Species Complex: Classification and Conservation in American Environmental History

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Abstract: How does the classification of biological organisms shape efforts to conserve them? This essay addresses this key question through the scientific, administrative, and legal histories of steelhead and rainbow trout. Members of the diverse salmon family, these two fish have different life histories and physical appearances, but since the 1930s scientists have considered them the same species. Over the past 150 years, however, their histories diverged. Today, rainbow trout are bred by the millions in hatcheries and are among the world's most common and widespread fish, while steelhead are listed as threatened or endangered all along the West Coast of the United States. Their remarkable story shows that conservation is not merely a political struggle over things that exist in nature; it is a perennial competition to prove the existence and define the very nature of those things that are the focus of such struggles. Biological taxonomy and classification are central to these debates, as they are to environmental history and the history of science more generally.

In his third State of the Union address, delivered on 25 January 2011, U.S. President Barack Obama told a joke meant to highlight common ground between the Democratic and Republican parties on the problem of waste and inefficiency in government. To make his point about the need to streamline federal programs, he cited his "favorite example: The Interior Department is in charge of salmon while they're in freshwater," Obama announced, with a mixture of derision and disbelief, "but the Commerce Department handles them when they're in saltwater. I hear it gets even more complicated once they're smoked."¹

Obama's zinger met with bipartisan laughter, and the following day dozens of news outlets covered the story. Many concluded that although there clearly was room for improvement in federal fishery programs, the president's account caricatured a long-standing administrative arrangement. Since the 1970s, the U.S. Fish and Wildlife Service (FWS), in the Department of

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¹ For a video of President Barack Obama delivering his 2011 State of the Union salmon joke see http://www.youtube.com /watch?v=BFcWz9eyovA.

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the Interior, had managed terrestrial and freshwater species, whereas the National Oceanic and Atmospheric Administration (NOAA), in the Department of Commerce, had managed all marine species, including anadromous fishes that migrate between fresh and salt water. The two agencies often collaborated with each other and with the states, but at least in theory they had well-defined authorities based on the characteristics and habits of the species they managed.²

Yet the president's comment pointed to a far deeper challenge. Salmon is not a single species with a single set of problems and solutions, as he implied in his pitch for bureaucratic simplification. It is a widespread and diverse family with some 228 recognized species that includes many kinds of fishes commonly known as salmon, as well as dozens of varieties of whitefish, char, and trout. Some types of fishes in this family live their entire lives in freshwater, others are anadromous, and a few consist of individuals that may pursue either of these two lifehistory strategies. All of them have complicated evolutionary histories, developmental stages, and population structures. Some have overlapping ranges, and several hybridize in the wild.³ (See Figure 1.)

The diversity and complexity of these fishes has long frustrated scientists and managers. Since the eighteenth century, researchers have worked to identify distinct salmon species, subspecies, and populations and to understand the relationships among them. These researchers have learned much, but many basic questions remain unanswered. Without a settled picture of the salmon family's history and taxonomy, agency officials have struggled in practice to delegate their responsibilities, defend their actions, and institute credible management programs.⁴

Historians of science and science studies scholars have long noted the importance of taxonomic systems that name and arrange objects in nature. Such systems purport to represent nature as it is; but, as the historian Harriet Ritvo has observed, they tend to say as much about the people doing the classifying as they do about the things being classified. Taxonomic systems thus reflect not only the natural order but also cultural history, social structures, and political power.⁵

Students of environmental politics, however, including many environmental historians, have been slow to adopt this view or appreciate its consequences. Taxonomic debates — contests

² For an example of national media coverage of Obama's salmon joke see Elizabeth Shogren, "Obama's Salmon Quip: The Truth Is Murky," *All Things Considered*, National Public Radio, 26 Jan. 2011. For the standing arrangement see "Memorandum of Understanding between the U.S. Fish and Wildlife Service, United States Department of the Interior, and the National Marine Fisheries Service, National Oceanic and Atmospheric Administration, United States Department of Commerce, Regarding Jurisdictional Responsibilities and Listing Procedures under the Endangered Species Act of 1973," 28 Aug. 1974.

³ Thomas P. Quinn, *The Behavior and Ecology of Pacific Salmon and Trout* (Seattle: Univ. Washington Press, 2005). For a full list see Fishbase.org: Family Salmonidae–Salmonids.

⁴ There is a large literature on salmon in American and Canadian environmental history. Important examples include Arthur McEvoy, *The Fisherman's Problem: Ecology and Law in the California Fisheries*, 1850–1980 (Cambridge: Cambridge Univ. Press, 1990); Joseph E. Taylor, *Making Salmon: An Environmental History of the Northwest Fisheries Crisis* (Seattle: Univ. Washington Press, 2001); Lissa K. Wadewitz, *The Nature of Borders: Salmon, Boundaries, and Bandits on the Salish Sea* (Seattle: Univ. Washington Press, 2012); David Montgomery, *King of Fish: The Thousand-Year Run of Salmon* (New York: Basic, 2009); David F. Arnold, *The Fishernen's Frontier: People and Salmon in Southeast Alaska* (Seattle: Univ. Washington Press, 2002); David Montgomery, *King of Fish: The Thousand-Year Run of Salmon* (New York: Basic, 2009); David F. Arnold, *The Fishernen's Frontier: People and Salmon in Southeast Alaska* (Seattle: Univ. Washington Press, 2009); and Matthew D. Evenden, *Fish versus Power: An Environmental History of the Fraser River* (Cambridge: Cambridge Univ. Press, 2004). ⁵ Numerous historians of science and science studies scholars have made this key point. Examples of related works include Harriet Ritvo, *The Platypus and the Mermaid and Other Figments of the Classifying Imagination* (Cambridge, Mass.: Harvard Univ. Press, 1997); Michel Foucault, *The Order of Things: An Archaeology of Human Sciences* (New York: Vintage, 1970); Peter J. Bowler, *The Norton History of the Environmental Sciences* (New York: Norton, 1992); Geoffrey C. Bowker and Susan Leigh Star, *Sorting Things Out: Classification and Its Consequences* (Cambridge, Mass.: MIT Press, 1999); D. Graham Burnett, *Trying Leviathan: The Nineteenth-Century New York Case That Put the Whale on Trial and Challenged the Order of Nature* (Princeton, N.J.: Princeton Univ. Press, 2007); and Carol Kaesuk Yoon, *Naming Nature: The Clash between Instinct and Science* (New York: Norton, 2009).



Figure 1. Thirty-three named forms of North American trout in the salmon family. A typical rainbow trout appears in the top row on the left-hand side, a mature female steelhead appears in the middle of the top row, and a mature male steelhead appears in the second row from the top on the right-hand side. Courtesy of Joseph Tomelleri.

to establish systems for classifying the natural world and sorting objects or processes into categories within those systems—are only a footnote in most environmental histories. Scholars in this field have tended to present taxonomic debates either as early framing stages in the development of more recent political conflicts or as technical disputes limited to small groups of wonky experts. As a result, they have treated conservation history largely as a series of controversies about access to and control over tangible things—land, water, trees, wildlife, fish that, apart from any symbolic value they may hold, still plainly exist in the world around us. Everyone agrees on what these things are, just not what to do with them or who should have the power to decide.⁶

This essay argues that taxonomic debates are a central and enduring feature of environmental politics. They occur in the scientist's search for truth, the bureaucrat's quest for ordered management, and the lawyer's pursuit of justice. They are central to conservation. And they should play a far greater role in our understanding of environmental history.

Salmon offer an ideal example of this point, and no member of the salmon family better illustrates it than steelhead and rainbow trout, which together form the subject of this essay. Both spawn in streams along the Pacific Rim, from Mexico to Siberia, where they interbreed and produce fertile offspring that may be genetically indistinguishable and appear identical as juveniles. Those that complete their entire life cycles in freshwater are called rainbow trout. In streams with access to the ocean, some young fish in these populations migrate downstream—nobody knows exactly why—undergo dramatic physiological changes, then enter the ocean, where they remain for one to three years. These anadromous fish are called steelhead. By the time steelhead return to coastal streams to spawn, which they can do more than once, they may be five times the size of adult rainbows and look more like salmon than trout. In some areas, steelhead and rainbows exhibit transitional life-history strategies, such as migrating between freshwater streams and brackish estuaries, that further blur the distinctions between them.⁷

Steelhead and rainbows thus pose a conundrum. They are not the exactly same thing, but they are not entirely different either. They are two forms on a continuum of salmon diversity that includes a bewildering collection of shape-shifting individuals, alternate life-history pathways, erratic migratory runs, linked breeding populations, and closely related species. Biologists refer to this as a "species complex": a collection of populations that are differentiated enough to qualify as more than one species but that have fuzzy boundaries and lack full reproductive isolation.

