Fisheries Management and Ecology

WILEY

Fisheries Management and Ecology

REVIEW OPEN ACCESS

Genetic and Ecological Management of Pacific Salmon Fisheries for the 21st Century

Randall E. Brummett[1] | Ian G. Cowx[2] | Devin M. Bartley[3]

[1]Oregon Anglers Alliance, Florence, Oregon, USA | [2]Hull International Fisheries Institute, University of Hull, Hull, UK | [3]Department of Fisheries & Wildlife, Michigan State University, East Lansing, Michigan, USA

Correspondence: Randall E. Brummett (brummett.randall@yahoo.co.uk)

Received: 24 April 2025 | **Revised:** 28 February 2026 | **Accepted:** 10 March 2026

Keywords: Adaptation écologique | Approche écosystémique | Ecological adaptation | Ecosystem approach | Native salmon | Phenotypic plasticity | Plasticité phénotypique | Repeuplement | Saumon indigène | Stocking

ABSTRACT

Based on ecological adaptation theory, tremendous effort is being spent on measures that are eliminating salmon hatcheries and fishing opportunities with the intention of protecting wild runs deemed to be of particular genetic importance to the survival of the species. New research in evolutionary biology and evidence from long-term field studies do not support these policies. Natural ecosystem variability and the complex life histories of salmon argue instead for a model based on epigenetic and phenotypic plasticity coherent with neutrality theory. Under a plasticity model, hatcheries managed within the carrying capacity of recipient streams and according to best genetic and rearing practices are not predicted to represent a threat to wild salmon, consistent with observations from the field. In addition, the scale of over-fishing and habitat destruction in the 19th and 20th centuries, compounded by projected climate change, strongly suggest that closing hatcheries justified by ecological adaptation theory is likely to further undermine genetic integrity, ecosystem productivity, and economic value of salmon, and is unlikely to result in exploitable (recreational and commercial) populations as seen in the past. Fisheries research that considers a full range of evolutionary, ecological, and social considerations is more likely to inform policy that addresses diverse values associated with Pacific salmon.

RÉSUMÉ

Sur la base de la théorie de l'adaptation écologique, d'énormes efforts sont déployés pour des mesures visant à éliminer les écloseries de saumons et les opportunités de pêche, dans le but de protéger les montaisons jugées d'une importance génétique particulière pour la survie de l'espèce. De nouvelles recherches en biologie évolutive et les résultats de études de terrain sur le long terme n'étayent pas ces politiques. La variabilité naturelle des écosystèmes et les cycles de vie complexes du saumon plaident plutôt pour un modèle basé sur la plasticité épigénétique et phénotypique, cohérent avec la théorie de la neutralité. Selon un modèle de plasticité, les écloseries gérées suivant la capacité de charge des cours d'eau destinataires et les meilleures pratiques génétiques et d'élevage ne représentent pas une menace pour le saumon sauvage, conformément aux observations sur le terrain. De plus, l'ampleur de la surpêche et de la destruction des habitats aux XIXe et XXe siècles, aggravée par le changement climatique projeté, suggère fortement que la fermeture des écloseries justifiée par la théorie de l'adaptation écologique est. susceptible de saper davantage l'intégrité génétique, la productivité des écosystèmes et la valeur économique du saumon, et qu'il est. peu probable que cela aboutisse à des populations (récréatives et commerciales) exploitables comme auparavant. La recherche halieutique qui prend en compte un large éventail de considérations évolutives, écologiques et sociales est. plus susceptible d'éclairer des politiques qui traitent des diverses valeurs associées au saumon du Pacifique.

Fisheries Management and Ecology, 2026; 0:1–13
https://doi.org/10.1111/fme.70069

1 | Introduction

Stocking of fish is a widely used tool used across the world to support and enhance fish biodiversity and fisheries production (Lorenzen 2008, 2014; Lorenzen et al. 2012; Cowx et al. 2023). There is, however, much controversy over the use of stocking, not least because of the potential genetic impact of introducing hatchery-reared fish on native species (McGinnity et al. 2004; Baskett et al. 2013; Claussen and Philipp 2023). This is despite many fisheries across the globe being maintained or enhanced by stocking, for example, large–scale, culture-based fisheries in Asia (De Silva 2003; De Silva and Funge-Smith 2005) or to mitigate against environmental degradation such as supplementing Atlantic salmon populations in rivers impacted by dam development in Sweden (Eriksson and Eriksson 1993) and the Columbia River (Jaeger and Scheuerell 2023). By contrast, the perception exists among many fisheries scientists, policy makers and members of the public, for example in the Pacific Northwest for salmon (genus *Oncorhynchus*), that hatcheries are an "ecological disaster" (c.f. Taylor III 1999). Taking this to the point of having no hatchery system (c.f. Myers et al. 2004) precludes the use of an important tool in the fisheries management toolbox (Molony et al. 2005), a perspective that Harrison and Berseth (2024) argue needs to be moderated to enable appropriate use of hatcheries and adapt to "salmon futures".

In the Pacific Northwest, there is no doubt that much of the massive effort that the government put into hatcheries from the 1890s through the 1920s was wasted due to bad technology, bad biology, political interference and sabotage (see Taylor III 1999 for an extensive review). Taylor III (1999) also documented how extensive the hatchery programmes were, scattering billions of salmon eggs, fry and fingerlings throughout the state and around the world in a rather haphazard and opportunistic fashion driven by the need of officialdom to look like something was being done to address public calls for action (Leitriz 1970; Traylor 2009), exacerbated by the effort wasting issues mentioned above.

Also clear from the history of hatcheries, however, is that when done correctly and in places where salmon are able to find suitable habitat over their lifecycle (Lorenzen et al. 2012; Venditti et al. 2018; Hinrichsen and Paulsen 2020; Cowx et al. 2023), they can work to both supplement struggling runs (Bosch et al. 2007; Gray and Charleston 2011; Koch et al. 2022) and establish and maintain populations (Nuetzel et al. 2023). For example, Jones et al. (2018) found that up to 94% genetically comingled wild and hatchery coho (*Oncorhynchus kisutch*) in the Salmon River were rapidly able to establish an all-wild run. Large and economically important, naturally sustaining salmon populations based originally on hatchery fish have been established in the US Great Lakes, New Zealand, Chile and Argentina (Groot and Margolis 1991; Riva Rossi et al. 2012; Jonas 2022). Over 50,000 naturally spawned hatchery origin coho swam through the fish ladder at Willamette Falls in 2024 (ODFW (Oregon Department of Fish and Wildlife) 2024), meaning that > 4000 adult hatchery fish managed to complete their life cycle in a place where coho had not previously been recorded. Some 68% of fish caught by recreational anglers and 75% by commercial fishers in Oregon, and 65%–75% of salmon captured in Washington fisheries come from hatcheries (Table 1). There seems ample evidence that whatever hatchery origin fish may lack or have in excess, they are able to prosper in natural habitats.

