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

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Abstract.—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. Headwater streams comprise 79% of U.S. stream networks; wetlands outside of floodplains comprise 6.59 million ha in the conterminous United States. 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 American 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 would face severe threat under the Waters of the United States rule recently proposed by the Trump administration.

Headwaters in a Nutshell

- Headwater streams comprise 79% of U.S. stream networks; wetlands outside of floodplains comprise 6.59 million hectares 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 revised WOTUS rules and would have severe and long-lasting negative consequences for fisheries and environmental conditions throughout the USA.

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 Cty. [SWANCC] v. Army Corps of Engineers*, 531 U.S. 159, 2001). However, federal jurisdiction over non-navigable waters 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 2015a), which included a detailed review by an EPA Science Advisory Board (SAB) of technical experts from the public ("SAB Review") (SAB, Letter to Gina McCarthy. October 17, 2014. SAB Review of the Draft EPA Report Connectivity of Streams and Wetlands to Downstream Waters: A Review and Synthesis of the Scientific Evidence), the Obama administration issued the Waters of the U.S. (WOTUS) Rule in 2015, which clarified the jurisdiction of the Clean Water Act to include protections for intermittent 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 2015a).

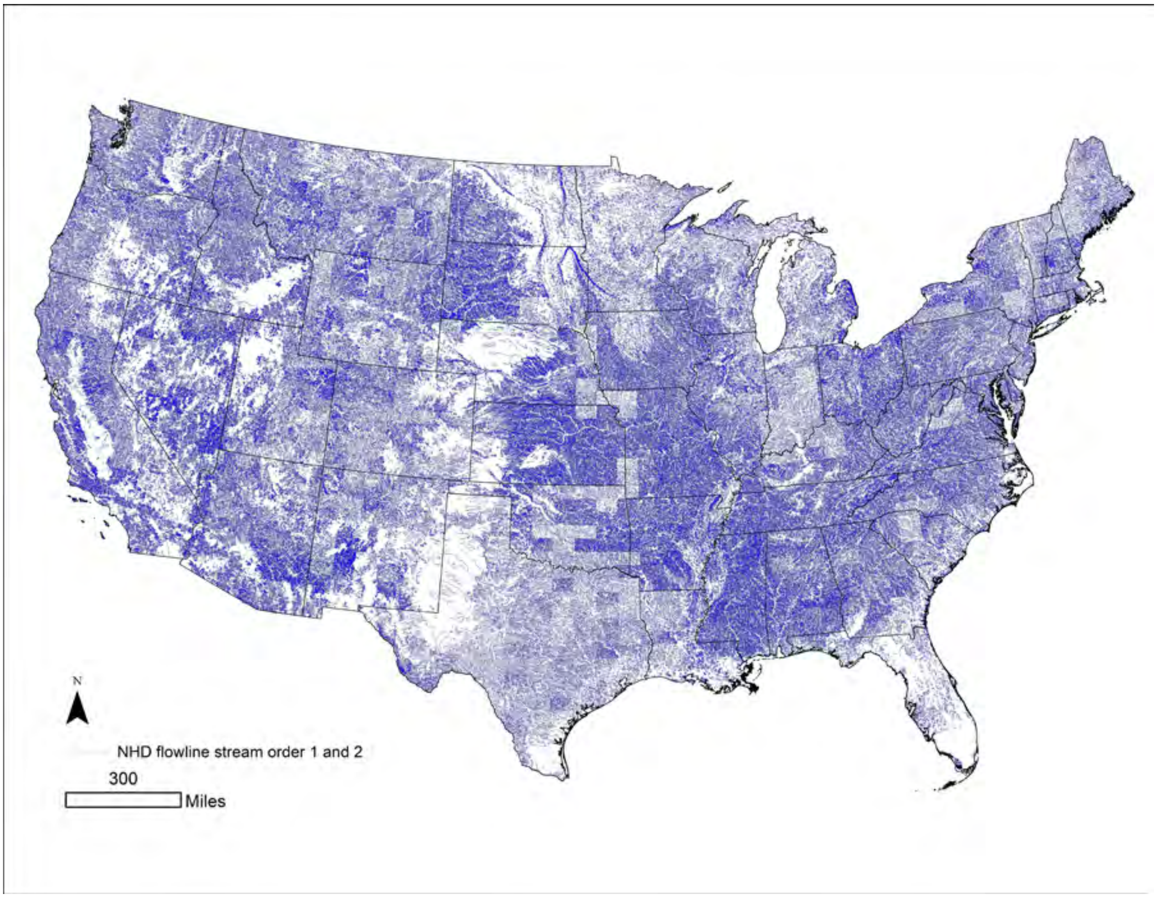

Figure 1. Map of 1st- and 2nd-order tributaries (a stream lacking a tributary and a stream with only first-order tributaries, respectively) comprising river networks of the conterminous U.S. as characterized by the 1:100,000 scale National Hydrography Dataset Plus Version 2 (NHDPlusV2, USEPA and USGS 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 U.S. (e.g., Indiana vs. 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.

On February 28, 2017, the Trump administration issued an executive order directing the U.S. Environmental Protection Agency (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, US EPA, 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 hectares 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 et al. 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.

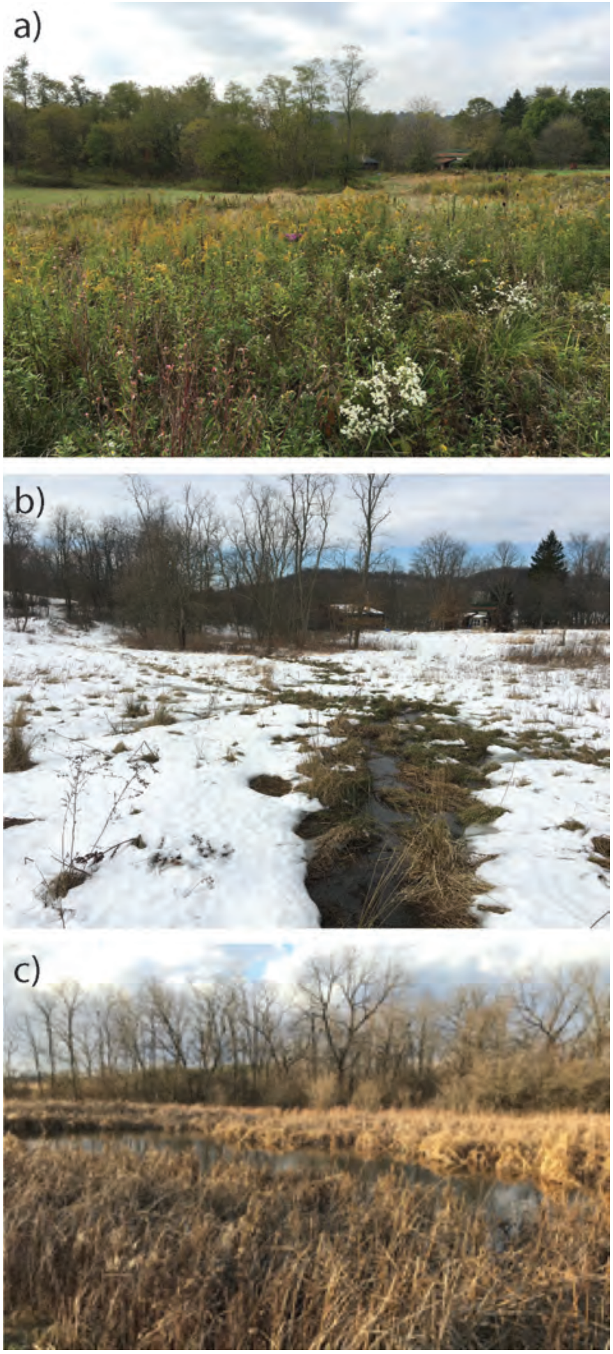

Figure 2. Wetlands outside of floodplains—such as the headwater/source wetland (a) in summer and (b) winter in Pennsylvania and the (c) prairie wetland in Ohio—would be particularly vulnerable to loss of protections. Photo credits: P.D. Shirey: a,b; S.M.P. Sullivan: c.