Despite their biological affinities, over the past 150 years these two fishes' histories diverged. Rainbows became one of the most widely cultivated vertebrate animals on Earth, supporting a multibillion-dollar aquaculture industry and bringing untold pleasures to recreational fishermen on six continents. In the process, they have transformed aquatic ecosystems and hybridized with local native trout varieties, creating a global biological juggernaut that the science writer Anders Halverson has called "an entirely synthetic fish." During this same period, steelhead declined throughout much of their former range, mainly owing to habitat degradation and the construction of barriers that block their migratory corridors and spawning grounds. Steelhead have all but disappeared from hundreds of streams, including some that once hosted annual runs in the tens of thousands.⁸

⁶ The literature on conservation history is vast. For examples of how environmental historians who study conservation have avoided taxonomy or treated it as a marginal concern see any of the works on salmon history listed in note 4, above. In *An Entirely Synthetic Fish* (New Haven, Conn.: Yale Univ. Press, 2010), Anders Halverson touches on taxonomic issues related to rainbow trout, but mainly with reference to hybridization of native fish with hatchery strains.

⁷Quinn, Behavior and Ecology of Pacific Salmon and Trout (cit. n. 3).

⁸ Halverson, Entirely Synthetic Fish (cit. n. 6).

Herein lies the paradox: If steelhead and rainbow trout are the same species, then *it* ranks among the most successful vertebrates on Earth in an age of human-induced global environmental change. If *they* are different, then rainbow trout constitute an exotic feral species throughout most of their current range, while steelhead are threatened with extinction all along the West Coast of the United States. The landmark federal Endangered Species Act (ESA) of 1973 seeks to protect all species and the ecosystems on which they depend. For steelhead, which are now listed as threatened or endangered under the ESA in watersheds from San Diego to Seattle, complying with this law could mean major changes in the vast water capture, storage, and delivery systems that have helped build and sustain the modern American West, including some of the world's most productive agricultural regions and largest metropolitan economies. Much depends on how we choose to classify and conserve these curious fish.

BIOLOGY: WHAT'S IN A NAME?

The scientific names of Pacific salmon species have a long and convoluted history. In 1740 Georg Wilhelm Steller, a Bavarian naturalist traveling on an ill-fated Russian naval expedition commanded by the Danish-born explorer Vitus Bering, described five varieties of salmon native to the Kamchatka Peninsula in eastern Siberia. Steller derived the species names for these fish from phonetic translations of those used by the area's native Koryak people. Indigenous groups around the North Pacific harvested salmon for consumption and trade, and they possessed detailed ecological knowledge. The inhabitants of each region had their own names for the kinds of fish that lived there, so the Koryak nomenclature represented just one among many indigenous taxonomies.⁹

Steller died in 1746 before he could return home and complete his work. The manuscript from his voyage attracted considerable interest, however, and by 1768 it had been published in Russian, English, and French. In 1792 the German physician Johann Walbaum described several varieties of Pacific salmon using a collection of specimens from East Asia. Walbaum combined the generic name *Salmo*, which Linnaeus had proposed in 1758, with Steller's Koryak-derived species names. In 1836 the Scottish surgeon John Richardson again described the genus *Salmo*, this time using specimens collected in North America. Twenty-four years later George Suckley, an American who had worked with the U.S. Army's Pacific Railroad Survey, wrote two additional reports attempting to classify the Pacific salmon. Yet all of this work failed to settle the questions of how many species existed and how they should be arranged. By 1866 Albert Günther, of the British Museum, could lament that "no other group of fishes . . . offers so many difficulties to the ichthyologist, with regard to the distinction of species as well as to certain points in their life history." The salmon family, he concluded, exhibited "almost infinite variations."¹⁰

In 1879 Spencer Baird, the first chief of the U.S. Fishery Commission, asked two young ichthyologists, David Starr Jordan and Jordan's former student Charles Henry Gilbert, to conduct a comprehensive study of the fish fauna along the West Coast of the United States. Jordan and Gilbert accepted the offer and soon began a yearlong survey that established a foundation

⁹ For more on Steller's expedition see Georg Wilhelm Steller, *Steller's History of the Kamchatka*, ed. M. W. Falk (Fairbanks: Univ. Alaska Press, 2003); Steller, *Journal of a Voyage with Bering*, 1741–42 (Palo Alto, Calif.: Stanford Univ. Press, 1993); Robert J. Behnke, *Trout and Salmon of North America* (New York: Free Press, 2002); and Halverson, *Entirely Synthetic Fish*, pp. 52–54. On indigenous ecological knowledge see McEvoy, *Fisherman's Problem* (cit. n. 4); and Wadewitz, *Nature of Borders* (cit. n. 4). ¹⁰ Gerald R. Smith and Ralph F. Stearley, "The Classification and Scientific Names of Rainbow and Cutthroat Trouts," *Fisheries*, 1989, 14(1):4–10; Albert Günther, *Catalogue of Fishes in the Collection of the British Museum*, Vol. 6 (London: Trustees of the British Museum, 1866), p. 3; and Vladimir Tchernavin, "Skulls of Salmon and Trout: A Brief Study of Their Differences and Breeding Changes," *Salmon and Trout Magazine*, 1937, 88:235–242.

for fish biology and management in that vast region. Their work also helped gain them considerable notoriety. In 1890 Jordan became the first president of Stanford University, and soon thereafter he appointed Gilbert to one of Stanford's first faculty positions.¹¹

Like their predecessors, Jordan and Gilbert encountered challenges in classifying the Pacific salmon. To solve these problems, they adopted three approaches. They examined physical features to distinguish between similar specimens. They drew maps to identify cohesive groups based on geographic patterns. And they studied salmon behavior and life history to distinguish river and lake (freshwater resident) forms from marine migratory (anadromous) forms. The first two of these approaches were well established, but the third was far less reliable—and the authors knew it.

In 1881 Jordan and Gilbert published a list with thirteen species of Pacific salmon, including three closely related types. *Salmo irideus*, or rainbow trout, was a common freshwater fish of mountain and coastal streams; *Salmo gairdneri*, or steelhead, was a larger, possibly anadromous, salmon-like trout found in major rivers; and *Salmo purpuratus*, known today as the cutthroat trout, was the region's most widespread and variable species, though observers often mistook it for one of the other two. In 1898 Jordan, then working with Barton W. Evermann, a future director of the California Academy of Sciences, revised this arrangement on the basis of new information indicating that cutthroat trout were limited to the Western Hemisphere. They restored John Richardson's original name for the cutthroat trout, *Salmo clarkii*, and split it from its Asian cousin, the Kamchatka trout, which they then lumped with the Atlantic salmon, *Salmo scalar*. The Scottish writer and Conservative politician Sir Herbert Maxwell might have had this switch in mind when he complained, five years later, that it was "discouraging to have to confess that there is no genus of fish about which there is so much conflict of opinion among ichthyologists as there is about that of *Salmo*."¹²

Scientists were not the only group whose conflicting vocabularies revealed the limits, contingencies, and instabilities of their knowledge about nature. In the late nineteenth and early twentieth centuries the sciences were still coalescing into disciplines, and their boundaries remained fluid and fuzzy. Ichthyology, like ornithology, had a long tradition of popular lore and local knowledge, and professional scientists depended on information provided by amateur naturalists. Yet popular knowledge also encompassed a dizzying array of terminology. Rainbow trout could be called redband trout or California brook trout. Steelhead were known as hardheads, black salmon, silver salmon, salmon trout, summer salmon, or sea-run rainbows. Sundowners were steelhead found in coastal lagoons, and half-pounders were steelhead that had ventured into the ocean—but only for a few months before returning to streams. Cutthroat trout were called Oregon brook trout or lake trout when they were not being confused with steelhead. Chinook salmon, a close relative of steelhead and rainbow trout, had at least nine common names.¹³

¹¹ Smith and Stearley, "Classification and Scientific Names of Rainbow and Cutthroat Trouts," p. 5.

¹² David S. Jordan and Charles H. Gilbert, "Notes on the Fishes of the Pacific Coast of the United States," *Proceedings of the United States National Museum*, May 1881, 4:29–70; Jordan and Barton W. Evermann, "The Fishes of North and Middle America," *Bulletin of the United States National Museum*, 1898, 47(3):2183–3136; William Converse Kendall, "What Are Rainbow Trout and Steelhead Trout?" *Transactions of the American Fisheries Society*, 1921, 50:187–199; and Herbert Maxwell, *British Fresh-Water Fishes* (London: Hutchinson, 1904), p. 179.

¹³ For examples of some of these names in use see Charles Frederick Holder, Recreations of a Sportsman on the Pacific Coast (New York: Putnam, 1910); Holder, The Angler's Guide: How and Where to Fish (New York: Field and Stream, 1909); David S. Jordan and Barton W. Evermann, American Food and Game Fishes (New York: Doubleday, Page, 1902); Jordan and Gilbert, "Notes on the Fishes of the Pacific Coast of the United States," p. 38; Kendall, "What Are Rainbow Trout and Steelhead Trout?"

