Strongholds for Pacific salmon: A proactive conservation strategy for ecosystem health, food security, biodiversity, and climate resilience

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ABSTRACT

Nested within the linked global crises of biodiversity loss and climate change are threats to cultural and ecological keystones such as Pacific salmon *Oncorhynchus* spp., a group of species with widespread ecological, cultural, and economic value. Wild salmon can rally public support for ecosystem protection and link place-based conservation efforts to global biodiversity and climate benefits. Realizing these benefits depends on leveraging broad support for salmon conservation to advance forward-looking approaches that safeguard food security, biodiversity, and climate resilience. Here we provide insights from the multidecadal implementation of a proactive wild salmon ecosystem conservation strategy at the scale of the North Pacific Rim. This approach is a necessary complement to policies focused on preventing species extinction after populations and habitats are degraded and it provides globally significant contributions to biodiversity and climate targets including recent 30 × 30 goals of the Convention on Biological Diversity.

INTRODUCTION

The growth of the global human population, industrialization, and intense extraction of natural resources have brought about the Anthropocene, placing earth's natural systems under unprecedented and mounting pressures (Folke et al., 2021). Together, these forces are contributing to an accelerating rate of biodiversity loss and an erosion of resilience in natural systems supporting human well-being (IPBES, 2019). Recognition of this crisis has led to widespread calls for transformation in industrial economies to reverse the degradation of our planet and the life it sustains (Díaz et al., 2019). Among many urgent priorities, a global movement to protect large ecologically intact terrestrial and marine ecosystems and imperiled biodiversity has emerged as a top priority (Maxwell et al., 2020; Venter et al., 2014). This movement towards large-scale land and ocean protections has taken many forms, but most recently has been integrated within the Global Deal for Nature, a timebound, science-driven global effort to protect 30% of the planet by 2030 (i.e., "30×30"; Baillie & Zhang, 2018; Dinerstein et al., 2019). Amidst the effort to preserve critical ecological function and climate regulation are lessons to be learned from long-term, large landscape conservation efforts, including those focused on specific taxa that can serve as flagships for conserving biodiversity and protecting broad social-ecological benefits.

Pacific salmon *Oncorhynchus* spp. (hereafter "salmon") have been at the forefront of calls for landscape conservation and species protections for more than a century (e.g., Stone, 1892). Salmon are considered ecological and cultural "keystones" because they support hundreds of aquatic and terrestrial species, and Indigenous and local communities across a vast arc of watersheds extending from California through Alaska and across to the Russian Far East and Japan (Garibaldi & Turner, 2004; Wilson & Halupka, 1995). The ecological, economic, and cultural health of the North Pacific Rim depends in large part on the annual migrations of salmon, which collectively number in the hundreds of millions of adults and billions of juvenile salmon moving across the freshwater and marine interface (Ruggerone & Irvine, 2018; Wilson et al., 2023).

However, ongoing declines—and more recently, sudden crashes—in systems like the Sacramento, Klamath, Fraser, Skeena, Yukon, and Amur rivers that historically boasted extraordinary salmon abundance signal an alarming erosion in ecosystem health and highlight significant conservation challenges (e.g., Atlas et al., 2023; Price et al., 2021; Yoshiyama, 1999). Salmon-bearing watersheds generate services that humans depend on, such as clean water, flood storage, commerce, and carbon sequestration, among others. Consequently, declines in salmon populations signal broader implications for

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ecological, economic, and human health, including the loss of livelihoods, food security, and erosion of the cultural identities of Indigenous and local communities. That these declines have occurred despite the continuing and widely recognized importance of salmon to humans and ecosystems (Reid et al., 2022; Waldman & Quinn, 2021), including strong public support for salmon recovery (Lewis et al., 2019), makes the ongoing loss of wild salmon stocks one of the more vexing species conservation challenges of our time.

Proximate drivers of salmon decline are well documented and include major impacts from landscape conversion and habitat loss, a legacy of fisheries overharvest, salmon hatcheries, and climate change (e.g., Lichatowich, 1999; Montgomery, 2003; Waldman & Quinn, 2021). Salmon declines are most severe in the southern portions of their range where human populations are largest—in Japan, California, Oregon, and Washington. However, accelerating climate impacts and ecosystem change across the northern hemisphere have recently caused widespread episodic mortality and reduced salmon productivity even in regions like Alaska with relatively low levels of human development (L. A. Jones et al., 2020; von Biela et al., 2022). Consequently, salmon declines are no longer limited to southern latitudes but are now observed throughout their historical range.

Losses in salmon abundance, habitat quality, and availability have triggered major conservation efforts to prevent the extinction of populations listed under laws such as the U.S. Endangered Species Act (ESA) and Canadian Species at Risk Act. Since the 1970s, these laws have provided legal authority for conservation, allowing endangered species advocates to stop activities that further threaten wild salmon populations or degrade their habitats. More recently, amendments to these laws and other federal responses, including the U.S. Pacific Coastal Salmon Recovery Fund (established in 2000), began promoting the recovery of ESA-listed populations by funding extensive habitat restoration and other conservation efforts. In many of the most industrialized watersheds on the West Coast, the U.S. and Canadian federal governments now spend hundreds of millions of dollars annually to address habitat loss and salmon population declines through watershed restoration and the production of hatchery-reared salmon (Jaeger & Scheuerell, 2023). Although policies and programs arising from these and other federal initiatives have promoted widespread investment in salmon recovery and watershed restoration, to date, no listed Pacific salmon populations have recovered to the point where they can be removed from federal protection, and many populations have been extirpated or are facing "imminent extinction" (Gustafson et al., 2007; Katz et al., 2013).

Given the challenge of salmon recovery under reactive policies like the ESA and the Species at Risk Act, proactive approaches are needed to protect remaining core areas of wild salmon diversity and abundance to maintain their contributions to social–ecological systems. This complementary approach of protecting intact and functioning salmon habitats and populations has a long history in the debate over how to protect wild salmon (e.g., Stone, 1892) but has only recently been implemented. In recent decades, the strategy has been called the "salmon stronghold strategy" (Rahr & Augerot, 2006; Rahr et al., 1998).