Nevertheless, US hatchery programs have long come under fire for producing "inferior" fish (US Department of Commerce 1934). Although no species of salmon is in imminent danger of extinction (IUCN (International Union for the Conservation of Nature) 2025), since 1991, 28 populations (runs) of the genus *Oncorhynchus* have been listed as threatened or endangered evolutionarily significant units (ESU: A population or group of populations that is substantially reproductively isolated from other conspecific populations and that represents an important component of the evolutionary legacy of the species (Federal Register 1991)) under the Endangered Species Act (ESA; NOAA (National Oceanographic and Atmospheric Agency) 2024) with hatchery activity on these runs consequently curtailed as a precaution (Araki et al. 2007; Garcia de Leaniz et al. 2007). There are a number of studies that define any difference between wild-spawned and hatchery-spawned salmon as negative regardless of the long-term effect on run size (c.f. McMillan et al. 2023) or contribution to maintaining a specific stock (Harrison and Berseth 2024). In the literature reviewed for this and other analyses (c.f., Riddell et al. 2024), there were no documented examples of hatchery influenced salmon genetically undermining wild salmon populations such that they collapsed as predicted by, *inter alia*, Reisenbichler and McIntyre (1977), Araki et al. (2007) and Baskett et al. (2013).

Ensuring that the genetic and ecological theory driving policy is aligned with empirical data from the field is a prerequisite for successful management. Over half of the budget of the Oregon Department of Fish and Wildlife (ODFW) comes from fishing/hunting licences and commercial fishing fees (ODFW (Oregon Department of Fish and Wildlife) 2021–2023). This funding depends on state agencies managing fisheries, not just fish. A salmon fishery is an ecosystem that includes, *inter alia*, birds, insects, crayfish, trees, orcas, bears, pinnipeds, and people. The Indigenous economy modified salmon habitat through fire, timber harvesting, hunting, gathering, and agriculture while depending upon fish for their sustenance and capturing in the Columbia and Oregon coastal rivers an estimated 25,500 t of salmon, equal to 6–11 million fish out of an estimated total of 13–19 million (Schalk 1986; Meengs and Lackey 2005). The modern economy likewise interacts with and is mutually dependent upon salmon. After all the dams, irrigation, pollution,

TABLE 1 | Proportion of Catch of Hatchery Origin (Highland Economics 2022).

	Oregon	Washington
Recreational		
Freshwater Salmon/ Steelhead	68%	65%
Saltwater salmon	68%	70%
Commercial		
Salmon	75%	75%

gravel and woody debris removal, logging, mining, poldering, and draining of wetlands and rampant over-fishing, Oregon's average salmon harvest from 2015 to 2020 was only slightly over 1 million fish but still contributed half a billion dollars per annum to Oregon's economy, mostly through recreational fishing value chains (TRC (The Research Group LLC) 2021, Highland Economics 2022).

The literature contains numerous reviews of the research (e.g., McGinnity et al. (2004), Araki et al. (2008), Rand et al. (2012), Baskett et al. (2013) and Christie, Ford, and Blouin (2014)) that support the elimination or reduction of hatchery supplementation. The present analysis is not intended to review those papers again, but rather to bring to light more recent research from fisheries science and studies from evolutionary and molecular biology that question some of those studies and to help readers understand why the theory driving much of salmon hatchery management policy is not generally supported by observations from the field, and why it is necessary to reconsider the policy towards stocking, as highlighted by Harrison and Berseth (2024).

Here we address the use of hatcheries in the recovery, maintenance, and augmentation of salmonid fisheries. Specifically we examine policies calling for the cessation of hatchery supplementation and the requirement for hatcheries to match precisely the original genetic structure of salmonid populations, and propose an additional concept based on phenotypic plasticity of salmonids that would allow hatchery supplementation to rebuild and maintain viable fisheries.

2 | Ecological Adaptation Versus Plasticity

The debate over the importance of having pure-bred wild salmon in a river revolves around the concept of ecological adaptation (Galtier 2024). Here we define "pure- bred wild salmon" and similar terms to mean fish that naturally breed in rivers, streams, or lakes with no input from hatchery supplementation in any generation.

While numerous publications document genetic differences among the runs of Pacific salmon and steelhead (Smith 2014; NOAA (National Oceanographic and Atmospheric Agency) 2024; Waples et al. 2008), the selective advantage of those genetic differences is harder to determine, and neutrality theory argues that most of these differences are of limited importance to survival and fitness (Kimura 1968; Ohta 2011). Ecological adaptation happens when a set of genes and their regulation/expression machinery make a salmon run particularly well adapted to the ecology and hydrology of a specific stream. According to this model, natural selection works on the genome to remove maladaptive genes and increase the frequency of those genes that make native fish more fit (i.e., have higher reproductive success). Interbreeding with hatchery fish that are not carriers of adaptive genes would then tend to dilute the level of adaptation in resultant offspring (Tave 2024). On the evolutionary downside of ecological adaptation are as follows: (1) inbreeding in small and/or pioneering populations and, (2) environmental instability, both of which mean that if a population becomes too well adapted to a particular stream, they become vulnerable to change in the ecosystem (Hartl 1980).

While Pacific salmon have high genetic variability due to a whole genome duplication approximately 90 million years ago (Rougemont et al. 2020), environmental instability and the serial extirpation and reestablishment of runs over geological history (see below), mean that all salmon runs suffer from founder effects, reductions in overall genetic diversity resulting from the fact that, in the early years of a run, the number of spawning individuals straying into a new habitat represents only a fraction of the total genetic diversity in a species (Waples et al. 2008; Subramanian and Kumar 2023). Likewise, runs that have been reduced to an effective breeding number (Ne) of less than 150 cannot be considered to represent the pangenome of the original run (Hartl 1980). *Salmo* runs of up to 1200 fish have been shown to be dependent upon influx through straying for their persistence (Fraser et al. 2007). According to population genetics theory, it takes for salmon, at least 4000 migrating individuals with no external gene flow for a population to maintain stable genetic differentiation from a generic parental population (Altukhov et al. 2000). Once isolated, deleterious mutations accumulate (Couce et al. 2024) and null alleles (those gene variants not actively under natural selection) drift to fixation (Hughes 2008; Nei et al. 2010), reducing genetic diversity (Hartl 1980). Genes under selection that are essential to survival are conserved over many generations and maintained in the population at more or less constant frequencies (Couce et al. 2024) by epistasis (Ardell et al. 2024) or "canalization", genetically and/or epigenetically programmed molecular mechanisms that buffer the effects of environmental perturbation on genotype to maintain functional phenotypes (Takahashi 2019; Condic et al. 2024).

A number of studies have focused on the extent to which wild salmon genomes might be negatively affected by introgression of hatchery genotypes (McMillan et al. 2023; Riddell et al. 2024). An early example is Reisenbichler and McIntyre (1977) who documented differences between wild type steelhead (*Oncorhynchus mykiss*) and hatchery/wild F1 hybrids in tributaries of the Deschutes River. In their study of survival and growth of swim-up fry produced by 4–13 pairs of adults in four streams and a hatchery pond, these authors documented highly variable outcomes but managed to demonstrate overall survival of about 6% more fish per wild clutch than per hatchery clutch, and a similar difference in juvenile growth (hatchery × wild hybrids being larger). The authors note that the results were inconsistent and differences in survival and growth were more heavily influenced by stream conditions than breeding, but built a model showing what could theoretically happen to wild steelhead populations in the long term (Figure 1).