To make matters even more complicated, professionals and amateurs shared an extensive vocabulary describing the developmental stages of fish in the salmon family. Salmon and trout begin life as eggs before becoming alevins (larvae), fry (newborns), and then parr (juveniles), by which time they are considered fingerlings. Trout remain in freshwater, but anadromous juveniles become smolts when they undergo physiological and morphological changes that enable them to survive in the ocean. Adults that return to breed are spawners, and those that have already spawned and are returning to the ocean are kelts or downstreamers. Fish that can survive to reproduce more than once, like steelhead, are iteroparous spawners.¹⁴ (See Figure 2.)

Beyond all of these taxonomic and developmental distinctions lay a broader debate about the evolutionary history of the salmon family. Were freshwater resident trout and anadromous salmon fundamentally different, comprising distinct branches of the evolutionary tree, or were they more like two leaves on the same twig—alternate forms that might arise in any species of this family?

From the 1880s to the 1920s, some of the country's most prominent fish biologists wrestled with this question in reference to steelhead and rainbow trout. Jordan, who originally attempted to classify Pacific salmon in part on the basis of whether they migrated to the ocean, later concluded that rainbows were probably just immature steelhead. Evermann called these two forms "identical," but he conceded that the matter was complicated because some subspecies of rainbow trout had freshwater resident populations with no anadromous counterparts. William C. Kendall, from the U.S. Bureau of Fisheries, regarded the steelhead as one among many kinds of rainbow trout. By 1934 Alan C. Taft, of the California Department of Fish and Game, predicted that researchers would never discover a clear division between steelheads and rainbows, because they were merely two overlapping versions of the same species.¹⁵

But if steelhead and rainbow trout were the same species, then why did these two forms arise, and how did they interact and persist when so few other vertebrate species can pursue such distinct life-history pathways? Answering this question would require a better understanding of the role of freshwater to saltwater migration in the salmon family.

Medieval authors were among the first to speculate about whether salmon that migrated to the ocean as juveniles returned, or "homed," to their natal streams as adults. By 1930 most experts agreed that salmon homed, but they did not know how or why these fish did so, the precision or reliability of this behavior, or the role it played in the fishes' population biology and evolutionary history. Over the next several decades, a series of studies found that most young salmon that enter the ocean perish, but more than 95 percent of those that survive return to their places of birth to spawn. When they are in the open ocean salmon use celestial and geomagnetic signs to navigate, but at close range they locate their home streams using chemicals found in the water as olfactory beacons. Since generations of fish return to the same natal stream, they may become adapted to the local conditions there. The small percentage of fish that stray to streams other than those of their birth are probably at a reproductive disadvantage compared to those that find their way home, but the few strays that successfully mate in

p. 187; and "Steelhead One of Most Highly Esteemed Gamesters to Be Found in Local Streams," Santa Barbara New Press, 3 Mar. 1952, p. C-11.

¹⁴ Quinn, Behavior and Ecology of Pacific Salmon and Trout (cit. n. 3).

¹⁵ Smith and Stearley, "Classification and Scientific Names of Rainbow and Cutthroat Trouts" (cit. n. 10), pp. 6–7; Barton W. Evermann, "Rainbow or Steelhead," *Forest and Stream*, 1922, 92:116; Kendall, "What Are Rainbow Trout and Steelhead Trout?" (cit. n. 12); Alan C. Taft, "California Steelhead Experiments," *Trans. Amer. Fisheries Soc.*, 1934, 64:248–251; and C. Tate Regan, "The Systematic Arrangement of the Fishes of the Family Salmonidae," *Annals and Magazine of Natural History*, 1914, 13:405–408.



Figure 2. A stylized depiction of the life histories of steelhead and rainbow trout originating in a California stream.

unfamiliar streams contribute to gene flow and can colonize vacant habitats, such as those that opened up as the glaciers retreated at the end of the last ice age.¹⁶

Biologists once hoped that they would discover an "anadromy gene" that would enable them to distinguish freshwater resident from anadromous fish in the salmon family. Most now believe that anadromy, like other forms of migration, results from a complex combination of nature and nurture, genetic predisposition and environmental cues. Genetic research has, however, offered other important insights. Steelhead and rainbow trout populations are relatively well connected throughout much of their range owing to occasional straying, but they also contain genetic diversity surpassing that of most other salmon species. The extent to which steelhead and rainbow trout interbreed seems to vary by stream and population. But steelhead and rainbows from the same stream interbreed more frequently, and are thus more closely related, than either does with its analogous form in neighboring streams.¹⁷

Genetic research also has helped clarify the place of steelhead and rainbow trout in the salmon family. In the early 1980s, steelhead and rainbows were still classified with Atlantic

¹⁶ Alan C. Taft and Leo Shapovalov, "Homing Instinct and Straying among Steelhead Trout (Salmo gairdneri) and Silver Salmon (Oncorhynchus kisutch)," California Fish and Game, 1938, 24:118–125; Shapovalov, "The Homing Instinct in Trout and Salmon," Proceedings of the Sixth Pacific Science Congress of the Pacific Science Association, 1941, 3:317–322; and Quinn, Behavior and Ecology of Pacific Salmon and Trout (cit. n. 3), pp. 85–94, 299–303.

¹⁷ Quinn, Behavior and Ecology of Pacific Salmon and Trout, p. 308; Anthony J. Clemento, Eric C. Anderson, David Boughton, Derek Girman, and John Carlos Garza, "Population Genetic Structure and Ancestry of Oncorhynchus mykiss Populations above and below Dams in South-Central California," Conservation Genetics, 2009, 10:1321–1336; and Ian Williams, Gordon H. Reeves, Sara L. Graziano, and Jennifer L. Nielsen, "Genetic Investigation of Natural Hybridization between Rainbow and Coastal Cutthroat Trout in the Copper River Delta, Alaska," Trans. Amer. Fisheries Soc., 2007, 136:926–942.

salmon and brown trout in the genus *Salmo*, although their species name had changed from *irideus* to *gairdneri*. In 1984, however, a Japanese geneticist showed that the Kamchatka trout, which Jordan and Evermann had separated from the cutthroat trout eighty-six years earlier, was in fact a subspecies of steelhead and rainbow trout that occasionally interbred with other subspecies. This led to a scientific name change for steelhead and rainbow trout from *gairdneri* to *mykiss*. Two years later, another study revealed that coho and Chinook salmon were both more closely related to steelhead and rainbow trout than they were to other species of Pacific salmon. In 1988 the American Society of Ichthyologists and Herpetologists concluded that steelhead and rainbow trout belonged in the Pacific group of the salmon family and should have the new name *Oncorhynchus mykiss*. This is the name that stands today.¹⁸

And yet, the most important question remained: Why did some steelhead and rainbow trout—unlike almost all other vertebrate species—produce offspring with the potential to live such different kinds of lives? The answer can be found in their environment. Steelhead and rainbows occur in more diverse, and more marginal, habitats than any other salmon species. Consider the conditions that *O. mykiss* faces in semiarid Southern California, where it is the only salmon species hardy enough to persist. During dry years, or even regular dry seasons, creeks turn to dusty arroyos and sandbars form at river mouths, blocking passage between sea and stream. This region's freshwater streams have little food but also few predators. They are safe places to be born, and the trout that stay there can maintain small populations for years in isolated pools, waiting for the next deluge. Marine ecosystems, conversely, have plenty of food but lots of hungry predators. Most steelhead that migrate to the ocean perish there, but those that survive return to their natal streams as robust and fertile adults. The ability to access diverse resources, through varied survival tactics, thus increases the likelihood that a population will endure in bad times and flourish in good times. Having multiple life-history options is a "bethedging" strategy for coping with a dynamic environment.¹⁹

The long history of efforts to classify fish in the salmon family involved anatomy, geography, behavior, and genetics. Yet the most profound insight from this work was ecological. The diversity and complexity of the steelhead and rainbow trout's habitats selected for the diversity and complexity of their populations, life histories, and bodies. Beginning in the mid-nineteenth century, humans transformed these habitats in ways that altered the ecological equation, undermining the very evolutionary logic that explained the coexistence of steelhead and rainbow trout as a single species.

MANAGEMENT: THE CONSERVATION OF WHAT?