The salmon stronghold strategy complements ongoing salmon recovery efforts by identifying and conserving the healthiest remaining wild salmon populations and the high value ecosystems and human communities they support (Rahr et al., 1998). The approach emphasizes the role of human stewardship in maintaining and restoring wild salmon diversity and abundance to provide ongoing benefits to human livelihoods and cultures, as well as ecosystems. Here, we first outline key elements of the salmon stronghold strategy and offer insights into protecting wild salmon ecosystems grounded in 25 years of placed-based conservation efforts around the North Pacific Rim. We also highlight the broader conservation benefits that result from preserving Pacific salmon at the center of social-ecological systems. Conserving intact Pacific salmon watersheds and allowing them to maintain or recover their full ecological potential is likely to be especially beneficial in helping to address broader environmental crises facing humanity by slowing the pace of biodiversity loss and climate change. In turn, policies aimed at biodiversity conservation and climate stabilization may be more tangible and appealing if linked with flagship species like Pacific salmon that have widespread ecological, cultural, and economic value.

SALMON STRONGHOLD CONSERVATION

Salmon strongholds are watersheds within major salmon ecoregions (Augerot, 2005) that have relatively high levels of wild salmon abundance, productivity, and diversity, and habitat quality capable of sustaining resilient wild salmon populations (Figure 1). The purpose of the salmon stronghold strategy is to secure the multidecadal ecological health of these watersheds, their native salmonids and local human communities. Salmon stronghold conservation, therefore, aims to maintain the social and ecological processes that underpin habitat integrity and salmon population resilience (Bottom et al., 2009; K. Connors, 2023), including the need for: (1) habitat protection and restoration, (2) conservation of wild salmon biodiversity, and (3) institutional capacity and local leadership to connect salmon and people, creating layers of protection for both habitat and wild salmon populations, and defending conservation by repelling future threats to strongholds over time.

Habitat protection and restoration

The resilience of wild salmon populations rests in large part on the availability of intact freshwater and estuarine habitats that are needed for reproduction and juvenile rearing (Bisson et al., 2009; Price et al., 2024). Productive salmon watersheds comprise a shifting mosaic of complementary habitats, from headwaters to estuaries, that are clean, seasonally cool, complex, and connected (e.g., Brennan et al., 2019; Rine et al., 2016). These characteristics facilitate high juvenile survival and growth, which bolster populations in the face of unfavorable marine conditions and provide compensatory population growth in freshwater habitats when spawner abundance is depressed by low marine survival (Bisbal & McConnaha, 1998; Bottom et al., 2009). Freshwater and estuarine habitats may also produce carryover effects that improve salmon performance during the marine phase of their life cycle (Gosselin et al., 2021). For example, high freshwater growth rates can increase marine

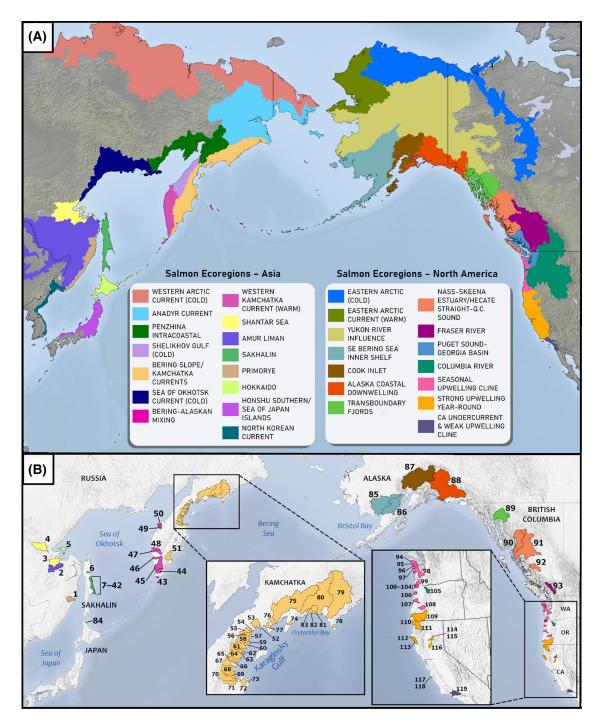


Figure 1. (A) The historical range of Pacific salmon and major salmon ecoregions (modified from Augerot, 2005), and (B) wild salmon strongholds identified during the initial phase of stronghold strategy implementation. Additional details for numbered salmon stronghold watersheds in (B) are given in Table S1 (see online Supplementary Material).

survival, which is positively size-biased in many instances (e.g., Wilson et al., 2021; but see Ulaski et al., 2020) and estuaries may act as stopover habitats facilitating high juvenile growth prior to the onset of lengthy marine migrations (Moore et al., 2016). These connected and seasonally complementary habitats provide opportunities for variable juvenile life histories, spreading risks of collapse or poor performance from ecological disturbance (K. K. Jones et al., 2021). Connectivity across heterogenous freshwater habitats also stabilizes interannual production of salmon, as productivity shifts among locations within dynamic watersheds over time (Brennan et al., 2019; Reeves et al., 1995). Consequently, conservation of the processes that maintain heterogeneity and connectivity across complementary freshwater habitats within watersheds (e.g., fires, floods, and fish migration and movement) through the establishment of protected areas, comprehensive land-use planning, and the designation and long-term protection of critical habitat is central to maintaining the resilience of wild salmon populations (Brennan et al., 2019; Moore, 2015; Reeves et al., 1995).

Salmon biodiversity conservation

Pacific salmon biodiversity is the variety of life expressed by salmon, encompassing variation from species to populations to phenotypes and genes. The high degree of inter- and intraspecific salmon diversity benefits people and ecosystems by buffering populations from short-term fluctuations in survival and abundance (Moore et al., 2015; Schindler et al., 2010), stabilizing fisheries and the availability of salmon for terrestrial and aquatic consumers (Nesbitt & Moore, 2016; Ruff et al., 2011), and underpinning salmon populations' adaptive capacity to respond to climate change and ecological disturbances (Braun et al., 2016; Greene et al., 2010; Stockwell et al., 2003). Conservation strategies can sustain these substantial benefits by minimizing risks from three primary threats to salmon biodiversity: (1) habitat loss and homogenization, which, as described in the previous section, erodes opportunities for local adaptation and the expression of diverse life histories (Beechie et al., 2006; McClure et al., 2008; Zarri et al., 2022); (2) mixed-stock marine fisheries, which can reduce inter- and intrapopulation diversity through overharvest and depletion (B. M. Connors, Malick, et al., 2020; Moore et al., 2021); and (3) hatchery propagation, which domesticates wild genotypes, reduces salmon genetic and phenotypic diversity, and reduces fitness in the wild (e.g., Christie et al., 2014; McMillan et al., 2023).