A series of studies on the Hood River has been particularly influential in shaping salmon hatchery policy in Oregon. Studying differences between hatchery and wild steelhead (*Oncorhynchus mykiss*) broodstock, Blouin (2003) found that brooders born and raised in a hatchery produce an F_1 generation that is relatively less fit than wild fish, but also showed that offspring of wild captured broodstock reared in the hatchery compare favorably with native fish, returning in equal numbers in two out of 3 years (1995–1997). A subsequent analysis of the F_2 generation (Araki et al. 2007) found wild-spawned males to be superior in 1998 (48 returning fish), wild-spawned females superior in 1999 (15 returning fish),

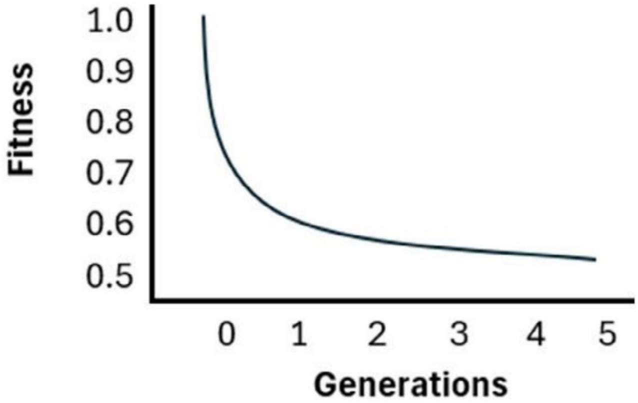

FIGURE 1 | Predicted decline in fitness from introgression of hatchery genes into wild salmon populations (after Baskett et al. 2013).

TABLE 2 | Change (Δ) in traits as a result of artificial selection in hatcheries.

Species	Selection pressure[a]	Δ per generation	References
O. mykiss	90%	+11% growth rate	Leeds et al. (2016)
O. mykiss	90%	+7% growth rate	Kause et al. (2005)
O. kisutch	90%	+15% body weight	Hershberger et al. (1990)
O. kisutch	90%	+3.5 days spawn date	Neira et al. (2006)
O. mykiss	5% (?)	−40% fitness	Araki et al. (2007)

[a] Under selection, either natural or artificial, change is driven by letting only those individuals with the desired trait reproduce. At 90%, only 10% of the fish, those having the highest percentage of beneficial genes, reproduce; at 10%, 90% of fish reproduce, conserving almost all genetic variability. Araki et al. (2007) used only one parent of hatchery origin.

and no difference in 2000 (133 returning fish). The authors estimated a fitness decline of 40% after what was effectively a half generation of hatchery influence, a much larger effect than can typically be induced by even intense artificial selection (Table 2). Incorporation of this number into an ecological adaptation model as above predicts a large and rapid collapse of the population (McGinnity et al. 2004, Baskett et al. 2013; Figure 1), prompting policy makers to curtail hatchery production and invest in trying to keep hatchery fish destined for harvest off the spawning grounds.

Following up on these studies, Courter et al. (2022) used a long-term (1992–2010) dataset of Hood River winter steelhead to show that the presence of hatchery fish had no persistent negative effect on wild fish abundance, but in most years nearly doubled the number of fish in the river (Figure 2). Likewise, Jaeger and Scheuerell (2023) studying returns on investment to hatcheries and habitat restoration in the Columbia River basin between 1970 and 2020 found that steelhead, Chinook, coho and sockeye salmon populations were significantly increasing, largely due to constant levels of stocking hatchery fish.

Hess et al. (2012) and Janowitz-Koch et al. (2019) evaluated the effects of a Chinook salmon supplementation programme in Johnson Creek, Idaho and estimated the demographic and phenotypic factors influencing fitness. Using methods similar to Araki et al. (2007), but over a much longer period (19 years: 1998–2016), these authors generated pedigrees from returning adults to determine whether origin (hatchery or natural) or phenotypic traits (timing of arrival to spawning grounds, body length, and age) significantly predicted reproductive success across multiple years. This supplementation programme with 100% natural-origin broodstock provided a long-term demographic boost to the population (mean of 4.6 times in the first generation and mean of 2.5 times in the second generation). Overall, when spawning in nature, hatchery-origin fish demonstrated a trend towards lower reproductive success compared to natural-origin fish, but when hatchery-origin fish successfully spawned with natural-origin fish, they had similar reproductive success compared to wild pairs (first-generation relative reproductive success was 1.11 for females, 1.13 for males; second-generation relative reproductive success was 1.03 for females, 1.08 for males).

Berejikian and Van Doornik (2018) conducted a 17-year before-after-control-impact experiment to determine the effects of a captive rearing program for steelhead on a key indicator of natural spawner abundance (redds). The supplemented population exhibited a significant (2.6-fold) increase in redd abundance in the generation following supplementation. Four non-supplemented control populations monitored over the same period exhibited stable or decreasing trends in redd abundance. Expected heterozygosity in the supplemented population increased significantly. Estimates of the effective number of breeders increased from a harmonic mean of 24.4 in the generation before supplementation to 38.9 during supplementation. A smaller but significant increase persisted after ending supplementation Berejikian et al. (2025).

Exploring options for the reintroduction of Chinook salmon above Cougar Dam on the McKenzie River, Dayan et al. (2024) used genetic parentage analysis to compare the reproductive success of three groups: hatchery origin fish, wild-born F_1 fish from the same hatchery and naturally spawning salmon from below the dam. F_1 offspring of naturally spawning hatchery origin fish produced nearly as many adult offspring as natural origin fish and 1.8 times more adult offspring than hatchery spawned and reared fish. Thus, a single generation in the wild increased fitness for the descendants of hatchery origin Chinook salmon to match that of natural origin fish. Another finding from this work is that the hatchery origin returning spawners were smaller than wild spawned fish, a statistic that is rarely reported, but essential to understanding the often over-riding influence of maternal over genetic effects in survival (Heath et al. 1999).

Research conducted in natural environments is expensive, long-term, and fraught with scientists' inability to control more than a few variables. Spatial and temporal fluctuations in productivity and abundance confound assessments. Consequently, studies are generally short-term, sample sizes are small, and variances large. Overall, the literature on salmon genetics and hatchery management reveals very high