Since the mid-nineteenth century, human populations along the West Coast of the United States have simplified and transformed the region's aquatic ecosystems to render them more predictable and productive. These changes drove a wedge between the steelhead and rainbow trout, allowing rainbows to become ubiquitous while devastating steelhead. And so even as these two fish were becoming the same species in the eyes of scientists, their histories diverged. Today, rainbow trout rank among the most successful vertebrate animals on Earth, but

¹⁸ Halverson, Entirely Synthetic Fish (cit. n. 6), pp. 54–56; Quinn, Behavior and Ecology of Pacific Salmon and Trout, p. 26; Robert J. Behnke, "Relationships of the Far Eastern Trout, Salmo mykiss walbaum," Copeia, 1966, 2:346–348; Toshio Okazaki, "Genetic Divergence and Its Zoogeographic Implications in Closely Related Species Salmo gairdneri and Salmo mykiss," Japanese Journal of Ichthyology, 1984, 31:297–311; and R. M. Bailey and C. R. Robins, "Changes in North American Fish Names, Especially as Related to the International Code of Zoological Nomenclature, 1985," Bulletin of Zoological Nomenclature, 1988, 45:92–103.

¹⁹ Quinn, Behavior and Ecology of Pacific Salmon and Trout, pp. 209, 220, 253, 276.

steelhead are considered threatened or endangered all along the West Coast of the United States, especially in the southern reaches of their range, where few remain.²⁰

Human relations with steelhead and rainbow trout date back to long before European contact. For reasons that remain mysterious, the archaeological record contains little evidence of this species at Native American sites. But indigenous people harvested enormous quantities of salmon, and some of these fish must have been steelhead and rainbow trout. According to one estimate, Native Americans captured up to 8.5 million pounds of Chinook salmon annually in California's Central Valley alone, a figure comparable to the commercial hauls of the nineteenth and twentieth centuries. Salmon populations in certain areas may have suffered under such intense pressure. By the mid-nineteenth century, however, declines in Native American populations and their traditional lifeways probably enabled salmon populations to recover and unleashed the bounty reported by so many Anglo-American newcomers.²¹

The West Coast's salmon runs impressed early explorers and settlers, but these observers soon realized that the region's aquatic ecosystems—with their large annual fluctuations in water levels and clear, cold, swift-flowing streams—were less diverse and productive than those on the East Coast. One late nineteenth-century study found more fish species during a single day in a small tributary of the Mississippi River than scientists had identified in all of California west of the Sierra Nevada. The Sierra Nevada itself, a mountain range with more than a dozen major rivers and some seven thousand lakes, contained only forty native fish species. Many nineteenth-century authors thus described the state's waters as beautiful but barren. The onset of commercial fishing and canning only made this worse. By 1879 David Starr Jordan estimated that the Sacramento River watershed, which once hosted the second largest salmon fishery on the West Coast, did not contain "one-twentieth the number of fish that it did twenty years ago."²²

In 1870 the California legislature established a Commission of Fisheries and a nationwide coalition founded the American Fish Culture Association. Two years later, Congress created a federal commission to study "the cause of the decrease of the seacoast fishes and those of the rivers and lakes with suggestions as to the best methods of restoring the same; and active measures looking toward the propagation and multiplication of the useful food fishes, either by restocking depleted waters or by introducing desirable species into new waters." Between 1871 and 1896, government agencies and "acclimatization societies" in California imported

²⁰ On the transformation of aquatic ecosystems in California and the West see Donald J. Pisani, *From the Family Farm to Agribusiness: The Irrigation Crusade in California and the West*, 1850–1931 (Berkeley: Univ. California Press, 1984); Donald Worster, *Rivers of Empire: Water, Aridity, and the Growth of the American West* (Oxford: Oxford Univ. Press, 1985); Norris Hundley, *The Great Thirst: Californians and Water*, 1770s–1990s (Berkeley: Univ. California Press, 2001); and Marc Reisner, *Cadillac Desert: The American West and Its Disappearing Water* (New York: Penguin, 1983). Under the ESA, the word "endangered" means that a species is in danger of extinction throughout all or a portion of its range; the word "threatened" means that, without further intervention, the species is likely to become endangered in the future. Although the "threatened" designation connotes a lower level of concern, threatened and endangered vertebrates both qualify for the same level of legal protection.

²¹ Ronald M. Yoshiyama, Frank W. Fisher, and Peter B. Moyle, "Historical Abundance and Decline of Chinook Salmon in the Central Valley Region of California," North American Journal of Fisheries Management, 1998, 18:487–521; and William Preston, "Post-Columbian Wildlife Irruptions in California: Implications for Cultural and Environmental Change," in Wilderness and Political Ecology: Aboriginal Influences and the Original State of Nature, ed. Charles E. Kay and Randy T. Simmons (Salt Lake City: Univ. Utah Press, 2002), pp. 111–140.

²² Jerry C. Towle, "Authored Ecosystems: Livingston Stone and the Transformation of California Fisheries," *Environmental History*, 2000, 5:54–74, on p. 60 (quoting Jordan); Bay Institute of San Francisco, *From the Sierra to the Sea: The Ecological History of the San Francisco Bay-Delta Watershed* (Novato, Calif.: Bay Institute, 2003), pp. 2.7, 2.11, 3.2–3.3; and McEvoy, *Fisherman's Problem* (cit. n. 4), pp. 46, 67, 78.

twenty-one exotic fish species. Fourteen of these remain in the state's waters, and at least seven make significant contributions to recreation or commerce.²³

Fish culturists also sought to propagate and distribute useful native species. In 1872 the U.S. Fish Commission's West Coast director, Livingston Stone, received a \$5,000 congressional appropriation to build a salmon egg collecting station. Stone found an ideal site on the McCloud River, a tributary of the Sacramento River draining the slopes of Mount Shasta in Northern California. This was not the first such station in California, but it was the most ambitious. If successful, Stone argued, this station would help restore salmon in American waterways, providing an essential public resource and reducing the need for onerous fishing regulations. Stone thus sought to replace the *in situ* conservation of native fish populations with the *ex situ* production of hatchery stocks for use whenever and wherever necessary.²⁴

Stone's initial project met with mixed results. Over a decade, he shipped at least forty-five million Chinook salmon eggs to twenty-nine states and several million more to Australia, New Zealand, Germany, and elsewhere. He emerged as an internationally respected figure in the fish culture movement and a tireless booster for West Coast salmon. Yet by 1879 he reluctantly admitted that not a single new self-sustaining run had emerged from his transplanted stock. The whole experiment had been "a stupendous surprise and disappointment." So that summer Stone devised a new plan. He set out on horseback to find a site for a second station on one of the McCloud's rugged headwater tributaries. This time he would shift his focus to rainbow trout.²⁵

By 1885 Stone had sent rainbow eggs to thirty-three states and at least six countries. In several cases the introduced fish spawned, establishing new freshwater populations. Stone's achievements inspired a raft of similar projects and led to increased public investment. During the first century of fish culture in California, for example, the state established at least 169 egg collecting stations and hatcheries. By 1914 the superintendent of these facilities, W. H. Shebley, could brag that, in just the past year, his staff had stocked California's lakes and streams with more than thirty-seven million salmon and trout—or about sixteen fish for every one of the state's human residents.²⁶

Recreational fishing grew rapidly in the United States during the early twentieth century. California began requiring angling licenses in 1913; by 1936 the state had issued annual tags to three hundred thousand fishermen and by 1965 it tallied 1,588,000 active licenses. Around half of these fishermen caught trout, and most of the fish they hooked were rainbows. Hundreds of businesses opened near popular fishing sites to provide supplies, amenities, and advice to anglers. After World War II, state and federal fish and game agencies lobbied for increased funding, pointing to these economic benefits. They also acquired army surplus equipment from the glut of machines rusting in postwar military depots — including several aircraft, which officials used to drop trout into hundreds of remote and previously fishless alpine lakes. By the 1970s there were few bodies of water in the American West that had not been stocked with hatchery fish.²⁷

²³ Towle, "Authored Ecosystems," pp. 54–74; U.S. Commission of Fish and Fisheries, *Propagation of Food Fishes*, 1874–1875 (Washington, D.C.: Government Printing Office, 1876), p. viii; and Peter B. Moyle, "Fish Introductions in California: History and Impact on Native Fishes," *Biological Conservation*, 1976, 9:101–118.

²⁴ Towle, "Authored Ecosystems," p. 62; and Halverson, Entirely Synthetic Fish (cit. n. 6), pp. 12–47.

²⁵ Halverson, Entirely Synthetic Fish, p. 36.

²⁶ McEvoy, Fisherman's Problem (cit. n. 4), pp. 101–116; Earl Leitritz, "A History of California's Fish Hatcheries—1870–1960," Fish Bulletin 150 (Sacramento: California Department of Fish and Game, 1970); Halverson, Entirely Synthetic Fish, pp. 58–59, 82–84; and "Plant Millions of Fish," Los Angeles Times, 3 Nov. 1914, p. II-9.

²⁷ Halverson, Entirely Synthetic Fish, p. 91; and Robert L. Butler and David P. Borgeson, "California 'Catchable' Trout Fisheries," Fish Bulletin 127 (Sacramento: California Department of Fish and Game, 1965).