Mixed-stock marine fisheries intercept fish during their oceanic feeding migrations, harvesting salmon from multiple species and populations, often far from the watersheds where the fish were produced and with limited information on which populations are being intercepted (Beacham et al., 2020; Moore et al., 2021). This system has limited management control over which specific stocks are harvested, often resulting in the overharvest of weak or at-risk salmon populations, and eroding the abundance, productivity, and biodiversity contributions of many small or less productive populations (e.g., Hilborn, 1985; Price et al., 2021; Walters et al., 2008).

Salmon hatcheries compound these conservation risks through indirect and direct effects on wild salmon biodiversity. Although hatcheries can contribute economic and social benefits via expanded fisheries opportunities in some cases (Radtke & Davis, 2000; Flagg, 2015), or short-term demographic rebuilding (Berejikian & Van Doornik, 2018; Johnson et al., 2020), indirect impacts of hatcheries occur when fisheries targeting hatchery salmon also intercept weak or at-risk wild stocks (Naish et al., 2007; Walters et al., 2008). Direct effects of hatchery salmon include numerous documented evolutionary and ecological impacts on wild salmon populations, including, but not limited to, rapid domestication and reduced fitness in the wild (Araki et al., 2007, 2009; Ford et al., 2023), introgression of maladaptive genetic variation through interbreeding with wild salmon populations (Besnier et al., 2022; Kitada, 2014; Quinn et al., 2002), and resource competition between hatchery and wild salmon at multiple spatial scales (e.g., Beamish & Neville, 2021; B. M. Connors, Malick, et al., 2020; Ruggerone et al., 2021).

Institutional leadership and strength

Stewardship of natural resources is most effective and equitable when local communities benefit from conservation and management and are deeply involved in monitoring and decision making (Berkes, 2003; Pinkerton & John, 2008; Thompson et al., 2020). Given the rich diversity of humansalmon relationships that exist around the Pacific Rim, and the fact that salmon, their habitats, and the human communities that depend on them are interconnected living systems, a foundational element of their conservation is a strong "immune response" in the form of local leadership that can effectively recognize and defend against emerging threats to the ecological integrity of salmon watersheds while incrementally adding "layers" of protection to wild fish populations and their habitats over time. Supporting Indigenous-led approaches to stewardship can be particularly effective at securing social-ecological resilience and protecting biodiversity (Frid et al., 2016; Lee et al., 2019; Polfus et al., 2016). For example, the network of salmon strongholds we described below intersects the boundaries of over 100 Indigenous language groups across the North Pacific Rim (Supplemental Material 1), representing a long and diverse history of interdependence between salmon and people and sophisticated systems of salmon management (Atlas et al., 2021; Carothers et al., 2021). This ongoing close-knit relationship means that Indigenous communities are often the first to recognize and mobilize against environmental threats to salmon ecosystems (e.g., Atlas et al., 2021; Moore et al., 2015; Vierros et al., 2020). This capacity for local defense of wild salmon strongholds is built by supporting, strengthening, and amplifying the voices and leadership of local Indigenous communities.

Institutional leadership and strength also reside in nongovernmental organizations (NGOs) and stakeholders who are committed to the long-term health of their salmon watersheds. While NGOs can help secure conservation agreements established in law and policy, it is the role of government agencies to enforce these agreements. These agencies play a critical role securing salmon stronghold durability and should be the focus of support, scrutiny, accountability, and vigilance. New threats, such as large-scale mining and road building, are often accompanied by political pressure on these agencies, and existing conservation agreements can be vulnerable to erosion. There is, therefore, a need for effective local leadership to mobilize public support for proactive and defensive actions in wild salmon ecosystems, as well as a need for connecting local leadership to broader-based organizations (e.g., national and international NGOs, Indigenous organizations) to most effectively influence regional, national, and international decision-making bodies.

IMPLEMENTING A SALMON STRONGHOLD STRATEGY

Salmon conservation focused on habitat protection, salmon biodiversity conservation, and institutional capacity is being implemented to prevent significant degradation of targeted salmon strongholds from Russia to California. Here, we describe stronghold strategy implementation based on the experience of Wild Salmon Center's conservation programs, the goal of which has been to work with government agencies, NGOs, and Indigenous and local communities to establish a durable network of salmon stronghold watersheds distributed across the North Pacific Rim (Figure 1; Augerot, 2005). This approach is based on the principle that a successful long-term strategy for wild salmon conservation in the face of an uncertain climate and human activities requires both place-based conservation at the watershed scale, including local capacity for sustained stewardship, and a network of stronghold watersheds representing salmon biodiversity across their native range (Mantua & Francis 2004; Pinsky et al., 2009; Rahr & Augerot, 2006).

The initial phase of this strategy included identifying a distributed network of the most intact remaining salmon watersheds on which to focus conservation investments. To guide stronghold identification, the Wild Salmon Center led an effort in the mid-2000s to quantify the conservation value of salmon watersheds at the scale of the North Pacific Rim based on measures of salmon abundance and diversity (Pinsky et al., 2009). Regional assessments were then performed to select strongholds in the Russian Far East, Pacific Northwest, and California through processes and forums that varied by state but that included input from NGOs, government agencies, and Indigenous leaders (e.g., Belyaev & Zvyagintsev, 2007; Pavlov et al., 2010; WSC, 2012, 2015). In other regions, strongholds were selected by Wild Salmon Center for focused conservation investment based on their regional and global importance for salmon abundance, diversity, and habitat quality. For example, whereas Alaska has many watersheds that could be considered salmon strongholds, Wild Salmon Center's place-based conservation efforts have focused on large rivers draining to Bristol Bay, and the Susitna, Copper, and Taku rivers, each of which are regional centers of exceptional salmon abundance and diversity (e.g., Bristol Bay produces more than half of the world's Sockeye Salmon Oncorhynchus nerka with recent adult returns as high as 79 million fish; Tiernan et al., 2022). Thus, in largely ecologically intact regions like Alaska, we acknowledge that salmon strongholds included within Wild Salmon Center's current stronghold network are a subset of watersheds that have similarly high conservation value (Pinsky et al., 2009). Stewardship of these focal watersheds can serve as models for protecting the social-ecological resilience of other regional watersheds as capacity grows for expanding the network of recognized strongholds.

