policy is a critical issue for AFS. Fisheries 43:527–532.

Snodgrass, J. W., A. L. Bryan Jr., R. F. Lide, and G. M. Smith. 2001. Factors affecting the occurrence and structure of fish assemblages in isolated wetlands of the upper coastal plain, USA. Canadian Journal of Fisheries and Aquatic Sciences 53:443–454.

Solomon, L. E., Q. E. Phelps, D. P. Herzog, and C. J. Kennedy. 2013. Juvenile alligator gar movement patterns in a disconnected floodplain habitat in Southeast Missouri. American Midland Naturalist 169:336–344.

Sommer, T. R., M. L. Nobriga, W. C. Harrell, W. Batham, and W. J. Kimmerer. 2001. Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival. Canadian Journal of Fisheries and Aquatic Sciences 58:325–333.

Staletovich, J. 2018. Florida confirms toxic red tide spreading along Atlantic coast. Miami Herald 3 October 2018. Available: https://www.miamiherald.com/news/local/environment/article219419020.html (November 2018).
Steward, A. L., D. von Schiller, K. Tockner, J. C. Marshall, and S. E. Bunn. 2012. When the river runs dry: human and ecological values of dry riverbeds. Frontiers in Ecology and the Environment 10(4):202–209.
Stoddard, J. L., D. V. Peck, A.R. Olsen, D. P. Larsen, J. Van Sickle, C. P. Hawkins, R. M. Hughes, T.R. Whittier, G. Lomnicky, A. T. Herlihy, P. R. Kaufmann, S. A. Peterson, P. L. Ringold, S. G. Paulsen, and R. Blair. 2005. Western streams and rivers statistical summary. EPA 620/R-05/006, U.S. Environmental Protection Agency, Washington, D.C.
Stumpff, L. M. 2001. Protecting restorative relationships and traditional values: American Indian tribes, wildlife, and wild lands. Pages 63–71 *in* A. Watson, and J. Sproull, editors. 7th World Wilderness Congress Symposium. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest & Range Experimental Station, Port Elizabeth, South Africa.
Sullivan, S. M. P. 2012. Geomorphic-ecological relationships highly variable between headwater and network mountain streams of northern Idaho, United States. Journal of the American Water Resources Association 48:1221–1232.
Sullivan, S. M. P., K. Hossler, and C. M. Cianfrani. 2015. Ecosystem structure emerges as a strong determinant of food-chain length in linked stream-riparian ecosystems. Ecosystems 18:1356–1372.
SWANCC (Solid Waste Agency of Northern Cook County) v. Army Corps of Engineers, 531 U. S. 159, 2001.
Tango, P. 2008. Cyanotoxins in tidal waters of Chesapeake Bay. Northeastern Naturalist 15:403–416.
Tiner, R. W. 2003. Estimated extent of geographically isolated wetlands in selected areas of the United States. Wetlands 23:636–652.
United States. 1972. Federal Water Pollution Control Act (Clean Water Act). 33 U.S.C §§ 1251 et seq.
USEPA (U.S. Environmental Protection Agency). 2009. Section 404 of the Clean Water Act. Geographic information systems analysis of the surface drinking water provided by intermittent, ephemeral, and headwater streams in the U.S. U.S. Environmental Protection Agency. Washington, D.C.
USEPA (U.S. Environmental Protection Agency). 2013. Water: Rivers & Streams. Available: https://archive.epa.gov/water/archive/web/html/streams.html. (November 2018).
USEPA (U.S. Environmental Protection Agency). 2015. Connectivity of Streams and Wetlands to Downstream Waters: A Review and Synthesis of the Scientific Evidence Technical Report, EPA/600/R-14/475F. US Environmental Protection Agency, Washington, D.C.
USEPA (U.S. Environmental Protection Agency). 2016a. National rivers and streams assessment 2008–2009: a collaborative survey. EPA/841/R-16/007. U.S. Environmental Protection Agency. Office of Water and Office of Research and Development, Washington, D.C.
USEPA (U.S. Environmental Protection Agency). 2016b. National Lakes Assessment 2012: a collaborative survey of lakes in the United States. EPA 841-R-16-113. U.S. Environmental Protection Agency, Washington, D.C.
USEPA and USGS (U.S. Environmental Protection Agency and U.S. Geological Survey). 2012. National hydrography dataset plus – NHDPlus. Edition 2.10. Available: http://www.horizon-systems.com/NHDPlus/NHDPlusV2_data.php. (February 2018).