Of all the fish cultivated during the nineteenth and twentieth centuries, none became more ubiquitous than the rainbow trout. Wild-born rainbows remained common along the northern Pacific Rim, but they were few compared to the billions produced in hatcheries each year. Today, some hatchery rainbows spend their entire lives in aquaculture ponds, where they are raised on synthetic feed to be harvested for sale and consumption. As of 2010, the rainbow trout was the world's tenth most valuable aquaculture species, with more than \$3.4 billion in annual profits, and the fourteenth largest by weight, with 781,582 tons produced. Since most propagated fish do not reproduce or even survive long in the wild, hatcheries still also manufacture tens of millions of rainbows for regular stocking of lakes and streams. With a range that spans six continents and hundreds of thousands of water bodies, the rainbow trout now ranks as one of the most abundant and widespread vertebrates on Earth.²⁸ (See Figure 3.)

Steelhead have experienced a different fate. Biologists have documented only a few possible cases of hatchery-bred rainbows producing steelhead offspring that migrate to the ocean and back. This means that virtually all steelhead are born in the wild in their ancestral streams. Over the past 150 years, steelhead numbers have plummeted throughout most of their range, owing to a complex combination of factors that have degraded or eliminated their habitats, including erosion, pollution, water diversion, the destruction of coastal estuaries, and the modification of stream channels. Despite these multiple pressures, however, robust steelhead runs continued in some areas for decades. Many observers have thus concluded that the single factor most directly associated with the steelhead's collapse is the construction of dams.²⁹

Beginning in the late nineteenth century, Americans embarked on a vast program to reengineer the rivers of the Intermountain West and Pacific Coast. Western North America is not a uniformly arid region, but compared to the eastern half of the continent the availability of water there is highly unevenly distributed in space and time. It accumulates in remote mountains during the winter and spring, where and when people need it least. Bureaucrats and engineers set out to fix this problem by altering and simplifying the region's hydrology on an unprecedented scale. One of their most common approaches was to construct dams that would capture and store water, prevent floods, and, wherever possible, produce hydroelectric energy.

A few small West Coast dams date to California's Mission era, but the region's first major water projects appeared in the San Francisco Bay Area around 1870. Lake Chabot, a 315-acre reservoir formed by damming San Leandro Creek in the Oakland Hills in 1875, was one of the most ambitious early projects. (This was the same stream where, twenty years earlier, the naturalist William P. Gibbons collected the fish specimen he used for the first scientific description of a rainbow trout.) The size and number of the state's water projects increased during the twentieth century. Many dams received congressional authorization and funding as part of the federal Central Valley Project, starting in the 1930s, or the State Water Project, beginning in the 1950s. These included monumental structures, such as Shasta Dam on the Sacramento River, which holds the state's third largest body of water, and Oroville Dam on the Feather River, which at 742 feet is the country's tallest dam. State and federal government agencies, as

²⁸ Clemento et al., "Population Genetic Structure and Ancestry of Oncorhynchus mykiss Populations" (cit. n. 17), p. 1321; and Food and Aquaculture Organization, Yearbook 2010 (New York: United Nations, 2010), p. 30.

²⁹ Peter B. Moyle, Joshua A. Israel, and Sabra E. Purdy, Salmon, Steelhead, and Trout in California: Status of an Emblematic Fauna (Davis, Calif.: Center for Watershed Sciences, 2008); and William S. Leet, Christopher M. Dewees, Richard Klingbeil, and Eric J. Larson, eds., California's Living Marine Resources: A Status Report (Sacramento: California Department of Fish and Game, 2001), pp. 418–425. This interpretation differs somewhat from Joseph E. Taylor's more multicausal argument in Making Salmon (cit. n. 4). For my own research related to this point see Peter S. Alagona, Scott Cooper, Matthew Stoecker, Peggy Beedle, and Mark Capelli, "The History of Steelhead and Rainbow Trout in the Santa Ynez River Watershed," Bulletin of the Southern California Academy of Sciences, 2012, 111:163–222.



Figure 3. The historic range of steelhead and rainbow trout (diagonal lines) and the current global range of rainbow trout by country (stippled pattern). Courtesy of Sheila Wiseman.

well as cities, firms, and private citizens, constructed countless additional impoundments and diversions. The era of dam building lasted for about a century. By the time the state completed its last major project, in the late 1970s, it had more than thirteen hundred of the nation's approximately seventy-nine thousand named dams and several of its biggest. Today, only one major California river, the Smith, located in the remote northwest Coast Ranges near the Oregon border, remains undammed.³⁰ (See Figure 4.)

Many dams were expensive pork-barrel projects with few social or economic benefits. Cumulatively, however, they provided water for tens of millions of people, increased flood protection for vulnerable communities, facilitated the economic development of the country's most populous and urban state, and helped California build the world's largest and most diverse agricultural economy. Controversy surrounded these projects almost from the beginning, but the general consensus, until at least the 1960s, was that their benefits exceeded their costs to society.³¹

These dams proved devastating, however, for the region's anadromous fishes, which depend on natural cycles in streamflow and access to headwater spawning habitats. Steelhead were especially hard hit, but their collapse was not a surprise.

As early as the 1870s, the California legislature sought to mitigate the effects of dams on fisheries. In 1915 it increased these efforts by passing Fish and Game Code Section 5937, requiring that the state's dams "allow sufficient water at all times" to pass through or around their structures "to keep in good condition any fish that may be planted or exist below the dam." But dam operators, who believed that conserving anadromous fish was incompatible with their core mission of water conservation, often ignored this policy. They argued that the code was nonbinding and that it conflicted with other requirements in California's complex water-law system. They also claimed that stocking reservoirs with rainbow trout and other hardy, hatchery-bred fishes would more than compensate for the loss of steelhead. With the Division of Fish and Game too weak to advance its case, many dam operators refused to dedicate even a drop of water for ecological values downstream.³²

Steelhead numbers continued to plummet—by more than 90 percent in many watersheds and up to 99 percent in Southern California. Biologists lamented this decline, but as the decades wore on, despite their concern, they dedicated less and less time to analyzing or reversing the problem, other than working to improve hatchery strains. From the 1930s through the 1960s, scientific journals and government agencies in the United States published only a handful of studies on fish species that were not used for commerce or recreation. Steelhead, which never supported a major commercial fishery and faded into lore among recreational anglers as their numbers dwindled, received little attention.³³

This changed in the 1970s, when a new generation of scientists and managers, some claiming membership in the young field of conservation biology, began expanding their work to include biological diversity and native species, even in cases where such species had little

³⁰ For more on these dams see Pisani, From the Family Farm to Agribusiness (cit. n. 20); Worster, Rivers of Empire (cit. n. 20); and Reisner, Cadillac Desert (cit. n. 20).

³¹ For an infamous early dam controversy see Robert W. Righter, *The Battle over Hetch Hetchy: America's Most Controversial Dam and the Birth of Modern Environmentalism* (Oxford: Oxford Univ. Press, 2005).

³² Roger Di Silvestro, "Steelhead Trout: Factors in Protection," *BioScience*, 1997, 47:409–414; and Karrigan S. Börk, Joseph F. Krovoza, Jacob V. Katz, and Peter B. Moyle, "The Rebirth of California Fish and Game Code Section 5937: Water for Fish," *University of California, Davis, Law Review*, 2012, 45:809–913.

³³ For an example of officials giving up on steelhead in the southern portion of their range see P. A. Douglas, California Department of Fish and Game District Fisheries Biologist, to U.S. Fish and Wildlife Service Region 5 Fisheries Management Supervisor, 8 Apr. 1953, Center for Ecosystem Management and Restoration, Southern Steelhead Document Archive, Oakland, California. For increasing attention to noncommercial and nonsporting fish see Peter B. Moyle and Jack E. Williams, "Biodiversity Loss in the Temperate Zone: Decline of the Native Fish Fauna of California," *Conservation Biology*, 1990, 4:275–284.

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Figure 4. The locations of California's more than thirteen hundred named dams. Dams create barriers to fish migration on almost every major stream in the state. Courtesy of Sheila Wiseman.

apparent economic value. Recreational fishing groups took up the cause as well. Such groups had many influential members and generated vital revenue for small-town economies near popular fishing areas, but they had long supported the creation of reservoirs stocked with hatchery fish. For their members, productivity trumped diversity. Some, however, began to see the quest for wild native fish as a purer, more traditional, and more challenging brand of their sport. Commercial fishers, who worried that habitat destruction was damaging what remained of the West Coast's marketable salmon fishery, also advocated restoration efforts in addition to their long-standing support for hatcheries. This coalition of scientists, recreationists, and commercial fishers soon began lobbying for new government programs and regulations that would

expand the legal framework for conservation. Such efforts, they hoped, might even restore one of the West Coast's rarest and most prized sporting fish, the steelhead.³⁴

LAW: CONSERVATION FOR WHOM?