To date, Wild Salmon Center and collaborating organizations have made conservation investments in 119 watersheds that encompass approximately 51 million ha, or roughly 10% of the historical range of Pacific salmon (Supplemental Material 1). The network of stronghold watersheds is distributed within 17 of 27 level-3 salmon ecoregions (Supplemental Material 1; Figure 1). These river systems produce average annual returns of approximately 120 million wild salmon (approximately 25% of the 1995–2015 global annual average; Ruggerone & Irvine, 2018) and include many of the planet's most important producers of Chinook Salmon *O. tshawytscha*, Sockeye Salmon, Coho Salmon *O. kisutch*, Masu Salmon *O. masou*, and steelhead *O. mykiss*, as well as some of the last strongholds for threatened Siberian Taimen *Hucho taimen* and Sakhalin Taimen *Parahucho perryi*, the world's largest salmonids (Sloat, 2023).

Stronghold watersheds generally have higher ecological integrity than other watersheds within the same respective ecoregions. For example, linear mixed models that include a random effect of salmon ecoregion and fixed effects for

habitat metrics reveal that at the time of their selection (~ 2009), stronghold watersheds had a significantly smaller human footprint index (HFI), an index of cumulative human pressures on the landscape (Venter et al., 2019; detailed methods and results for theses analyses are provided in Supplemental Material 2). Stronghold watersheds also had significantly less hatchery influence (Augerot, 2005) than other watersheds. Between 2009 and 2020, the HFI decreased or did not change in 91% of the strongholds analyzed (Supplemental Material 2). Interestingly, although stronghold watersheds have lower HFI, they currently have significantly less protected land area than other ecoregional watersheds (Supplemental Material 2). This finding supports the urgency of adding layers of new land protections or other effective area-based conservation measures before there are imminent threats to these high-value salmon watersheds.

A consistent guiding principle for the protection of stronghold watersheds has been an emphasis on proactive conservation initiated before immediate threats posed by development can damage salmon ecosystem health. Specific conservation actions have necessarily included a range of approaches that reflect differences in the environmental, social, and political contexts of multiple states, provinces, and countries. For example, the intensity of human influences on salmon watersheds varies greatly across the vast range of Pacific salmon and this dictates the types of habitat conservation actions that are necessary and possible. In areas with little human impact, proactive habitat protection and land use planning has proven the most effective way to safeguard watershed function (Rahr & Augerot, 2006). This includes designating areas of limited human use, such as protected areas, parks, or similar reserves through local, national, or Indigenous law, and working with local communities to ensure that human activities minimize risks to habitat forming processes (Sanderson et al., 2022). In sparsely populated and largely publicly owned lands of the Russian Far East, Alaska, and northern British Columbia, whole watershed reserves with comprehensive "ridge to reef" habitat protections remain important conservation targets (Case study 1; Rahr & Augerot, 2006). However, most salmon strongholds in the central and southern parts of the Northern Pacific Rim have intermediate levels of human influence and thus require mixed strategies of habitat protection and restoration (Abel et al., 2007; Sanderson et al., 2022). For example, coastal watersheds in western North America often have headwaters on federal lands that function as reserves (e.g., national parks, wilderness areas, forest lands managed for late-successional characteristics), but downstream areas have mixed land ownership and landscapes fragmented by urbanization, logging, and agriculture (e.g., Burnett et al., 2007). Here, both land use laws and voluntary landowner agreements (e.g., U.S. habitat conservation plans) have helped ensure that ongoing land use minimizes risk to habitat forming processes. In addition, processed-based restoration of habitat heterogeneity and connectivity can link upstream reserves to complementary and critically necessary downstream habitats throughout river networks. As levels of human influence increase across salmon strongholds, habitat conservation strategies necessitate a shift from preservation (e.g., reserves) towards a greater role for restoration and ongoing stewardship, with corresponding increases in cost, time, and difficulty (Sanderson et al., 2022).

Consequently, in strongholds that have required increased investment in restoration, conservation activities are coordinated at the watershed scale to avoid independent, small-scale activity and to ensure that limited available resources contribute to the recovery of watershed-scale resilience (e.g., WSC, 2022a).

The second major element of the stronghold strategy is the conservation of wild salmon biodiversity. This has focused on establishing wild salmon health as the management priority for governmental fisheries management agencies, including commitments to maintain salmon biodiversity within and between populations and ensure spawner escapement goals are sufficient to sustain productive salmon fisheries (Hilborn et al., 2003; Mantua & Francis, 2004; Nesbitt & Moore, 2016).

A key strategy for conserving salmon biodiversity and sustaining fisheries is transitioning a larger share of fishery harvests from high risk mixed-stock marine fisheries to terminal and selective fisheries (B. M. Connors et al., 2019; Freshwater et al., 2020; Moore et al., 2021). Indeed, most precolonial Indigenous fisheries were conducted in-river using terminal and selective fishing technologies, which facilitate strong management control over the specific salmon stocks that are harvested (Atlas et al., 2021; Morin et al., 2022; White, 2011). These fisheries were largely sustainable for thousands of years before the arrival of Europeans in western North America, and some rivaled early commercial fisheries in their magnitude (Campbell & Butler, 2010; Craig & Hacker, 1940; Glavin, 1996) but were outlawed and displaced by colonization (Atlas et al., 2021; Harris, 2001). Thus, there is a strong historical precedent for harvest in terminal and selective fisheries and opportunities to revitalize and expand the role of these fishing methods in salmon strongholds around the North Pacific Rim (Atlas et al., 2021).

In addition to efforts to transfer harvest away from mixedstock fisheries and towards terminal and selective fisheries, strategies to achieve salmon biodiversity conservation have included incentive-based and regulatory approaches to managing the impacts of fisheries harvest and salmon hatcheries. In the Russian Far East, most salmon are harvested in terminal fisheries using trap nets near the shore or beach seins, but enforcement of fishing regulations can be challenging. The participation by most of the region's commercial fishing companies in seeking certification by the Marine Stewardship Council has incentivized wild salmon biodiversity conservation. Likewise, on Russia's Sakhalin Island, commercial fishing groups, conservation advocates, and scientists from Moscow State University designated the Wild Salmon Territory, a region comprised of 36 rivers in western Sakhalin where commercial fishing companies support local antipoaching efforts, the production of salmon in hatcheries is prohibited, and managing for salmon biodiversity is the primary goal (VNIRO, 2022). Similarly, in the Pacific Northwest, where salmon hatcheries proliferated during the damming of many major salmon producing rivers in the mid-20th century, the designation of wild fish management areas (also called wild salmonid gene banks) to block future hatchery development in the few relatively unimpacted watersheds has been an important conservation strategy within salmon strongholds for reducing the evolutionary and ecological risks posed by hatchery programs (Case study 2).