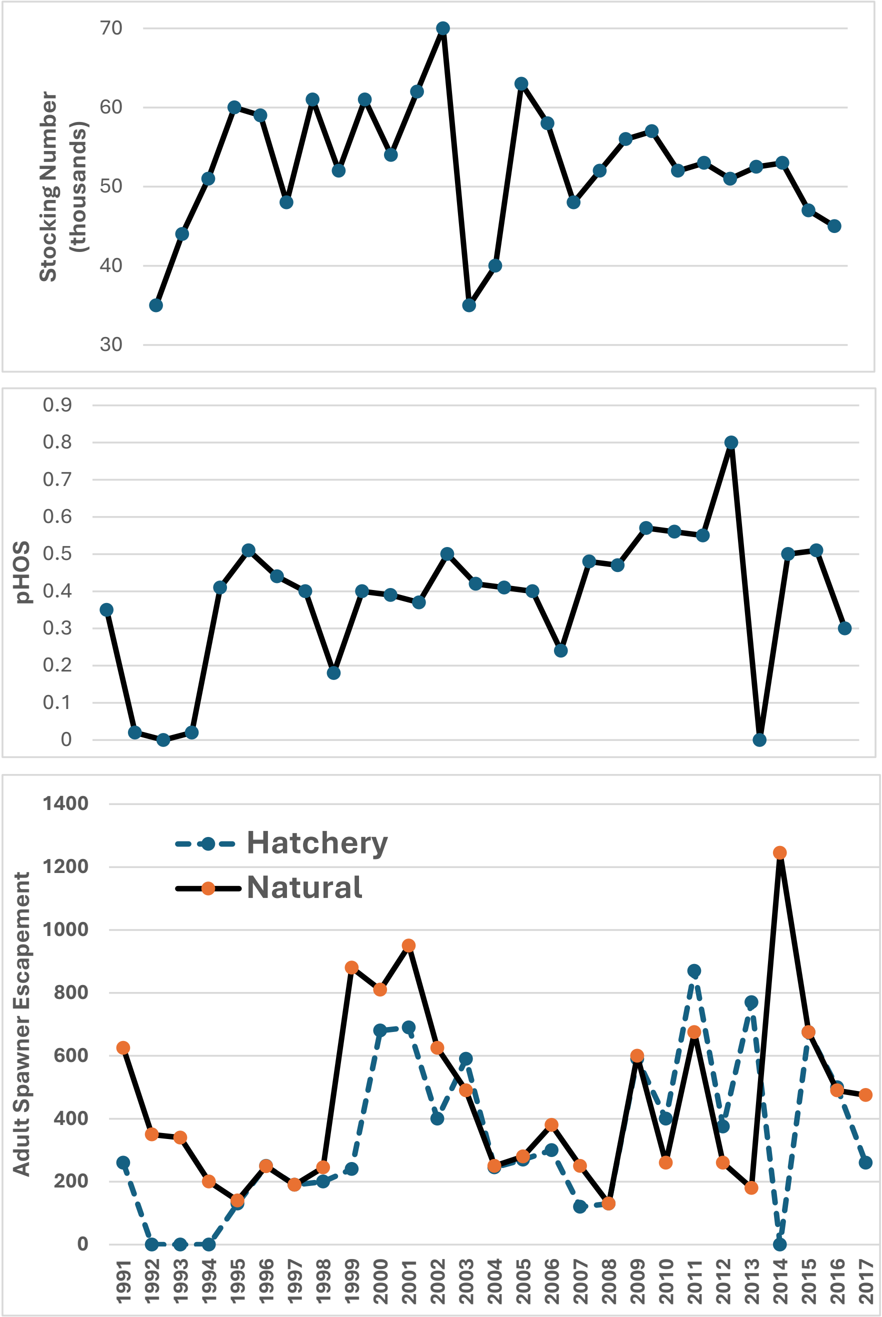

FIGURE 2 | Number of hatchery juveniles planted into the Hood River (top), percentage of hatchery origin fish on the spawning grounds (pHOS; middle) and spawner escapement of natural and hatchery-origin winter steelhead in the Hood River (bottom). Removal of the Powerdale Dam is indicated by the dashed vertical line on the lower figure. Number of wild juveniles was unknown, but releases of 40,000–70,000 hatchery juveniles had no measurable negative effect on wild run size (adapted from Courter et al. 2022, used with permission).

variability driven by instability of the ecosystems upon which salmon depend. Ocean conditions vary over decadal cycles, rivers and streams vary year to year, and regularly suffer catastrophic run failures due to such factors as droughts, fires, floods, and landslides (Leitriz 1970).

Generally speaking, genotypic changes that produce measurable differences in morphology take hundreds of generations (Vøllestad and Primmer 2019) and reproductive isolation takes hundreds of thousands of generations (Momigliano et al. 2017). That is not to say that adaptation has not occurred in Pacific salmon. There are genetic signals of adaptation to migration distance and timing (autumn vs. spring run) (Hecht et al. 2015; Thompson et al. 2019), but no studies have identified genotypes adaptive enough to create a run with characteristics that would make it particularly well-suited to a specific stream. Ford et al. (2008) found that natural selection in hatcheries and the wild was significant and similar for weight and run timing in coho, but not significant for other morphological characteristics. For Chinook, even 100 generations—about 500 years—span a period during which few, if any, riverine habitats in the Pacific Northwest have remained stable enough for long enough to foster specific adaptation (Netboy 1974). As a result of various populations being in various states of decline and recovery, one should expect to find what we see in the literature: short-term (3–5 years) studies showing more differences between hatchery and wild fish than longer term (> 15 years) studies.

The explanation generally given for inferior reproductive success of hatchery born salmon is domestication selection, release of natural selection or outbreeding depression (c.f., Araki et al. 2007). Survival in hatcheries is generally over 90%, so meaningful selection is only occurring at the point of choosing broodfish. Members of the genus *Oncorhynchus* tend to semelparity, so it is not possible to maintain broodfish under hatchery conditions. Of North American *Oncorhynchus*, only rainbow trout/steelhead (both *O. mykiss*) are completely iteroparous and able to be maintained in hatcheries, but outside of trout farming for table-fish, broodstocks of these are held at low densities and only inadvertently selected. Only iteroparous Atlantic salmon (*Salmo salar*) broodstocks have been held continuously in hatcheries and purposefully domesticated in the classic sense (c.f. Encyclopedia Britannica https://www.britannica.com/science/domestication). In semelparous *Oncorhynchus*, inadvertent selection can happen only if the runs are segregated such that broodstock are taken from returning hatchery fish where individual families from reduced numbers of broodstock are over-represented (Christie et al. 2012; Christie, French, et al. 2014), and then only at very slow rates because selection pressure is very low (Table 2). Although we have no heritability estimates for natural fry survival in salmon reported in the literature, the vast majority of early life history mortality in most species is either developmental or random (Snyder et al. 2021). Natural egg to fry mortality in Chinook and coho averages over 70% (Groot and Margolis 1991). All natural selective pressures occurring post-release affect hatchery and wild spawned fish equally, so the window over which natural selection could differentially occur is rather narrow.

The genus *Oncorhynchus* diverged from *Salvelinus* about 20 million years ago and the species we see today date from about 10 million years ago (Macqueen and Johnston 2014). Rainbow trout/steelhead diverged from a common ancestor about 10 million years ago and the Pacific salmons diverged from rainbow trout/steelhead about 5 million years after that (Macqueen and Johnston 2014). Natural selection applied over a sufficiently long period to invoke lasting genotypic changes is probably not happening to any great extent within individual runs (Rougemont et al. 2020), but mostly at the level of species and ecotype (autumn vs. spring run) (Lansing 2017; Thompson et al. 2020). The life history and, to a certain extent, size and appearance of the various salmon reflect this. Pink (*O. gorbuscha*) and chum (*O. keta*) characteristically inhabit short, steep rivers; Chinook prefer long rivers; coho are more opportunistic but are most common along medium size coastal rivers; sockeye (*O. nerka*) inhabit river systems that include lakes. Beyond this level of differentiation from the ancestral form, ecosystem variability is likely too high and too frequent for genetic variability to evolve into some alternative stable genotype.

Taken together, these observations suggest that an alternative to ecological adaptation might be at play (Araki et al. 2007 on-line supplementary materials). Rather than incrementally adapting to stable stream habitats, phenotypic plasticity (Fusco and Minelli 2010) explains how Genotype × Environment (GxE) interactions help animals instead adapt to environments that are inherently unstable, such as those in stream ecosystems of the Pacific Northwest (Hutchings 2011). In steelhead, for example, numerous genes associated with fitness were up-regulated in fish with a hatchery background (Christie et al. 2016). Rather than targeting genes that make a fish more fit under stable conditions, natural selection under a phenotypic plasticity model targets topologically associated domains that enable fish to detect environmental conditions and respond in different ways according to the situation (Vøllestad and Primmer 2019; Stankowski et al. 2024). Genetic diversity is still required for this response, and best management practices in hatcheries need to ensure this diversity (Bell et al. 2008), although perhaps not to the extent of matching the wild genotype.