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 a 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; Staletovich 2018; Zimmer 2018). For wetlands outside of floodplains, global estimates indicate continued loss of >30% since 1970 (Dixon et al. 2016).

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 1983; Meyer and Wallace 2001; Colson et al. 2008), thus posing serious risk to ecological and societal benefits (Creed et al. 2017). 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.

Although the proposed rule in part uses a hypothetical model developed in the SAB Review (SAB, Letter to Gina McCarthy. October 17, 2014) that illustrates how gradients in connectivity might be used to provide a semi-quantitative evaluation of the downstream impacts of changes to streams and wetlands (Figure 3, pg. 54) to support lack of protection for wetlands outside of floodplains (i.e., wetlands lacking a surface connection to protected waterways), ephemeral streams, and some intermittent streams, it is important to clarify this model and put it in the full context of the SAB Review. As supported by the SAB Review (SAB, Letter to Gina McCarthy. October 17, 2014), connectivity between headwaters and downstream waterbodies does indeed reflect a gradient in the variability of the frequency, duration, magnitude, predictability, and consequences of physical, chemical, and biological connections. Conceptually, this connectivity gradient suggests that, comparing individual stream or wetland to individual stream or wetland, intermittent and ephemeral streams and non-floodplain wetlands have a decreased probability that changes at the location of interest will be transmitted to downstream waters as compared to perennial streams and floodplain wetlands, respectively (e.g., Figure 3, pg. 54). However, the SAB Review also notes 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. Treating the vast number of non-perennial streams and wetlands outside of floodplains as single units is akin to treating a capillary as an isolated anatomical part, ignoring their collective importance to the entire human circulatory system.

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 (Hill et al. 2014; Richardson and Danehy 2007; Sullivan 2012). 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 US$15.7 trillion per 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 per 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 at al. 2002; Wipfli and Gregovich 2002; Wipfli and Baxter 2010). The provisioning of 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* spp., 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 instream retention of nitrogen. Most nitrogen flowing through a drainage network is estimated to come from headwater streams; in the Northeast, 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 2009, 2016). Further loss of headwater systems is expected to have major negative consequences for biogeochemical cycles at local to continental and global scales.

Even ephemeral and intermittent headwaters provide important ecological functions and ecosystem services (Steward et al. 2012). In arid and semiarid 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 West.

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 (Lowe and Likens 2005; Liang et al. 2013; DeRolph et al. 2015; 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. 1996; 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* (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 (MDN) to headwater streams (Zhang et al. 2003). MDN 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). MDN is 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 have already been severely affected by multiple human activities, including channel alteration, water diversion, and land modification by agriculture, livestock grazing, mining, and urbanization (e.g., Beschta et al. 2013; Hughes et al. 2010, 2014, 2016). These land uses and others have eliminated countless headwater streams and wetlands that naturally once served as 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, 2016; Crawford et al. 2016). Wetland loss—including but not limited to wetlands outside of floodplains—across the USA is

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 and McIntyre 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.

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.

staggering, with some midwestern states (e.g., Illinois, Indiana, Ohio, Missouri) having lost more than 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 et al. 2018; 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 Pool-fish *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 affects 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 limited stages of 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 (Figure 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

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 ESA (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 supports 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.

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, endangered Chinook Salmon, and the endemic Or-