Institutional capacity, the third element of the salmon stronghold strategy, has been effective in advancing proactive salmon habitat and biodiversity conservation. This immune response provided by strong local conservation leadership has been critical in defending conservation gains in salmon strongholds (Case study 3). Logging, mining, and fossil fuel projects pose major threats to aquatic ecosystems and wild salmon, including increased stream temperatures, sediment run off from road building, and toxic leaching from mine tailings and oil and gas infrastructure (Brittingham et al., 2014; Cunningham et al., 2023; Seargent et al., 2022). In addition to cumulative effects of these activities on salmon watersheds during their operation, major industrialization can lock in economic and political structures that disrupt social-ecological systems based on wild salmon and reduce rural community resilience (Wilson, 2014). High oil, gas, lumber, and mineral prices, and corporate capture of natural resource policy has required deep investments in grassroots organizing and political engagement to defend wild salmon ecosystems. Illegal and unregulated harvest and impacts from salmon aquaculture also pose regional challenges to wild salmon stronghold stewardship (Krkošek et al., 2011; Webster, 2003). Consequently, in addition to proactive conservation measures, defensive efforts have been necessary to protect salmon strongholds from emerging threats. By strengthening local conservation leadership, most major threats to the current network of salmon strongholds have been blocked, including hard rock mining, liquefied natural gas terminals, hydroelectric development, commercial logging, illegal fishing, and fish hatchery development (Case study 3).

In the following case studies, we provide regional- and watershed-scale case studies to highlight approaches that have helped advanced habitat protection and salmon biodiversity conservation, and local conservation leadership that has helped secure the durability of wild salmon strongholds in three national contexts: Russia's Kamchatka Peninsula, British Columbia, Canada, and the U.S. Pacific Northwest. We then describe broader benefits of the salmon stronghold conservation for food security and livelihoods, biodiversity, and climate resilience.

Case study 1: whole-watershed protected areas for wild salmon

The breakup of the Soviet Union in the late 1980s and subsequent social and economic decline resulted in a wave of unregulated natural resource extraction and illegal fishing across much of the Russian Far East. Russia's Kamchatka Peninsula, which produces about 25% of the world's wild Pacific salmon (Ruggerone & Irvine, 2018) was hit especially hard. By the mid-1990s, industrial scale poaching, mostly for salmon caviar, matched or exceeded the legal harvest of salmon, capturing over 75% of the annual escapement in some of the larger rivers (Beamesderfer & Lajus, 2016). By 2010, a natural gas pipeline and road was constructed across western Kamchatka, providing salmon poachers access to remote and pristine river systems where much of Kamchatka's salmon abundance and genetic diversity is found.

Concerned about the fate of Kamchatka's spectacular park system, salmon rivers, and the Indigenous and local communities that depend on annual salmon runs, in 2000, the United Nations Development Program launched an international effort to secure protections for Kamchatka's park system and salmon biodiversity. The "Preservation of salmon biodiversity and sustainable development in Kamchatka" was led by Russian federal and regional government agencies, the Wild Salmon Center, and Moscow State University. The project's objective was the conservation and sustainable use of salmon biodiversity in four river systems on Russia's Kamchatka Peninsula (GEF, 1999).

Based on the recommendations of the Russian and international experts participating in the United Nations Development Program Project, the 218,854-ha Kol River watershed (watershed 46 in Figure 1) was selected to be a refuge and "natural laboratory" for salmon ecosystems because of its pristine condition, small human footprint, and the extraordinary inter- and intraspecific salmon biodiversity (Pavlov et al., 2010). The Kol is a highly productive salmon watershed, with high habitat complexity and juvenile fish production, as well as unusually high annual salmon run sizes (5–10 million fish/year) given the size of the watershed (Stanford & Gayeski, 2019).

The Kol Salmon Refuge was established as a whole watershed protected area in 2005 and has since been inscribed as part of the Volcanoes of Kamchatka World Heritage Site, the first World Heritage Site dedicated to salmon conservation (UNESCO, 2015). Soon after designation, the Kamchatka administration established a guard station where an access road crossed the river, blocking access for salmon poachers targeting salmon. Further cooperation between the managers of the Kol Refuge, licensed commercial fishermen, and the Ivanovy band of the Itelmen people eliminated most poaching from the Kol. Additional salmon conservation reforms were achieved in 2016, when the commercial salmon fishing company that controlled the rights to fish the mouth of the Kol (a terminal fishery using coastal trap nets and beach seining) agreed to adopt a fisheries improvement plan and conduct regular third party audits of its salmon fishing practices, and was subsequently certified as sustainable for Coho Salmon, Pink Salmon and Chum Salmon O. keta by the Marine Stewardship Council in 2016 (Beamesderfer & Lajus, 2016), and recertified in 2022 (Beamesderfer & Lajus, 2023).

Today, the Kol Refuge is managed by the Kamchatka Ministry for Natural Resources and remains the traditional hunting and fishing territory for the Ivanovy band of the Itelmen people, whose subsistence activities are maintained within the protected area. The Kol River ecosystem and its wild salmonid populations remain healthy. Since the designation of the Kol River as a protected watershed, the Wild Salmon Center and Russian partners have helped establish nine additional largescale protected areas for wild salmon totaling 3.1 million ha in Kamchatka and the Russian Far East, expanding the network of wild salmon strongholds with permanent protection in the region (WSC, 2022b).

Case study 2: Oregon coast genebanks for wild salmon

Most coastal rivers in the U.S. Pacific Northwest and California are now heavily influenced by hatcheries for salmon and steelhead production, creating significant risks for the conservation of wild salmon biodiversity (Rand et al., 2012). Of the rivers that remain free of hatchery programs, many are in western Oregon (Figure 2). However, because of increasing local pressure for more harvestable salmon and steelhead in the near term to support recreational fisheries, the expansion of hatchery programs has been proposed on many of these rivers. Recognizing this threat and the need for proactive measures to safeguard remaining wild salmon biodiversity, in 2014 and then in 2021, the Oregon Fish & Wildlife Commission approved major elements of a coastal multispecies conservation and management plan, including administrative rules identifying 42 out of 71 watersheds or subwatersheds as "wild fish emphasis areas" where wild salmon diversity became the primary management goal and future hatchery programs would be prevented (Figure 2; ODFW, 2014, 2021). This is now the largest network of "wild fish only" basins south of Canada and protects centers of genetic and life history diversity that will be essential to support the adaptation of wild salmon populations to the projected impacts of climate change.