Molecular, mostly epigenetic, mechanisms behind plasticity have been identified that compensate for both variable environments and small N_e resulting from population collapse or founder effects: reversable CpG DNA methylation and micro RNAs can switch genes on and off in response to environmental perturbation (Phillips 2008; Chomicki et al. 2024; Després et al. 2024; Jabbur et al. 2024; Stankowski et al. 2024; Tian et al. 2024) without the need for slow adaptation. Plasticity is common in nature: plasticity in neurons is behind memory formation and behavioural adaptation (Santoni et al. 2024; Akiki et al. 2024; Mederos et al. 2025). Under a phenotypic plasticity model, hatcheries that use best practices in the selection of broodstock and juvenile rearing (c.f. Bell et al. 2008; Lorenzen et al. 2010), including, where a genetically stable population can be found, rearing from natal river broodstock for a maximum of one generation in the hatchery (Lorenzen et al. 2012; Cowx et al. 2023), are not predicted to represent a threat to wild salmon, consistent with observations from the field.

Plasticity is neither a new nor radical idea (Gould and Eldredge 1977). Pioneering evolutionary geneticist Theodosius Dobzhansky (1937), pointed out: “One must constantly keep in mind the elementary consideration which is all too frequently lost sight of in the writings of some biologists; what is inherited in a living being is not this or that morphological character, but a definite norm of reaction to environmental stimuli.” GxE effects have been empirically demonstrated under controlled conditions in Atlantic salmon (Gonzalez et al. 2022) and among other fishes (Dunham et al. 1990). Importantly, for policy and management, plasticity is commonly reversible (Koch et al. 2023; Krabbe 2024).

3 | An Ecosystems Perspective

Many freshwater ecosystems of the Pacific Northwest are heavily dependent on salmon abundance. In mature runs, thousands of dead adult post-spawn salmon are commonly the major source of nutrients for stream ecosystems. Juvenile Chinook salmon and steelhead trout rapidly assimilate carcasses of spawned out salmon, obtaining, respectively, up to 25% and 57% of their nitrogen from carcasses (Kaylor et al. 2019). Within 3 weeks of carcass additions to streams in the upper Columbia River basin, growth rates of juvenile

Chinook and steelhead increased by 1.1–5 and 6–23 times, respectively. Increased growth rates and body size in response to carcass additions, coupled with a positive relationship between body size and survival, suggest that juvenile salmon productivity and survival are limited by depressed returns (Kaylor et al. 2019). Not just the salmon benefit from these marine nutrients; between 25% and 90% of the nitrogen in bones and fur of bears in the Columbia River Basin comes from salmon (Montgomery 2004; Kaylor et al. 2019). Riparian plant diversity is measurably influenced by the abundance of salmon leaving marine-derived nutrients behind after dying (Hocking and Reynolds 2011). In southeast Alaska, Sitka spruce growing on salmon-bearing stream banks grew 3 times faster than other spruce trees, meaning that the large logs needed to produce the best Chinook stream habitat can grow in 100 years instead of 300 (Montgomery 2004). Total prenuptial mortality of salmon averages around 97% (Groot and Margolis 1991), supporting a complex food web that includes many charismatic species such as eagles, bears, seals, and orcas. Oke et al. (2020) in a study of the climate-induced ecological impacts of reduced body length of Chinook (8.0%), coho (3.3%), chum (2.4%), and sockeye (2.1%) since 2010, estimated average per-fish reductions in nutrient transport of 28%. Salmon are what are known in ecology as a foundational species. As such, salmon habitat cannot be restored without salmon, requiring multiple years of stocking, either natural or artificial, to establish a run and explaining many failed attempts to create salmon runs outside of their native range.

Unlike the debate over the adaptive value of particular salmon genotypes, there is little argument about the futility of overstocking juvenile salmon into streams. While a short-term demographic boost is typical of hatchery supplementation, long-term establishment of wild-spawning runs depends on there being adequate spawning, nursing, growing and smolting habitat. Zabel et al. (2006) modelled climate and life history variables and identified juvenile carrying capacity as the most important variable in Chinook salmon population viability. Studying the effectiveness of conservation hatcheries on the Hood Canal (Berejikian et al. 2025) and in Idaho (Venditti et al. 2018) found that ecological limiting factors to carrying capacity across salmon lifecycles were the main constraints to increasing the number of wild-spawning salmon post supplementation by a conservation hatchery program. These ecosystems are partitioned into spawning, nursing, growing and smolting habitats, any one of which can be limiting (Venditti et al. 2018; Hinrichsen and Paulsen 2020), and are shared among a number of salmon and other species, competition among which can be bad for some or all at certain stages of their life cycle (Jones et al. 2018). Accepted ecological theory predicts that if fish populations that exceed some carrying capacity that optimises both size and abundance don't crash due to oxygen depletion, starvation or parasites, they will end up having smaller average size than usual (Bigler et al. 1996). There is no doubt that the carrying capacity of stream habitat in Oregon has been seriously eroded by poor land use management and depleted runs of nutrient-enriching salmon seed and carcasses. Given that current runs are, in the best years, still < 20% of pre-industrial salmon abundance (Hume 1893; Meengs and Lackey 2005) and spawning habitat has declined by 30%–70% (Meengs and Lackey 2005; Lichatowich 2013), it is reasonable to assume that salmon numbers in many waters could be significantly boosted if hatchery fish were available to enrich both the gene pool (Wilder et al. 2025) and the nutrient profile of salmon nursing habitats.

Closing hatcheries and thus reducing the numbers of fish in streams over some unknown number of years in hopes that they might eventually rebound would degrade the entire ecosystem for a long time, perhaps forever. If closures and regular environmental catastrophes, predicted to increase by all climate change models, reach a large enough number of adjacent streams, straying will be reduced below the 5% needed to avoid inbreeding depression and maintain genetic stability in the face of drift (Fraser et al. 2007). Without influx of new genetic diversity, populations of less than 1000–4000 migrating fish per year are likely to be in irreversible decline for both genetic and ecological reasons (McElhany et al. 2000; Fraser et al. 2007; Stokes and White 2014), and will gradually dwindle until some catastrophic environmental accident wipes them out, along with what remains of the plants, animals and home economies that depend upon them.

Stream habitats in the Pacific Northwest are not stable, and neither are salmon runs. The gravel essential to spawning success comes from bank erosion and landslides that regularly degrade spawning habitats and/or block streams for long periods. This gravel steadily moves downstream; a baseball-sized rock can move up to 7 km during heavy rains (Underwood 2012), meaning that without another landslide, a large percentage of the gravel essential for salmon spawning eventually washes out to sea. It only takes 3 years of blockage (for coho) or 5 years (for Chinook) for a run to be extirpated. The salmon need occasional landslides that can destroy salmon runs. Salmon are adapted to this Catch-22 situation.

To adapt to the wildly variable ecosystems in which they have thrived for millions of years, salmon have evolved a complex life history strategy: runs vary in timing, cohorts arrive serially on spawning beds and 1/2 to 3/4 of a salmon population is at any given time out at sea so that when some natural or manmade disaster erases the run in any particular year there is still a chance that things will work out better the following year. Under a phenotypic plasticity model, the occurrence of jacks, precociously spawning males, is an expected phenological response to abundant food and high early growth rates, which is why hatchery populations tend to produce more of them (Larsen et al. 2004). Ford et al. (2012) evaluated a large three-generation pedigree of an artificially supplemented population where hatchery fish represented 50%–80% of the spring-run Chinook that spawn in the Wenatchee River, Washington, and found that the fish with the highest reproductive success in captivity produce early maturing male offspring and that the percentage of these jacks explained observed differences in the reproductive success of wild versus hatchery fish. The evolutionary persistence of jacks, their importance in bridging spawning years within a population, the relatively high heritability of size at age, and the observation that females (for which size at age is more important to reproductive success than for males) argue for a GxE regulated phenotypic plasticity mechanism for maintaining jacks in a population (Hankin et al. 1993).