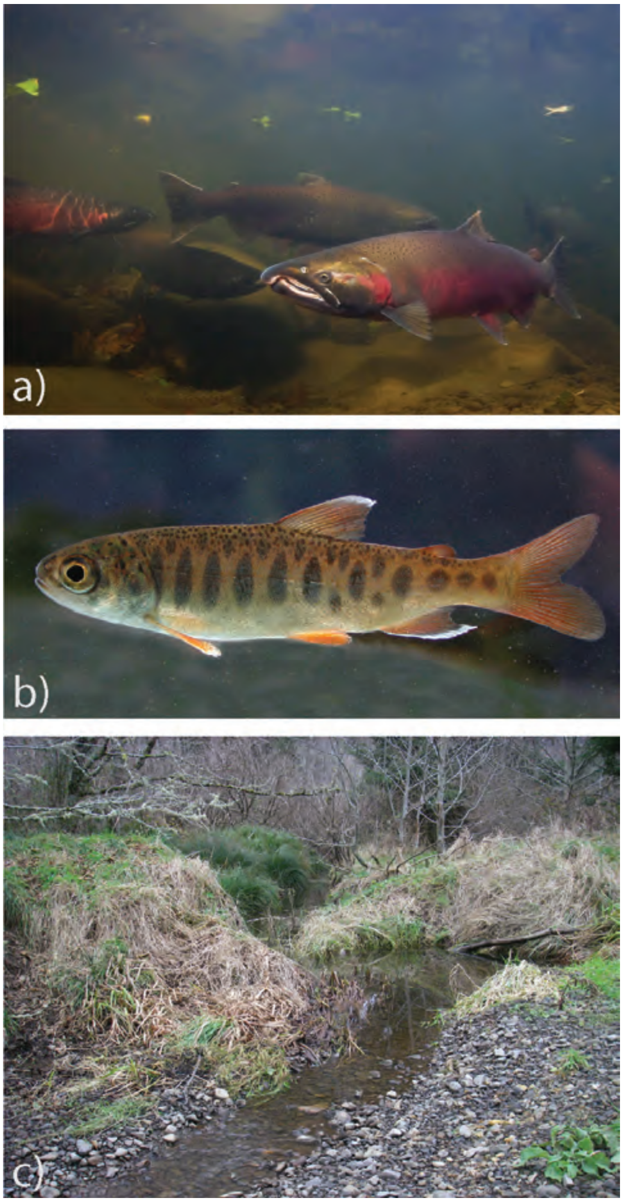

Figure 6. The Oregon Coast Coho Salmon (a; Jeremy Monroe, Freshwaters Illustrated) is an ESU (evolutionarily significant unit) listed as threatened under the ESA. Juvenile Coho (b; Lance Campbell); of several life history types use very small headwater habitats in coastal streams that are wet only in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

egon 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 leading to 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 are 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 *O. mykiss* 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 West, the many