Extensive monitoring of Oregon Coast (OC) Coho Salmon populations within this region demonstrates the substantial benefits of wild fish only designations for salmon resilience. Coho Salmon hatchery programs grew rapidly from the 1950s to the mid-1970s when commercial ocean fisheries appeared prolific and sustainable, but hatcheries replaced wild stocks as the primary producers of Coho Salmon during this period. In 1977, a shift in ocean conditions generated a 20-year period of poor marine survival for Coho Salmon, during which the abundance of both hatchery and wild Coho Salmon crashed, culminating in the closure of commercial fisheries and the listing of OC Coho Salmon as threatened under the ESA in 1998 (Lichatowich, 1999). In response to ESA listing, Coho Salmon hatchery programs were substantially reduced, returning the coastal watersheds from hatchery dominated production systems to a system based almost exclusively on natural production of wild salmon. In combination with habitat protection and restoration efforts, this has resulted in increased resiliency to disturbances such as poor ocean conditions, and an increase in population diversity (K. K. Jones et al., 2018; NOAA 2022). Although OC Coho Salmon have not yet recovered to levels warranting delisting, the curtailment of hatchery propagation and designation of wild fish only watersheds to prevent future hatchery impacts has significantly contributed to the increased abundance, diversity, and resilience of these populations.

Case study 3: local conservation leaders halt harmful industrial development in the Skeena River, British Columbia

The Skeena River (Figure 1, watershed 91) is the second-largest salmon producer in Canada and has supported First Nation fisheries for millennia (Gottesfeld & Rabnett, 2008). In the early 2000s, as Canadian federal investment in oil sands and natural gas extraction increased, the fossil fuel industry entered the Skeena River watershed with multiple proposed projects that threatened the watershed's critical salmon habitats. First announced in 2006, multinational companies proposed pipelines that would have transported diluted bitumen oil from interior Canada through the Skeena watershed to new terminals in coastal ports. Around the same time, proposed shale gas extraction at the headwaters of the Skeena, Nass, and Stikine rivers, a place known as the Sacred Headwaters to the area's First Nations, presented an imminent risk to the ecological health of these watersheds. First Nations and local conservation

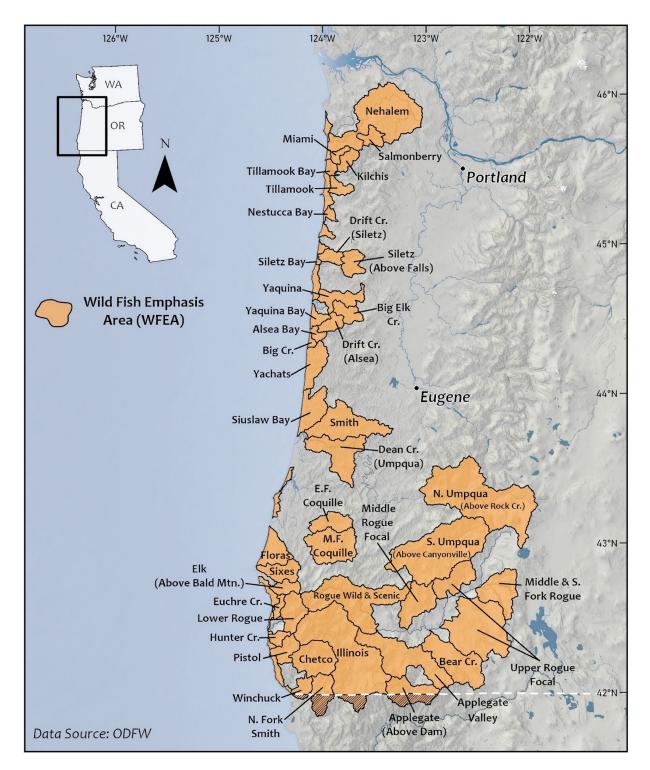


Figure 2. Designated wild fish management areas in Oregon coastal watersheds create the largest network of "wild fish only" salmon watersheds in the continental USA.

organizations in the Skeena region successfully asserted their opposition and mobilized public opinion to defeat these and multiple other industrial projects that posed serious threats to wild salmon. In the past decade, they also convinced the provincial government to reject a proposal to build an open-pit copper, gold, and molybdenum mine on the shores of Morrison Lake in the Babine River watershed, potentially jeopardizing the Skeena's largest Sockeye Salmon run (Friesen & Hontela, 2012). They also prevented a proposed liquefied natural gas terminal from being built on Lelu Island in the heart of the Skeena River estuary, one of Canada's most important wild salmon nurseries (Carr-Harris et al., 2015). This occurred despite oil and gas interests and the government offering a First Nation in the Skeena River estuary US\$1 billion to consent to construction of the controversial terminal (Moore et al., 2016). These efforts to defend the Skeena watershed are motivated by the deep historical and ongoing connection between people and salmon, rooted in a culture of reciprocity that contributes to ongoing social, cultural, and ecological resilience (Johnsen, 2009; Trosper, 2002). Financial and logistical support for the many First Nations and conservation organizations in the basin has been and will continue to be key for protecting a healthy Skeena River watershed from harmful development projects, unsustainable forestry, and other pressures into the future.

STRONGHOLD CONTRIBUTIONS TO FOOD SECURITY, BIODIVERSITY, AND CLIMATE RESILIENCE

The decline of wild salmon populations is nested within the linked global crises of biodiversity loss and climate change that threaten to disrupt nature's contributions to people (Diaz et al., 2019). A proactive approach to wild salmon conservation can secure durable protections for wild salmon ecosystems and the human communities that depend on them and has potential benefits extending well beyond the conservation of wild salmon, including contributions to global biodiversity and climate targets (Dinerstein et al., 2019) and prosperity for diverse cultures and economies that are intertwined with salmon ecosystems (Diaz et al., 2019; IPBES, 2019). As flagship species with widespread ecological, cultural, and economic value, wild salmon can rally public support for ecosystem protection and connect place-based conservation and restoration efforts to global biodiversity and climate benefits (Carrizo et al., 2017; Milner-Gulland et al., 2021). Realizing these wider benefits depends on effectively leveraging broad support for salmon conservation to advance forward looking approaches that safeguard food security, biodiversity, livelihoods, cultures, and climate resilience of ecosystems and human communities.