The West Coast's earliest fishing regulations appeared during the late nineteenth century, around the same time as the region's first biological surveys, fish culture efforts, and water projects. Despite the widespread changes under way in the region's aquatic ecosystems, these early conservation laws mostly assumed that the states could conserve wild fish populations by limiting take. They defined fishing seasons, catch limits, and allowable gear (explosives and poisons were outlawed early), but even these modest prohibitions lacked adequate penalties and enforcement.³⁵

During the first decade of the twentieth century, California law distinguished between steelhead and rainbow trout, assigning different seasons and catch limits to each. For anglers, whose numbers were growing by the year, this created a quandary. The *Los Angeles Times* mocked the state's distinction between steelhead and rainbows as "foolish[,]... for an angler has never found a bait which will attract one variety of trout and repulse another." As for the difference in fishing seasons, the *Times* asked if fishermen should somehow attempt to "shoo away" hungry rainbows during the month of April, when the law permitted fishing for steelhead but not their freshwater brethren.³⁶

Two questions were at stake in this early regulatory debate. Were steelhead and rainbows the same species? And, regardless of their taxonomic status, should the state regulate them in the same way? David Starr Jordan had recently stated that he believed the two were the same species, and, according to the *Times*, most anglers accepted Jordan's expert opinion. But consent was far from universal. Edwin L. Hedderly, of the *Los Angeles Herald*, for example, claimed that he had "not yet found a trout fisherman who agreed with this view." Fishermen may have differed on the taxonomic question, but they agreed that one set of regulations was essential so that well-meaning anglers would not risk violating the law. They got their wish, between 1909 and 1911, when the state reclassified all trout in coastal streams as steelhead and rainbows were the same species, the state would manage them as such.³⁷ (See Figure 5.)

Despite these early regulatory efforts, steelhead numbers dwindled in many watersheds. By 1940 John O. Snyder, another Jordan protégé and Stanford professor, could write that the "presence of dams and diversions is no doubt responsible in large measure for the depletion of trout and salmon. Protective laws and much firmness and diplomacy in their administration seems necessary if serious losses are to be prevented." The state legislature continued building its catalogue of fishing regulations, but such laws proved ineffective in addressing the environmental changes causing anadromous fish declines.³⁸

Efforts to protect anadromous fish on the West Coast hit rock bottom in the middle of the twentieth century, in the middle of California. Friant Dam, a linchpin of the Central Valley

³⁴ Halverson, Entirely Synthetic Fish (cit. n. 6).

³⁵ For overviews and discussions of these codes see early issues of *California Fish and Game*, beginning with the journal's first issues in 1914.

³⁶ "Fine Fishing for Steelhead," Los Angeles Times, 3 Apr. 1910, p. VII-7.

³⁷ "Arrest Waits Trout Fishers," Los Angeles Times, 1 Apr. 1909, p. 17; "Anglers, Attention! Native Fish Steelhead," *ibid.*, 31 Mar. 1909, p. I-3; "Fine Fishing For Steelhead," (Breer Catches Big Steelhead," Los Angeles Times, 5 Apr. 1910, p. I-7; and State of California, The Statutes of California and Amendments to the Codes Passed at the Thirty-Ninth Session of the State Legislature (Sacramento, Calif.: State Printing Office, 1911), pp. 188–189, 302–315, 520–563, 716–717, 1004–1006.

³⁸ John O. Snyder, "Trouts of California," California Fish and Game, 1940, 26:115.



Figure 5. Anglers with a day's catch of steelhead from the Santa Ynez River, once Southern California's largest steelhead fishery, in February 1913. Robust runs continued in the Santa Ynez until the middle of the twentieth century but ended with the completion of Bradbury Dam in 1953. Courtesy of the Lompoc Valley Historical Society.

Project completed in 1942 on the San Joaquin River, blocked access to 70 percent of the river's spawning habitat and transformed a sixty-mile section of streambed below the structure into a dry wash. The state Division of Fish and Game, with the support of 131 recreational fishing groups, wrote to the facility's operator, the federal Bureau of Reclamation, requesting that it release a small amount of water to maintain downstream fish habitat.³⁹

The bureau claimed that it would give the division's request full consideration, but it made clear that homes and farms, not fish, were its top priorities for water delivery. It also said it doubted whether state laws applied to federal water projects, such as Friant Dam. Dry conditions prevailed in California in the late 1940s, and in May 1948 the bureau's regional director, Richard L. Bloke, informed the division that he would not allocate any water for fish conservation. A year later, Bloke concluded that it was "a physical and financial impossibility to try and save the salmon in the San Joaquin River." Yet the fight continued. In 1951 California attorney general and future governor Edmund "Pat" Brown made it clear that he considered this a zero-sum game when he declared that California's Water Code, which appeared to support the bureau's position, trumped its Fish and Game Code. The division did not give up so easily, however, and the case dragged on until 1959, when the State Water Rights Board sided with Brown and the bureau. To justify its decision, the board offered circular logic: since the San Joaquin River's anadromous fish were, by then, essentially extinct, "failure to take action . . . will not destroy any existing runs nor prevent a possible later reestablishment."⁴⁰

³⁹ Börk et al., "Rebirth of California Fish and Game Code Section 5937" (cit. n. 32).

⁴⁰ Philip Garone, The Fall and Rise of the Wetlands of California's Great Central Valley (Berkeley: Univ. California Press, 2011),

p. 190; Everett G. Rank et al., Plaintiffs, v. (Krug) United States of America et al., U.S. District Court for the Southern District of

During the 1970s, fish advocates began to push for more proactive policies to restore West Coast salmon. In the years that followed, several court rulings in Washington and Oregon affirmed Native American fishing rights based on nineteenth-century treaties. This reduced the proportion of fish available for commercial harvests, but it also provided a legal tool for First Nations groups and their allies to compel government agencies to dedicate more resources for restoration. The famous Mono Lake Case, of 1983, forced California to recognize its public trust obligation to maintain fisheries and waterways for the benefit of its citizens, including its duty under Fish and Game Code Section 5937 to maintain fisheries Program Act aimed to increase populations of wild-born salmon, including steelhead, substantially by the end of the century. Congress followed, in 1992, with the Central Valley Project Improvement Act, which set the goal of doubling wild salmon populations in the project's catchment area.⁴¹

One of the most important legislative changes was the passage of the federal Endangered Species Act in 1973. At first, few observers realized the importance or potential impact of this law. By the end of the 1970s, however, the battle over the Tennessee Valley Authority's Tellico Dam project and its effects on an endemic fish called the snail darter revealed the act's farreaching scope. The ESA aimed to protect all native plant and animal species and the ecosystems on which they depend by prohibiting any activities that could jeopardize a listed species or adversely modify its habitat. The act soon gained a reputation as one of the United States' most powerful environmental laws and the most ambitious conservation statute ever enacted by any country.⁴²

Under the ESA, the lead federal agency, either the Fish and Wildlife Service or the National Oceanic and Atmospheric Administration, must first determine whether the group of organisms being considered for protection qualifies as a species. The ESA, which was amended in 1978 and 1982, defined a species as any full species or "subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife, which interbreeds when mature." The following year, the U.S. General Accounting Office recommended that Congress eliminate the ESA's "distinct population segment" provision because it was ripe for overuse by zealous listing agencies. Legislators declined to do so, citing an earlier House committee's view that it was "in the best interests of mankind to minimize the losses of genetic variations." Congress advised the agencies to list such populations "sparingly," but it provided little further guidance for how to do so—or even how to define a distinct population.⁴³

NOAA officials encountered instant problems in applying these policies to the salmon family. In 1981 the administration's Fred Utter wrote that although the ESA's definition of a species applied reasonably well to the salmon family, identifying distinct populations within species

California, 142 F. Supp. 1, 7 (1956); L. F. Chappell to Charles E. Casey, 24 Apr. 1944, California State Archives, Sacramento, Natural Resources—Fish and Game Commission, Executive Secretary's Files, U.S. Fish and Wildlife Service: 1944, 1948, 1951; Emil J. N. Ott, Jr., to Governor Earl Warren, 4 Mar. 1948, California State Archives, Natural Resources—Administration—Director, Director's Subject File, Friant Dam: 1948–50; and Richard L. Bloke to E. L. Macaulay, 6 May 1949, California State Archives, Natural Resources—Fish and Game Commission, Executive Secretary's Files, U.S. Agency Correspondence, Bureau of Reclamation: 1946, 1948, 1949.

⁴¹ William G. Clark, "Fishing in a Sea of Court Orders: Puget Sound Salmon Management Ten Years after the Boldt Decision," North Amer. J. Fisheries Management, 1985, 5(3B):417–434; John Hart, Storm over Mono: The Mono Lake Battle and the California Water Future (Berkeley: Univ. California Press, 1996); and Börk et al., "Rebirth of California Fish and Game Code Section 5937" (cit. n. 32).