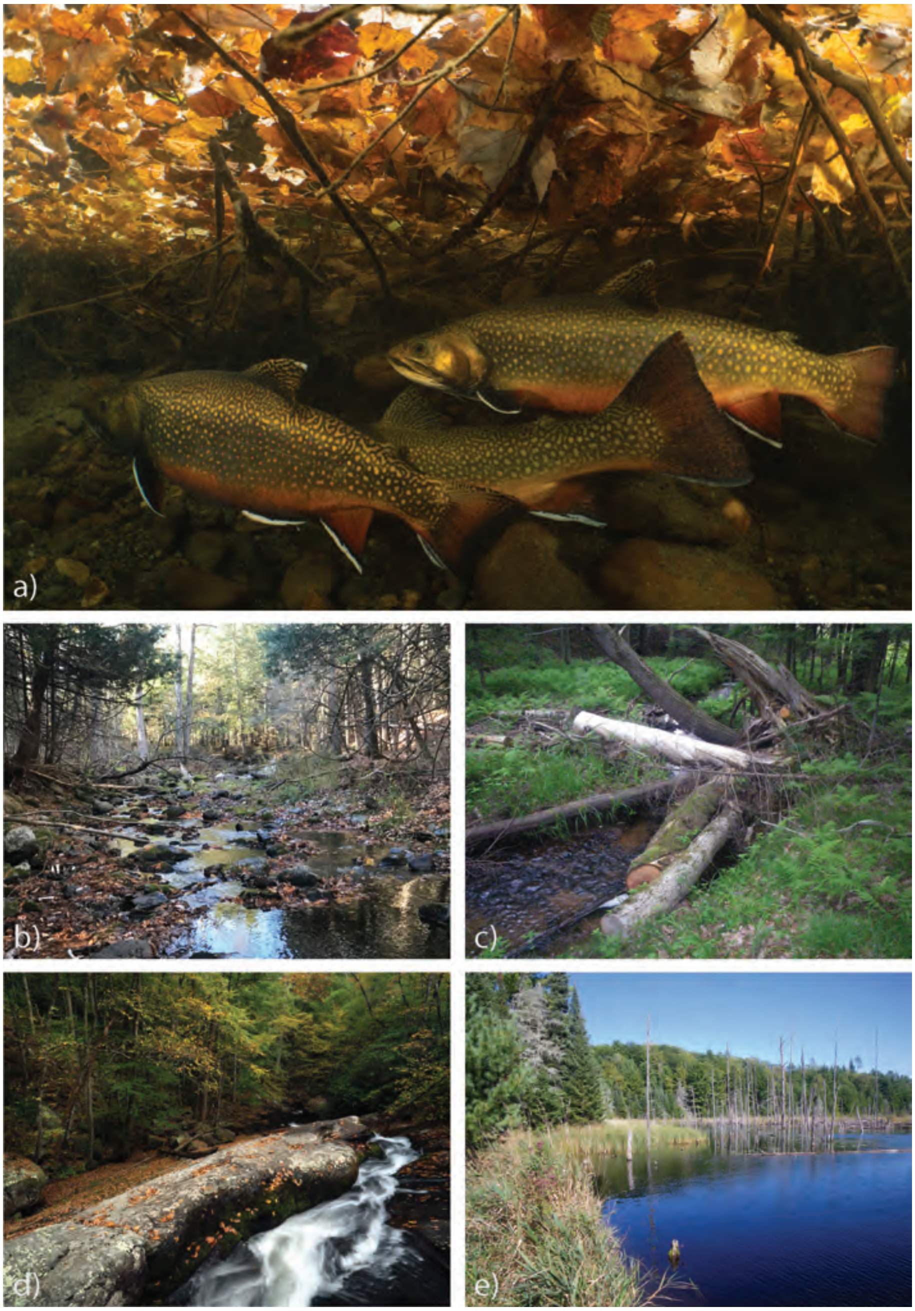

Figure 7. (a) Brook Trout *Salvelinus fontinalis* require cold, clear, and well-oxygenated water often found in headwater habitats (Photo Credit: David Herasimtschuk, Freshwaters Illustrated). Examples of headwater streams inhabited by Brook Trout are shown for (b) Maine, (c) Michigan, and (d) an Appalachian headwater stream. (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.

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 West are ephemeral, and yet are important habitats for fish during months when they have water (Figures 5 and 8). Some of the imperiled minnow species use highly intermittent backwaters in floodplain wetlands adjacent to stream channels for spawning and rearing (e.g., *Hybognathus* spp.; Falke et al. 2010, 2012; Medley 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

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 & 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 ESA.

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 (*U.S. 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 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 this species. Thermal habitats unique to mountain headwater streams throughout the West 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 USA can not only reduce the uncertainty and economic costs that come with an imperiled species being listed under the Endangered Species Act, 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 439,000 jobs and generating more than $63 billion across the United States in 2015 (USFWS 2012a; NMFS 2015). For instance, headwater tributaries in the western U.S. 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 100,000 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 West by the 2080s (Wenger et al. 2011b), 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 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 526,600 jobs nationwide (Allen et al. 2018). Economic contributions from freshwater fishing is also increasing, growing 11% since 2011 (Allen et al. 2018). It's also critical economic growth when compared to other sectors, collectively the outdoor recreation economy grew 3.8% in 2016 with the overall economy grew 2.8% during the same time period (Allen et al. 2016).

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).

Headwaters both directly and indirectly affect commercial fisheries. 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 27,000 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 20,000 full-time jobs (BBNC 2017). As mentioned previously, spawning Pacific salmon import MDN 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 2015–2017 (ASMFC 2017), 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 70,000 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 indigenous 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 American West (e.g., Boraas and Knott 2018). Salmon are also a traditional "first food," which are honored in many tribal traditions and are also 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 Koo-

Alewives in Maine

Alewives 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. 2011, 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 *Alosa aestivalis* are depleted and near historic lows (ASMFC 2017).

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

tenai 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 West. 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 systems and the ecosystem 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 *Alosa 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, the National Oceanic and Atmospheric Administration, 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 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 *Lampetra 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).

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 (Liebowitz 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. Although 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, we recommend that the U.S. Environmental Protection Agency 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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