4 | Conclusions

Pacific salmon have extremely high genetic variability due to a whole genome duplication approximately 90 million years ago (Rougemont et al. 2020), making them genetically flexible and robust, designed to survive in the harsh environment of the Pacific Northwest region of the United States. If we don't completely ruin their rivers and destroy the oceans, salmon will survive and could even thrive and restore wild runs. Without help, however, that is unlikely to happen for a very long time. Stray rates for wild fish are usually in the range of 4%–10% per generation (Groot and Margolis 1991). If the habitat is intact, a depopulated stream might bounce back quickly if a strong population of salmon resides close at hand (Fraser et al. 2007). That is not the current state of affairs in many migratory salmon river systems. Under most climate change models, we are facing a future of increased habitat variability, depopulated streams deprived of spawning gravel and stripped of their nutrients by the absence of salmon, and only small populations in a similar state of disrepair within straying distance. Poor survival upstream and consequent low numbers of fish in a cohort tend to produce higher stray rates away from the natal stream (Quinn and Fresh 1984), putting small populations into a downward spiral. Hatcheries practicing best management practice could replace degraded spawning habitat so that the 'close at hand' population would be a hatchery.

Given the complex life history of salmon and the natural and anthropogenic changes to salmon habitat, there is no one-size fits all stocking programme. In Oregon, the prevailing system of managing Evolutionarily Significant Units for specific genetic diversity and supposed ecological adaptation under the ESA is neither restoring native runs nor improving fishing (Smith 2014; Ford et al. 2025), the two pillars of the Oregon Department of Fish and Wildlife (ODFW) mission. Supposedly wild runs of Pacific salmon have been listed under the ESA for decades in Oregon and elsewhere in California and the Pacific Northwest; none have been delisted (Ford et al. 2025). Although evidence for inbreeding in hatchery lines is scant (Christie, French, et al. 2014), theory predicts that the practice of basing hatchery release numbers on the Proportion of Hatchery Origin fish on the Spawning grounds (pHOS) and obliging hatcheries to only use for broodstock the descendants of hatchery fish so as to minimise gene flow is actually accentuating any minor differences between wild and hatchery genotypes (Christie et al. 2012). Discounting arguments that there are political/economic incentives to maintain ESA listing, it appears that the ecological adaptation model needs rethinking. Recent research in evolutionary biology argues that the basic assumptions that genetic purity and high levels of dependence upon adaptive genes aligned to a specific spawning location are not the dominant driver of differentiation in salmon because of their complicated life histories (Primmer 2011). Neutrality theory (Hughes 2008; Galtier 2024) challenges the assumption that speciation in salmonids is adaptive and key to survival in variable and diverse habitats. Anderson and Weir (2022) found that less than 10% of speciation in vertebrates is driven by progressive evolutionary adaptation to new environments. Similarly, Holstad et al. (2024) found variation in genetic diversity explains only 12% of among-species divergence. Data from field studies show high variability among populations and between years, which is exactly what one would expect from a group of species like Pacific salmon that are adapted to violent environmental change.

Looking forward, predicted climate change adds further complexity. Courter et al. (2022) identified ocean conditions that force many of the local impacts of climate change as the main driver of steelhead run variability on the Hood River. The Sacramento, Klamath, and South Fork of the Umpqua have all suffered increasing drought and climate variability. Thawing permafrost is contaminating Alaskan rivers with toxic levels of metal oxides (O'Donnell et al. 2024). Salmon populations with no history of such environmental conditions are unlikely to harbour adaptations to them.

Evolution is not goal oriented. Natural selection works across a maze of structural variability in both protein-coding DNA (genes) and non-coding epigenetic DNA, some of which influences how, how many, and how much genes produce. In an ecological adaptation model that assumes some ideal level of specific adaptation to a particular spawning stream, small populations are bound to end in genetic disaster unless the environment stays exactly the same as fish become increasingly inbred when isolated from external geneflow. The small clear, cool-water streams that wind through pristine forests are highly variable, short-lived ecosystems and are not presently the same as they were when salmon evolved and diversified. Research from the field of evolutionary biology suggests that, rather than a slow accumulation of adaptive genes, highly conserved phenotypic plasticity across all species and populations is an integral and essential part of the salmon genome having evolved in response to the ever-changing stream habitats that define riverine ecology in the Pacific Northwest.

Salmon are adapted to ecosystems that have never stayed the same for any appreciable length of evolutionary time. It only takes a landslide, a fire, or a big tree falling over a small stream to disrupt a run for years, and it only takes 3–5 years of closure in the cases of coho and Chinook salmon, respectively, for a population over-adapted to a particular stream to be extirpated. The current species of salmon evolved from some generic salmonid pre-genitor about 20 million years ago at the time when tapirs, rhinos, and chalicotheres were being annihilated by cascade mountain building and rivers were full of pyroclastic mud. The last major glaciation, when the rivers of Alaska, British Columbia, and Washington were frozen to their beds, ended only 20,000 years ago, but the salmon survived in refugia and then re-expanded opportunistically as the ice melted (Rougemont et al. 2020). Some species are specialists with narrow ecological niches and limited geographic ranges, while others are generalists, feeding opportunistically and able to adapt to change. Salmon appear to be an example of the latter.

The idea of a "wild" salmon genotype or wild salmon fisheries in the Anthropocene is romantic and harkens to an Edenic nature, but is largely impractical for many fisheries (Harrison and Berseth 2024). Shouldn't there be more evidence that current hatchery practices regarding genetic resource management are harming wild populations? Why has ESA designation failed to delist endangered salmon species (Ford et al. 2025)? After decades of stocking, why do salmon reviews still write about 'potential harm' and 'possible negative impacts' to wild salmon

(Islam et al. 2022; Crowley et al. 2022, NPCC (Northwest Power and Conservation Council) 2023)? Harrison and Berseth (2024) advocate for rethinking the idea of a wild genotype in the face of fluctuating environments and human-salmon interactions and focus more on how hatcheries can support broader conservation and stewardship goals. For these broader and, in our opinion better goals, numbers of salmon need to be increased and hatcheries can play a role as long as they are not constrained by unrealistic mandates to (i) create wild fish, or (ii) avoid having hatchery fish breed with wild fish. Because of the diversity of salmon fisheries, how a hatchery could meet these broader goals will depend on context and the specific fishery, as well as good science.

Much of the criticism of stocking has been based on short-term studies that perceived any genetic difference between hatchery and wild fish as harmful. Short-term studies should lead to longer-term studies and monitoring actual impacts on a population/fishery, not just changes in genotypes, especially in systems as dynamic as the Pacific Northwest of the USA. Long-term monitoring is one aspect of a precautionary approach (aka adaptive management) that is widely supported by the North Atlantic Salmon Conservation Organisation (NASCO), the Convention on Biological Diversity and other organisations. The Food and Agriculture Organisation of the United Nations (FAO) described elements of a precautionary approach that is action in the case of uncertainty and calls for the establishment of (i) reference points, that is, what is wanted, for example, an Ne of 500 for hatchery broodstock, or what is not wanted, for example, inbreeding above $F = 0.15$; (ii) pre-agreed actions when reference points are reached or breached, for example, change hatchery protocols; and (iii) monitoring to assess progress towards the agreed reference points and actions (FAO 1995). This interpretation of the precautionary approach does not mean that just because there is risk or uncertainty the action is to do nothing. Hatcheries are one tool in recovering and maintaining salmon populations. In some cases, it may be the wrong tool, but the use of hatcheries should not be prohibited based on unrealistic visions of salmon or unclear science.