Food and livelihood security

Providing access to nutritious food is a global challenge, considering growing human populations and the increasing frequency of natural disasters affecting food production systems (Coughlan et al., 2014). Pacific salmon are among the planet's most important wild food systems and have provided substantial material contributions to humans for over 11,000 years, including provisioning the first Americans along Pacific coastal migration routes during the peopling of North America in the last glacial epoch (Praetorius et al., 2023; Sutton, 2017). As coastal glacial rivers stabilized and developed increased habitat complexity, the food security provided by salmon enabled relatively permanent settlements and the development of complex cultures in northeastern Asia and western North America (Cassidy, 2007; Lepofsky et al., 2005).

Indigenous and local communities continue to maintain vibrant ongoing relationships with wild salmon (Atlas et al., 2021; Molden et al., 2021). Further, commercial, recreational, and subsistence fishers of all cultural backgrounds reap immense benefits from wild salmon (Figure 3), as this group of species continues to support the harvest of hundreds of millions of fish annually (Ruggerone & Irvine, 2018). For example, salmon in Southeast Alaska support recreational, subsistence, and cultural fisheries with a combined annual economic impact of nearly \$1 billion (Clark et al., 2006). In Bristol Bay, Alaska,



Figure 3. Wild Pacific salmon contribute to global seafood markets, subsistence harvest in rural communities, and recreational and commercial fisheries. (Clockwise from upper left) Salmon sushi (iStock). Indigenous subsistence harvest in Alaska. Photo credit: Jeremy Monroe, Freshwaters Illustrated. A Skeena fly fisherman. Photo credit: Alamy. Alaska commercial fishermen. Photo credit: Perry Broderick.

the economic benefit of the world's largest Sockeye Salmon run is estimated to exceed \$2.2 billion (McKinley Research Group, 2021). Maintaining these benefits in the face of increasing human pressures, including climate change, will depend on proactive conservation and stewardship of relatively intact centers of wild salmon abundance and diversity (i.e., salmon strongholds) where biocomplexity spreads risk and enables adaptive responses and resilience to disturbance (Brennan et al., 2019; Hilborn et al., 2003; Munsch et al., 2022).

Biodiversity and 30×30 conservation goals

The proactive conservation of wild salmon strongholds also contributes to biodiversity conservation. Salmon are effective umbrella species, whose conservation confers benefits to many naturally co-occurring species across their expansive range and complex habitats (Branton & Richardson, 2014; Obester et al., 2022). Marine predators like northern resident and endangered southern resident killer whales Orcinus orca in the northeastern Pacific depend upon wild salmon (Figure 4; Ford et al., 2016), as do more than 2,000 fish eating killer whales in the Russian Far East (Filatova et al., 2019); brown bears Ursus arctos attain larger body size and higher reproductive output in locations where salmon are abundant (Bryan et al., 2013; Hilderbrand et al., 1999); and riparian tree growth is enhanced by marine derived nutrients delivered by returning salmon (Drake et al., 2002; Helfield & Naiman, 2001; but see Feddern et al., 2019). Each salmon stronghold lies within an ecoregion included in World Wildlife Fund's "Global 200"; a set of priority ecoregions that contain exceptional concentrations of species and endemics. Effective landscape-scale conservation within this diverse set of habitats would help conserve some of the most outstanding and irreplaceable biodiversity on the planet (Olson & Dinerstein, 2003). Further, nearly 70% of the strongholds' terrestrial area encompass lands identified as possessing critical



Figure 4. Pacific salmon support diverse terrestrial, aquatic, and marine consumers. (Clockwise from the top left) Alaskan brown bear with Sockeye Salmon. Photo credit: Dave McCoy. Steller's sea eagle. Photo credit: Igor Shpilenok. Bristol Bay Rainbow Trout and Sockeye Salmon eggs. Photo credit: Jason Ching. Southern resident killer whales. Photo credit: Rolf Hicker, Alamy.

biodiversity attributes, such as species rarity, distinct species assemblages, intact large mammal assemblages, habitat intactness, and climate migration corridors, but currently lack formal protections. Collectively known as the Global Safety Net, these areas are where conservation of unprotected biodiversity could be scaled to improve the resilience of ecosystems and secure terrestrial carbon stocks, both of which are essential in achieving recent climate targets (Dinerstein et al., 2019).

Slowing climate change and increasing climate resilience

The conservation of large intact landscapes, which absorb onethird of the world's carbon pollution every year, is also critical for reducing the rate of climate change (Griscom et al., 2017). Boreal forests, peatlands, and remaining intact temperature rainforests in salmon strongholds hold globally significant carbon stores, sequestering approximately 6.1 billion tons of carbon annually, equivalent to approximately 3.5 years of U.S. emissions at 2021 rates (Supplemental Material 1; Figure 5; Noon et al., 2022). Crucially, approximately 25% of this total includes ecosystem carbon at risk of being released by human activities and that would not be recovered by mid-century, when net-zero emissions need to be reached to avoid the worst climate impacts (Supplemental Material 1; Noon et al., 2022). This carbon sequestration capacity is bolstered by the ecological linkages that salmon sustain. These include marine nutrient contributions that increase riparian forest biomass and productivity (e.g., Helfield & Naiman, 2001; Kieran et al., 2021), highlighting the need to conserve ecological processes facilitated by wild salmon and other nature-based solutions as part of a holistic effort to curb climate warming. Articulating the value of protecting and restoring wild salmon strongholds as a pathway towards climate stabilization is a key opportunity and could further bolster the resources available for watershed stewardship if aligned with emerging markets for verifiable carbon sequestration.

While climate change is a global challenge requiring coordinated action among nations, resilience to climate change impacts is heavily influenced by regional and local drivers. Climate effects are attributable not only to increasing climate stress, but also to past and present local land use that influence landscape sensitivity to climate impacts (Munsch et al., 2022). For example, riparian forests, geomorphology, and other landscape features modify regional climate variation such that the environmental conditions that salmon and other organisms experience are unique to the characteristics of local habitats (Dralle et al., 2023; Griffiths et al., 2014; Sloat et al., 2017). Healthy aquatic and riparian ecosystems with intact hydrologic and floodplain functions, and connectivity across longitudinal habitat gradients can mitigate some of the negative climate impacts in freshwater (Beechie et al., 2013; Schoen et al., 2017; Sloat et al., 2017). Additionally, protection of riparian forests has been shown to substantially offset climate warming by reducing stream temperatures through shading effects (e.g., Wondzell et al., 2019). Thus, intact salmon watersheds with functional habitat forming processes provide the basis for watershed-scale climate resilience of wild salmon ecosystems and the fisheries they support (Brennan et al., 2019; Mantua & Francis, 2004).