USFWS (U.S. Fish and Wildlife Service). 2012a. 2011 National Survey of Fishing, Hunting, and Wildlife-Associated Recreation. U.S. Department of the Interior, Washington, D. C.
USFWS (U.S. Fish and Wildlife Service). 2012b. Revised recovery plan for the Lost River Sucker *Deltistes luxatus* and Shortnose Sucker *Chasmistes brevirostris*. Pacific Southwest Region U. S. Fish and Wildlife Service, Sacramento, California.
USFWS (U.S. Fish and Wildlife Service). 2014. Trout fishing in 2006: a demographic description and economic analysis: addendum to the 2006 national survey of fishing, hunting, and wildlife.associated recreation. Wildlife and Sport Fish Restoration Programs, Arlington, Virginia.
USFWS (U.S. Fish and Wildlife Service). 2015. Endangered and threatened wildlife and plants; removal of the Modoc Sucker from the federal list of endangered and threatened wildlife. Federal Register 80 235(December 8, 2015):76235–76249.
USFWS (U.S. Fish and Wildlife Service). 2017. Alabama Cavefish *Speoplatyrhinus poulsoni* 5-year review: summary and evaluation. Mississippi Ecological Services Field Office, Jackson.
USGS (U.S. Geological Survey). 2013. Water Basics Glossary. 2018. Available: https://water.usgs.gov/water-basics_glossary.html (November 2018).
Walsh, C. J., A. H. Roy, J. W. Feminella, P. D. Cottingham, P. M. Groffman, and R. P. Morgan. 2005. The urban stream syndrome: current knowledge and the search for a cure. Journal of the North American Benthological Society 24:706–723.
Wenger, S. J., D. J. Isaak, C. H. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, M. K. Young, M. M. Elsner, B. E. Rieman, A. F. Hamlet, and J. E. Williams. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. Proceedings of the National Academy of Sciences of the United States of America 108:14175–14180.
Whittle, P. 2018. Maine elver harvest surges past recent records for overall value. Portland Press Herald, Portland, Maine.
Wigington, P. J. Jr., J. L. Ebersole, M. E. Colvin, S. G. Leibowitz, B. Miller, B. Hansen, H. R. Lavigne, D. White, J. P. Baker, M. R. Church, J. R. Brooks, M. A. Cairns, and J. E. Compton. 2006. Coho Salmon dependence on intermittent streams. Frontiers in Ecology and the Environment 4:513–518.
Williams, J., H. Neville, A. L. Haak, W. T. Colyer, S. J. Wegner, and S. Bradshaw. 2015. Climate change adaptation and restoration of western trout streams: opportunities and challenges. Fisheries 40:304–317.
Wipfli, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 54:1259–1269.
Wipfli, M. S., and C. V. Baxter. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. Fisheries 35:373–387.
Wipfli, M. S., and D. P. Gregovich. 2002. Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. Freshwater Biology 47:957–969.
Woelfle-Erskine, C., L. G. Larsen, and S. M. Carlson. 2017. Abiotic habitat thresholds for salmonid over-summer survival in intermittent streams. Ecosphere 8(2):e01645.
Wohl, E. 2014. A legacy of absence: wood removal in U.S. Rivers. Progress in Physical Geography 38:637–663.
Woody, C. A., R. M. Hughes, E. J. Wagner, T. P. Quinn, L. H. Roulsen, L. M. Martin, and K. Griswold. 2010. The U.S. General Mining Law of 1872: change is overdue. Fisheries 35:321–331.
Zale, A. V., S. C. Leon, M. Lechner, O. E. Maughan, M. T. Ferguson, S. O'Donnell, B. James, and P. W. James. 1994. Distribution of the threatened Leopard Darter, *Percina pantherine* (Osteichthyes Percidae). The Southwestern Naturalist 39(1):11–20.
Zhang, Y. X., J. N. Negishi, J. S. Richardson, and R. Kolodziejczyk. 2003. Impacts of marine-derived nutrients on stream ecosystem functioning. Proceedings of the Royal Society B-Biological Sciences 270:2117–2123.
Zimmer, C. 2014. Cyanobacteria are far from just Toledo's problem. The New York Times (August 7). Available: https://www.nytimes.com/2014/08/07/science/cyanobacteria-are-far-from-just-toledos-problem.html (November 2018). AFS