⁴² Kenneth M. Murchison, *The Snail Darter Case: TVA versus the Endangered Species Act* (Lawrence: Univ. Press Kansas, 2007); and Shannon Petersen, *Acting for Endangered Species: The Statutory Ark* (Lawrence: Univ. Press Kansas, 2002).

⁴³ National Oceanic and Atmospheric Administration, "Policy on Applying the Definition of Species under the Endangered Species Act to Pacific Salmon," *Federal Register*, 20 Nov. 1991, 56(224):58612–58618.

presented a much more difficult task. The obvious solution was to equate the legal concept of a distinct population with the scientific concept of spawning runs associated with particular seasons and streams. But spawning runs are notoriously dynamic and complex processes, not well-defined objects. An even greater problem was that the spawning run approach applied poorly to steelhead and rainbow trout, a single species comprising two forms, only one of which migrated between fresh and salt water.⁴⁴

Robin Waples, of NOAA's Northwest Fisheries Science Center, proposed an alternate approach to address this conundrum. Citing work by the San Diego Zoo conservation geneticist Oliver A. Ryder, Waples argued that NOAA should define a distinct population segment as an Evolutionarily Significant Unit (ESU). To qualify as an ESU, a population would need to be "substantially reproductively isolated" from other populations of the same species and represent "an important component in the evolutionary legacy of the species."⁴⁵

In 1991 NOAA used this approach to list its first West Coast salmon distinct population, the Snake River sockeye run, as protected under the ESA. Over the next eight years it listed twentysix additional Pacific salmon populations. The agency also began mapping critical habitats, which are the areas it deemed necessary for these populations' survival. Critical habitat areas are not sanctuaries, but, according to the ESA, any federal or federally permitted project in these areas may not adversely modify the listed species' habitat within a critical habitat area. By the end of the decade, critical habitats for various salmon populations included tens of thousands of miles of streams, from the Mexican to the Canadian border.⁴⁶ (See Figure 6.)

These population listings and critical habitat designations provoked an uproar among farmers, municipalities, developers, and timber firms, which argued that ESA regulations would parch their communities and harm the economy. The solution, they said, was simple: the government should restore diminished populations by producing more hatchery stock. In 1993 NOAA responded by announcing that it would use hatchery stock for some research and recovery efforts, but it would only consider wild-born fish members of protected populations. It did not say how people should distinguish hatchery stock from wild-born fish in places where they both live.⁴⁷

This confusing policy failed to satisfy the agency's critics, which by this time also included fish advocates who claimed that hatchery stock diluted genetic lineages, spread diseases, increased competition, and reduced the fitness of wild-born populations. In 2001 a related case, *Alsea Valley Alliance et al. v. Donald L. Evans et al.*, reached the U.S. District Court in Oregon, which ruled that the ESA permitted the use of hatchery propagation as a kind of captive breeding. But it was not a total victory for NOAA. The court also ruled that the agency had violated the law by distinguishing between hatchery and wild-born fish, since in any given

⁴⁴ Fred M. Utter, "Biological Criteria for Definition of Species and Distinct Intraspecific Populations of Anadromous Salmonids under the U.S. Endangered Species Act of 1973," National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Mar. 1981.

⁴⁵ Robin S. Waples, "Pacific Salmon, Oncorhynchus spp., and the Definition of 'Species' under the Endangered Species Act," Marine Fisheries Review, 1991, 53(3):11–22; National Oceanic and Atmospheric Administration, "Policy on Applying the Definition of Species under the Endangered Species Act to Pacific Salmon" (cit. n. 43); and Oliver A. Ryder, "Species Conservation and Systematics: The Dilemma of Subspecies," Trends in Ecology and Evolution, 1986, 1:9–10.

⁴⁶ NOAA maintains a digital archive of all *Federal Register* documents pertaining to listing decisions and critical habitat designations at westcoast.fisheries.noaa.gov.

⁴⁷ National Oceanic and Atmospheric Administration, "Interim Policy on Artificial Propagation of Pacific Salmon under the Endangered Species Act," *Federal Register*, 5 Apr. 1993, 58(63):17573–17576.



Figure 6. Areas in which streams are either accessible or inaccessible to steelhead in California, based on the locations of artificial or natural barriers. The light gray labeled areas define the boundaries of steelhead "distinct population segments" protected under the Endangered Species Act. Thousands of miles of streams within these DPS areas are listed as "critical habitat," which means that NOAA considers them essential for steelhead conservation. Courtesy of Sheila Wiseman.

stream both would be part of the same interbreeding population and a distinct population was the smallest biological unit that could qualify for protection as an endangered "species."⁴⁸

⁴⁸ Alsea Valley Alliance et al. v. Donald L. Evans et al., U.S. District Court for the District of Oregon, 161 F. Supp. 2d 1154 (2001). For more on this case see Daniel Schneider, Hybrid Nature: Sewage Treatment and the Contradictions of the Industrial Ecosystem (Cambridge, Mass.: MIT Press, 2011).

This put NOAA in an awkward position. If it included hatchery stock in its listing decisions, then in a world where such facilities produced millions of fish each year no salmon population would ever qualify as endangered, even as the genetic stock became increasingly homogenized and the number of wild-born fish continued to decline. By April 2002 NOAA had received eight official petitions, based on the *Alsea* decision, asking it to reevaluate the status of seventeen Pacific salmon populations. The agency responded by launching a status review of its entire West Coast salmon program. After three years of study it concluded that, although some minor status changes were warranted, all twenty-seven populations should remain on the list, even with the inclusion of hatchery stock. Another round of lawsuits followed. This time, however, the U.S. District Court for Eastern California found that NOAA had acted reasonably, according to established procedures, and within its authority. The list would stand.⁴⁹

The status review also addressed the specific question of how NOAA should deal with steelhead and rainbow trout. The agency wrestled with this as early as 1997, when it listed the first steelhead population as protected under the ESA. Back then, it noted that "conclusive evidence does not yet exist regarding the relationship of resident and anadromous *O. mykiss.*" The law seemed to require that steelhead and rainbows, which were not "substantially reproductively isolated," be grouped and managed together. Yet because steelhead were still declining, NOAA argued that several populations of this species warranted protection to preserve their anadromous form. The FWS, which usually sided with NOAA, now protested, pointing out that the omnipresent rainbow trout, which fell partly under its authority, was anything but an endangered species. After some negotiation, the two agencies agreed that NOAA would list only the steelhead portion of any *O. mykiss* populations.⁵⁰

NOAA had made the same mistake twice. By distinguishing between different kinds of individuals—in this case steelhead and rainbow trout—in a single population, it once again violated the Oregon court's ruling that a population was the smallest unit eligible for listing under the ESA.

Desperate for a resolution, NOAA turned to an independent science advisory panel, which recommended a new strategy to comply with the law while conserving the anadromous form of the species. In streams with no barriers to migration, where steelhead and rainbows can freely interbreed and access the ocean, NOAA would manage them together as part of the same population. In streams with long-standing natural barriers, such as impassable waterfalls, NOAA would assume that the fish on the two sides of those barriers were different populations, with rainbow trout on the landlocked side and steelhead on the seaward side. In streams with recently erected barriers to migration, such as dams without fish ladders, the agency would evaluate each case individually. But because little data existed about the genetic linkages between recently divided upstream and downstream groups, the agency would have to assume that the two were separate populations unless provided with evidence indicating otherwise. Fish above the dams would be rainbows, and fish below the dams would be steelhead.⁵¹

⁴⁹ National Oceanic and Atmospheric Administration, "Endangered and Threatened Species: Proposed Listing Determinations for 27 ESUs of West Coast Salmonids," *Federal Register*, 14 June 2004, 69(113):33102–33179; and *California State Grange et al. v. National Marine Fisheries Service et al.*, U.S. District Court for Eastern California, 620 F. Supp. 2d 1111 (2008).

⁵⁰ National Oceanic and Atmospheric Administration, "Endangered and Threatened Species"; and California State Grange et al. v. National Marine Fisheries Service et al.

⁵¹ National Oceanic and Atmospheric Administration, "Endangered and Threatened Species"; *California State Grange et al. v. National Marine Fisheries Service et al.*; and Jody Hey, Ernest L. Brannon, Donald E. Campton, Roger W. Doyle, Ian A. Fleming, Michael T. Kinnison, Russell Lande, Jeffrey Olsen, David P. Philipp, Joseph Travis, Chris C. Wood, and Holly Doremus, "Considering Life History, Behavioral, and Ecological Complexity in Defining Conservation Units for Pacific Salmon: An Independent Panel Report, Requested by NOAA Fisheries," 13 June 2005.