In the modern world, a constituency of users is essential to the survival of species and ecosystems (Harrison and Berseth 2024). Birds overall have declined by some 29% since 1970, except for waterfowl that are actively hunted and protected by hunter-supported active management (Rosenberg et al. 2019). Globally, examples abound of ecosystems supposedly protected by exclusionary policies that have been lost or badly eroded (Barron et al. 2022). Without taxpaying and voting users, management and enforcement for wildlife is typically defunded, leaving poachers and developers free to exploit natural resources as they see fit.

Scepticism is an essential component of the scientific process. Data that contradicts the prevailing theory should lead to a re-evaluation of that theory. Based on the reasoning that: (1) evidence from actual fish counts in the field over extended periods of time does not support models built on assumptions of irremediable negative impacts of hatchery rearing, (2) the naturally high ecosystem variability and the complex life histories of salmon argue against an ecological adaptation model of evolutionary significance, and (3) phenotypic plasticity consistent with neutrality theory is increasingly supported in new theoretical and empirical research, we suggest that pathways to fishable wild salmon runs based on ecological adaptation theory are not realistic given the extent of natural ecological variability and the damage inflicted by economic development in the 20th century and projected impacts of climate change. We further assert that the science behind the current direction in salmon genetics and hatchery policy is not settled, and fisheries research needs to acknowledge this uncertainty and elaborate lines of study aimed at a new model of salmon fitness and population genetics, especially in relation to fisheries enhancement.

Funding

The authors have nothing to report.

Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors have nothing to report.

References

Akiki, R. M., R. G. Cornbrooks, K. Magami, et al. 2024. "A Long Noncoding eRNA Forms R-Loops to Shape Emotional Experience-Induced Behavioral Adaptation." *Science* 386: 1282–1289.

Altukhov, Y. P., E. A. Salmenkova, and V. T. Omelchenko. 2000. *Salmonid Fishes: Population Biology, Genetics and Management*, 354. Blackwell.

Anderson, S. A. S., and J. T. Weir. 2022. "The Role of Divergent Ecological Adaptation During Allopatric Speciation in Vertebrates." *Science* 378: 1214–1218.

Araki, H., B. A. Berejikian, M. J. Ford, and M. S. Blouin. 2008. "Fitness of Hatchery-Reared Salmonids in the Wild." *Evolutionary Applications* 1, no. 2: 342–355.

Araki, H., B. Cooper, and M. S. Blouin. 2007. "Genetic Effects of Captive Breeding Cause a Rapid, Cumulative Fitness Decline in the Wild." *Science* 318: 100–103.

Ardell, S. M., A. Martsul, M. S. Johnson, and S. Kryazhimskiy. 2024. "Environment-Independent Distribution of Mutation Effects Emerges From Microscopic Epistasis." *Science* 386: 87–92.

Barron, E. S., R. P. Chaudhary, S. Carvalho Ribeiro, et al. 2022. "Status of and Trends in the Use of Wild Species and Its Implications for Wild Species, the Environment and People." In *Thematic Assessment Report on the Sustainable Use of Wild Species*, edited by J. M. Fromentin, M. R. Emery, J. Donaldson, M. C. Danner, A. Hallosserie, and D. Kieling. IPBES Secretariat. https://doi.org/10.5281/zenodo.6451322.

Baskett, M. L., S. C. Burgess, and R. S. Waples. 2013. "Assessing Strategies to Minimize Unintended Fitness Consequences of Aquaculture on Wild Populations." *Evolutionary Applications* 6: 1090–1108.

Bell, J. D., K. M. Leber, H. L. Blankenship, N. R. Loneragan, and R. Masuda. 2008. "A New Era for Restocking: Stock Enhancement and Sea Ranching of Coastal Fisheries Resources." *Reviews in Fisheries Science* 16, no. 1–3: 1–9.

Berejikian, B. A., M. J. Malick, J. Lee-Waltermire, et al. 2025. "Conservation Hatchery Effects on the Abundance and Spawn Timing of Natural Steelhead Populations: A Replicated BACI Experiment in the Hood Canal Watershed." *Canadian Journal of Fisheries and Aquatic Sciences* 82: 1–16.

Berejikian, B. A., and D. M. Van Doornik. 2018. "Increased Natural Reproduction and Genetic Diversity One Generation After Cessation of a Steelhead Trout (*Oncorhynchus mykiss*) Conservation Hatchery Program." *PLoS One* 13, no. 1: e0190799.

Bigler, B. S., D. W. Welch, and J. H. Helle. 1996. "A Review of Size Trends Among North Pacific Salmon (*Oncorhynchus* spp.)." *Canadian Journal of Fisheries and Aquatic Sciences* 53: 455–465.

Blouin, M. S. 2003. "Relative Reproductive Success of Hatchery and Wild Steelhead in the Hood River. Bonneville Power Administration Final Project Report DOE/BP-00009245-1."

Bosch, W. J., T. H. Newsome, J. L. Dunnigan, et al. 2007. "Evaluating the Feasibility of Reestablishing a Coho Salmon Population in the Yakima River, Washington." *North American Journal of Fisheries Management* 27: 198–214.

Chomicki, G., G. Burin, L. Busta, et al. 2024. "Convergence in Carnivorous Pitcher Plants Reveals a Mechanism for Composite Trait Evolution." *Science* 383: 108–113.

Christie, M. R., M. J. Ford, and M. S. Blouin. 2014. "On the Reproductive Success of Early-Generation Hatchery Fish in the Wild." *Evolutionary Applications* 7, no. 8: 883–896. https://doi.org/10.1111/eva.12183.

Christie, M. R., R. A. French, M. L. Marine, and M. S. Blouin. 2014. "How Much Does Inbreeding Contribute to the Reduced Fitness of Hatchery-Born Steelhead (*Oncorhynchus mykiss*) in the Wild?" *Journal of Heredity* 105, no. 1: 111–119.

Christie, M. R., M. L. Marine, S. E. Fox, R. A. French, and M. S. Blouin. 2016. "A Single Generation of Domestication Heritably Alters the Expression of Hundreds of Genes." *Nature Communications* 7: 10676.

Christie, M. R., M. L. Marine, R. A. French, R. S. Waples, and M. S. Blouin. 2012. "Effective Size of a Wild Salmonid Population Is Greatly Reduced by Hatchery Supplementation." *Heredity* 109: 254–260.

Claussen, J. E., and D. P. Philipp. 2023. "Assessing the Role of Supplementation Stocking: A Perspective." *Fisheries Management and Ecology* 30: 583–591.

Condic, N., H. Amiji, D. Patel, et al. 2024. "Selection for Robust Metabolism in Domesticated Yeasts Is Driven by Adaptation to Hsp90 Stress." *Science* 385, no. 6706: 405.

Couce, A., A. Limdi, M. Magnan, et al. 2024. "Changing Fitness Effects of Mutations Through Long-Term Bacterial Evolution." *Science* 383: 383.

Courter, I. I., T. Chance, R. Gerstenberger, M. Roes, S. Gibbs, and A. Spidle. 2022. "Hatchery Propagation Did Not Reduce Natural Steelhead Productivity Relative to Habitat Conditions and Predation in a Mid-Columbia River Subbasin." *Canadian Journal of Fisheries and Aquatic Sciences* 79: 1879–1895.

Cowx, I. G., S. Funge-Smith, and A. J. Lynch. 2023. "Stocking Fish in Inland Waters: Opportunities and Risks for Sustainable Food Systems." *Fisheries Management and Ecology* 30: 555–563. https://doi.org/10.1111/fme.12656.