LIMITS TO THE STRONGHOLD STRATEGY

The stronghold strategy has secured significant conservation gains, but it is not without limits. Protection of wild salmon strongholds is complicated by the highly migratory life history of Pacific salmon, with populations traversing thousands of kilometers and crossing multiple political jurisdictions during their marine migrations (Vierros et al., 2020). For this reason, freshwater habitat protections alone cannot guarantee healthy wild salmon populations, particularly given ongoing risks from mixed-stock fisheries, salmon hatcheries, and from a rapidly warming and acidifying ocean that is impacting marine food webs. These threats occur outside salmon's natal watersheds and have the potential to undermine local conservation and recovery goals (Malick et al., 2017; Ruggerone et al., 2023). In these instances, cooperation to reduce overharvest in mixedstock fisheries are needed to meet conservation objectives for many salmon populations (B. M. Connors, Staton, et al., 2020; Moore et al., 2021; Walters et al., 2008). Likewise, the negative effects of crowding and competition in the North Pacific on wild salmon growth and survival are exacerbated by record numbers of wild Pink Salmon in response to ocean climate change (Ruggerone et al., 2023). Industrial-scale salmon hatcheries in multiple nations that release billions of juvenile hatchery fish annually exacerbate ocean impacts (B. M. Connors et al., 2024). These and other anthropogenic impacts on wild salmon in the North Pacific have the potential to undermine wild salmon conservation goals. Clearly, cooperation is needed across national and subnational jurisdictions to address these issues and allow local communities to reap the benefits of ongoing investments in local salmon stewardship (B. M. Connors et al., 2024; Schindler et al., 2008).

In this regard, geopolitical issues will also add uncertainty to the implementation of the salmon stronghold strategy. No Pacific Rim-wide salmon strategy can succeed without Russia,

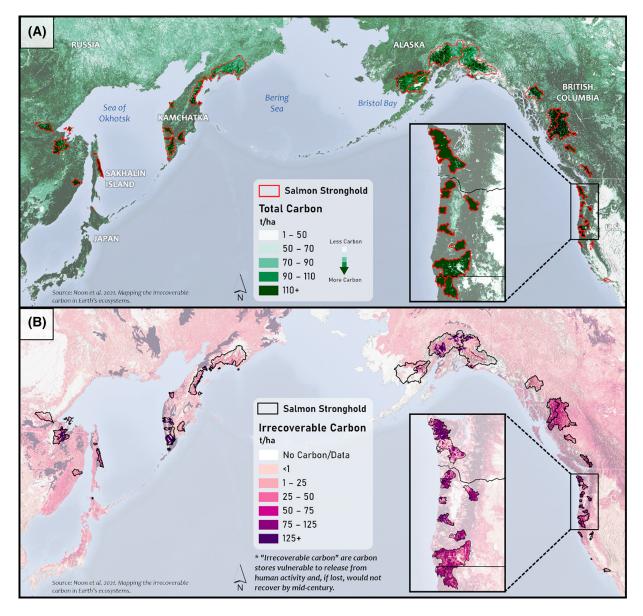


Figure 5. (A) The distribution of total carbon storage and (B) irrecoverable carbon in Pacific salmon strongholds. The Pacific salmon stronghold network sequesters approximately 6.1 billion tons of carbon annually, of which approximately 25% is carbon that is vulnerable to release from human activity and, if lost, would not be recovered by the mid-21st century.

which is home to rivers that produce roughly 40% of the worlds remaining wild salmon (Ruggerone & Irvine, 2018). The Wild Salmon Center has worked closely with Russian science and conservation leaders and government natural resource agencies for over two decades. While the deterioration of U.S.–Russia relations has put pressure on Russian conservation organizations and made it very difficult for international organizations to support Russian conservation and science efforts, most of the incountry efforts to establish new protected areas, traditional use areas and participate in wild salmon conservation management plans, including the Marine Stewardship Council, continue.

CONCLUSIONS

Salmon are a powerful symbol of watershed and community health, and for many individuals and communities, provide

one of the last real connections with natural systems. For this reason, the stronghold strategy has been effective at building on people's reverence for, and relationships with, wild salmon to secure broader ecosystem protections. The success of the strategy has also been driven in part by a willingness to make a multidecadal commitment to defending each stronghold watershed. Key to this endeavor is building the architecture of durability by layering in proactive habitat and wild fish agreements over time, while investing in the local leadership and institutional capacity to mount an immune response to future threats. Once agreements and management plans are in place to limit threats, and local communities are empowered to defend these gains, wild salmon strongholds can be considered to have reached a "durability threshold." This does not mean that the work of protecting a salmon stronghold is done, but that the major architecture for its long-term durability is in place.

This model has been effective, securing millions of hectares in new parks and reserves, thousands of stream kilometers with increased riparian forest protections, and the reform of commercial and recreational fisheries along both sides of the Pacific Rim. While the implementation of this strategy does not address all the myriad ecological challenges facing the vast North Pacific Rim, no comprehensive salmon conservation strategy will succeed without the proactive conservation of intact salmon watersheds. As we have documented, the outcomes of this approach have substantial benefits to biodiversity conservation, food security, and the health of Indigenous and local communities, the sequestration of irrecoverable carbon.

As of this writing, the global human population is projected to climb from 8 billion today to 9.7 billion by the year 2050 (UN, 2022). This will result in an escalation of impacts to salmon watersheds from the growing demands for seafood, energy, wood, clean water, agricultural products, and minerals. We expect that the growing human footprint, and natural resource dependent economies of the North Pacific Rim will put unprecedented pressure on salmon ecosystems. Watersheds that are not facing immediate threats today will likely face them within the next decade or two. History has shown that the cost of protecting these watersheds will become exponentially higher—and much more difficult—once major threats are in place. Proactive conservation of the planet's remaining centers of salmon abundance and diversity is urgently needed to maintain these species at the center of what remains a vibrant social-ecological system.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Fisheries* online.

DATA AVAILABILITY

Any data underlying this article that is not included as supplementary material will be shared on reasonable request to the corresponding author.

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None declared.

CONFLICTS OF INTEREST

This study is based entirely on publicly available data and does not involve any ethical considerations regarding human and animal subjects.

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