In 2010 a coalition of California farm groups and water agencies from the southern San Joaquin Valley, where State Water Project managers were struggling to provide water for irrigation during a series of dry years, appealed the Eastern California District Court's decision upholding ESA protection for five West Coast steelhead populations. This time, the plaintiffs argued that NOAA was required by law to treat all steelhead and rainbow trout in any stream as a single population, regardless of their access to the ocean. Such a change would require the removal of most, if not all, *O. mykiss* populations from the endangered species list.⁵²

Again on the defensive, NOAA argued that the ESA's purpose was to conserve biodiversity in many forms, including behavioral and ecological diversity, that steelhead were unlikely to persist without protection, and that interbreeding was a necessary but insufficient condition for defining a population as a species under the law. In its decision, the Ninth Circuit Court of Appeals admitted that it could not resolve the underlying questions, but it found the agency's arguments reasonable and cited a precedent of judicial deference to agency expertise in such technical and multifaceted cases. NOAA's policy would remain. After more than 250 years of research on salmon taxonomy, 150 years of managing steelhead and rainbow trout, and a century of legislating and regulating on behalf of this species, the default legal distinction between its two forms would depend not on morphology or behavior or evolution or genetics but on their positions upstream or downstream of a dam.⁵³

TO CLASSIFY AND CONSERVE

In February 2013, two years after President Obama's State of the Union salmon joke, the U.S. Government Accountability Office (GAO) published a report asking whether the FWS and the NOAA Fisheries unit should merge to make their work more efficient. It turned out that Obama was not the first to suggest such a change. The two agencies had many related duties, and this had prompted a series of proposals to combine or rearrange them. The GAO interviewed ten former Interior and Commerce Department secretaries and directors, as well as other officials from forty-three government agencies and nongovernmental organizations. In the end, however, it did not recommend a change. After studying the costs and benefits of various restructuring schemes, it concluded that there was no simple bureaucratic solution for managing complex species like steelhead and rainbow trout or their diverse habitats.⁵⁴

The case of steelhead and rainbow trout may seem like an extreme example of the role of taxonomy in environmental politics, but it is not unique. Taxonomic debates pervade every area of environmental science, management, and law that requires making distinctions between and mapping the relationships among related objects or processes. Such debates apply to landforms, waterways, climates, geologic epochs, and even planets. In the biological world, steelhead and rainbow trout are as close to the norm as they are to the exception. Plants and invertebrates both pose taxonomic challenges far greater than those for vertebrate animals. And even among the vertebrates, taxonomic debates still surround almost every family.

To demonstrate this point, consider the canids. Dogs are among the best-studied vertebrate animals, but scientists are still piecing together their evolutionary relationship with wolves. The two are considered separate species, having diverged from a common ancestor up to thirty thousand years ago. Yet, like rainbow trout and steelhead, dogs and wolves can interbreed

⁵² Modesto et al. v. Gutierrez et al., U.S. Court of Appeals for the Ninth Circuit, 619 F. 3d 1024 (2010).

⁵³ Ibid. For the judicial deference precedent see Chevron U.S.A., Inc., v. Natural Resources Defense Council, Inc., U.S. Supreme Court, 467 U.S. 837 (1984).

⁵⁴ Government Accountability Office, "Government Reorganization: Potential Benefits and Drawbacks of Merging the National Marine Fisheries Service into the Fish and Wildlife Service," GAO-13-248, Feb. 2013.

and produce fertile offspring, one is partly domestic while the other is almost exclusively wild, one became ubiquitous even as the other's populations declined, and one is part of a global industrial commodity system while the other is the focus of contentious place-based conservation efforts.

In the United States outside Alaska, wolves have been protected, in one form or another, since 1967, when the FWS published its first endangered species list. In 2013, however, the service proposed to reorganize its wolf conservation program by delisting the gray wolf, which it no longer considered a valid species under the ESA, declaring the Mexican wolf an endangered subspecies, maintaining the red wolf as an endangered species, and elevating the unlisted eastern wolf from a subspecies to a species. When several scientific, environmental, and industry groups objected, the service convened an advisory panel. This panel concluded that the proposal did not represent "the best available science," but it declined to offer an alternative.⁵⁵

Regardless of the outcome, the service is in for more wolf-related taxonomic headaches. The population of Mexican wolves, which has remained below a hundred individuals for most of the past few decades, is showing signs of inbreeding, leading to calls for fresh blood from more northern packs that belong to a different subspecies. Recent genetic research suggests that red wolves, which the FWS has been working to protect as a unique species for more than half a century, derive from a line of wolf–coyote hybrids no more than several hundred years old. And since at least the 1970s, eastern wolves have hybridized with coyotes and dogs, creating an even newer complex of wild canids along the Atlantic Seaboard. In the south, these hybrids have a greater proportion of dog and coyote genes; further north, they have a greater proportion of coyote and wolf genes. In many areas, however, local residents know these creatures simply as "coywolves": novel beasts that combine the physical prowess of a wolf with the wily adaptability of a coyote and none of the sweet cuddliness of a dog.⁵⁶

Species are still the primary focus of biodiversity science and conservation. For many observers, however, the case of steelhead and rainbow trout, like that of wolves and dogs, illustrates the shortcomings of this approach. Some argue that we should abandon the species concept altogether. Scientists in this camp note that there are at least two dozen species definitions in the current biological literature, none of which captures the full diversity and complexity of the phenomena it claims to describe. Critical conservationists see a different problem. They argue that instead of fetishizing species, as so often happens under the ESA and other laws, we should seek to maintain overall genetic diversity while nurturing healthy ecosystems that produce valuable goods and services.⁵⁷

⁵⁵ Fish and Wildlife Service, "Endangered and Threatened Wildlife and Plants; Removing the Gray Wolf (*Canis lupus*) from the List of Endangered and Threatened Wildlife and Maintaining Protections for the Mexican Wolf (*Canis lupus baileyi*) by Listing It as Endangered," *Federal Register*, 13 June 2013, 78(114):35664–35719. For the basis of this proposal see Steven M. Chambers, Steven R. Fain, Bud Fazio, and Michael Amaral, "An Account of the Taxonomy of North American Wolves from Morphological and Genetic Analyses," *North American Fauna*, 2012, 77(2):1–67; and National Center for Ecological Analysis and Synthesis, "Sponsored Independent Expert Peer Review of the Scientific Findings in the Proposed Rule: Removing the Gray Wolf (*Canis lupus*) *from* the List of Endangered and Threatened Wildlife and Maintaining Protections for the Mexican Wolf (*Canis lupus*) *baileyi*) by Listing It as Endangered," 23 Sept. 2013.

⁵⁶ Cally Carswell, "Line of Descent," *High Country News*, 8 Aug. 2016, pp. 14–20; Christopher J. Manganiello, "From a Howling Wilderness to Howling Safaris: Science, Policy, and Red Wolves in the American South," *Journal of the History of Biology*, 2009, 42:325–359; Dan Flores, *Coyote America:* A *Natural and Supernatural History* (New York: Basic, 2016), pp. 213–231; and Roland Kays, "Yes, Eastern Coyotes Are Hybrids, but the 'Coywolf' Is Not a Thing," *Conversion* (online), 13 Nov 2015.

⁵⁷ See, e.g., Brent D. Misheler, "Getting Rid of Species?" in *Species: New Interdisciplinary Essays*, ed. Robert A. Wilson (Cambridge, Mass.: MIT Press, 1999), pp. 307–315.

For environmental historians and historians of science, the story of steelhead and rainbow trout points to a bigger insight. Taxonomic debates are a fundamental feature of environmental politics. They can produce new scientific knowledge and foster more effective management, but they can also fuel bitter controversies, hobble administrative agencies, and lead to bizarre legal decisions. They can even shape the very stuff of nature itself, carving the subjects of conservation out of an infinitely variable world by giving them names, then transforming them through exploitation and management. Conservation history, in other words, is not merely a political struggle over things that exist in nature; it is a perennial competition to prove the existence and define the very nature of those things that are the focus of such struggles.

As for steelhead and rainbow trout, their story is far from over. Since the 1970s, laws and court decisions have redistributed political power from a few dominant institutions whose singleminded mission was to provide water for big cities and farms to arrangements that allocate water for a much broader range of people and purposes, including anadromous fish. Restoration projects with the potential to provide multiple social and ecological benefits are under way in many watersheds, and a small number of dams in the American West are being decommissioned. Bold conservation initiatives, such NOAA's Southern California Steelhead Recovery Plan, promise aggressive action on other fronts. But many dams remain critical infrastructure, and the specter of droughts and floods, which will probably occur more frequently and with greater severity owing to climate change, may limit support for some removal efforts. Finding even a modest place for steelhead in the contemporary Western waterscape will thus require further changes involving multiple interest groups and government agencies, taking decades to complete, and costing hundreds of millions of dollars. All of this depends, in part, on the way we choose to classify a humble fish that—in many ways, and like so many other creatures defies our most basic categories.⁵⁸

⁵⁸ National Marine Fisheries Service, Southern California Steelhead Recovery Plan Summary (Long Beach, Calif.: National Marine Fisheries Service, Jan. 2012).