Crowley, S. E., I. R. Bradbury, A. M. Messmer, S. J. Duffy, S. S. Islam, and I. A. Fleming. 2022. "Common-Garden Comparison of Relative Survival and Fitness-Related Traits of Wild, Farm and Hybrid Atlantic Salmon *Salmo salar* Parr in Nature." *Aquaculture Environment Interactions* 14: 35–52. https://doi.org/10.3354/aei0042.

Dayan, D. I., N. Sard, M. A. Johnson, C. K. Fitzpatrick, R. Couture, and K. G. O'Malley. 2024. "A Single Generation in the Wild Increases Fitness for Descendants of Hatchery-Origin Chinook Salmon (*Oncorhynchus tshawytscha*)." *Evolutionary Applications* 17: e13678. https://doi.org/10.1111/eva.13678.

De Silva, S. S. 2003. "Culture-Based Fisheries: An Underutilized Opportunity in Aquaculture." *Aquaculture* 221: 221–243.

De Silva, S. S., and S. J. Funge-Smith. 2005. *A Review of Stock Enhancement Practices in the Inland Water Fisheries of Asia*. RAP Publication No. 2005/12., 93. Asia Pacific Fishery Commission.

Després, P. C., A. K. Dubé, M.-E. Picard, J. Grenier, R. Shi, and C. R. Landry. 2024. "Compensatory Mutations Potentiate Constructive Neutral Evolution by Gene Duplication." *Science* 385: 770–775.

Dobzhansky, T. 1937. *Genetics and the Origin of Species*, 364. Columbia University Press.

Dunham, R. A., R. E. Brummett, M. O. Ella, and R. O. Smitherman. 1990. "Genotype–Environment Interactions for Growth of Blue, Channel and Hybrid Catfish in Ponds and Cages at Varying Densities." *Aquaculture* 85: 143–151.

Eriksson, T., and L.-O. Eriksson. 1993. "The Status of Wild and Hatchery Propagated Swedish Salmon Stocks After 40 Years of Hatchery Releases in the Baltic Rivers." *Fisheries Research* 18: 147–159.

FAO. 1995. *Precautionary Approach to Fisheries. Part 1: Guidelines on the Precautionary Approach to Capture Fisheries and Species Introductions*. FAO Fisheries Technical Paper No. 350/1, 52. FAO.

Federal Register. 1991. Volume 226 (54); 58491–58634.

Ford, M. J., J. J. Hard, B. Boelts, E. LaHood, and J. Miller. 2008. "Estimates of Natural Selection in a Salmon Population in Captive and Natural Environments." *Conservation Biology* 22, no. 3: 783–794.

Ford, M. J., S. T. Lindley, K. A. Barnas, et al. 2025. "Abundance Trends of Pacific Salmon During a Quarter Century of ESA Protection." *Fish and Fisheries* 26: 1087–1106. https://doi.org/10.1111/faf.70019.

Ford, M. J., A. R. Murdoch, and S. R. Howard. 2012. "Early Male Maturity Explains a Negative Correlation in Reproductive Success Between Hatchery-Spawned Salmon and Their Naturally Spawning Progeny." *Conservation Letters* 5: 450–458.

Fraser, D. J., M. W. Jones, T. L. McParland, and J. A. Hutchings. 2007. "Loss of Historical Immigration and the Unsuccessful Rehabilitation of Extirpated Salmon Populations." *Conservation Genetics* 8: 527–546.

Fusco, G., and A. Minelli. 2010. "Phenotypic Plasticity in Development and Evolution: Facts and Concepts." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 365: 547–556. https://doi.org/10.1098/rstb.2009.0267.

Galtier, N. 2024. "Half a Century of Controversy: The Neutralist/Selectionist Debate in Molecular Evolution." *Genome Biology and Evolution* 16: evae003. https://doi.org/10.1093/gbe/evae003.

Garcia de Leaniz, C., I. A. Fleming, S. Einum, et al. 2007. "A Critical Review of Adaptive Genetic Variation in Atlantic Salmon: Implications for Conservation." *Biological Reviews* 82: 173–211. https://doi.org/10.1111/j.1469-185X.2006.00004.x.

Gonzalez, C., J. Gallardo-Hidalgo, and J. M. Yáñez. 2022. "Genotype-By-Environment Interaction for Growth in Seawater and Freshwater in Atlantic Salmon (*Salmo salar*)." *Aquaculture* 548: 737674. https://doi.org/10.1016/j.aquaculture.2021.737674.

Gould, S. J., and N. Eldredge. 1977. "Punctuated Equilibria: The Tempo and Mode of Evolution Reconsidered." *Paleobiology* 3, no. 2: 115–151.

Gray, P., and M. Charleston. 2011. *Swimming Against the Tide; Restoring Salmon to the Tyne*, 298. Medlar Press Ltd.

Groot, C., and L. Margolis. 1991. *Life Histories of Pacific Salmon*, 564. UBC Press.

Hankin, D. G., J. W. Nicholas, and T. W. Downey. 1993. "Evidence for Inheritance of Age of Maturity in Chinook Salmon (*Oncorhynchus* *tshawytscha*).” *Canadian Journal of Fisheries and Aquatic Sciences* 50: 347–358.

Harrison, H. L., and V. Berseth. 2024. “A Commentary on the Role of Hatcheries and Stocking Programs in Salmon Conservation and Adapting Ourselves to Less-Than-Wild Futures.” *Fish and Fisheries* 25: 750–760.

Hartl, D. 1980. *Principles of Population Genetics*, 488. Sinauer Associates.

Heath, D. D., C. W. Fox, and J. W. Heath. 1999. “Maternal Effects on Offspring Size: Variation Through Early Development of Chinook Salmon.” *Evolution* 53, no. 5: 1605–1611.

Hecht, B. C., A. P. Matala, J. E. Hess, and S. R. Narum. 2015. “Environmental Adaptation in Chinook Salmon (*Oncorhynchus tshawytscha*) Throughout Their North American Range.” *Molecular Ecology* 24, no. 22: 5573–5595.

Hershberger, W. K., J. M. Myers, R. N. Iwamoto, W. C. Mcauley, and A. M. Saxton. 1990. “Genetic Changes in the Growth of Coho Salmon (*Oncorhynchus kisutch*) in Marine Net-Pens, Produced by Ten Years of Selection.” *Aquaculture* 85: 187–197.

Hess, M. A., C. D. Rabe, J. L. Vogel, J. J. Stephenson, D. D. Nelson, and S. R. Narum. 2012. “Supportive Breeding Boosts Natural Population Abundance With Minimal Negative Impacts on Fitness of a Wild Population of Chinook Salmon.” *Molecular Ecology* 21: 5236–5550.

Highland Economics, LLC. 2022. “Economic Contribution & Value of Hatcheries in Oregon & Washington.” https://hatchery-wild-coexist.com/wp-content/uploads/2022/11/HWCEconomicStudy.pdf.

Hinrichsen, R. A., and C. M. Paulsen. 2020. “Low Carrying Capacity a Risk for Threatened Chinook Salmon.” *Ecological Modelling* 432: 109223.

Hocking, M. D., and J. D. Reynolds. 2011. “Impacts of Salmon on Riparian Plant Diversity.” *Science* 331: 1609–1612.

Holstad, A., K. L. Voje, Ø. H. Opedal, et al. 2024. “Evolvability Predicts Macroevolution Under Fluctuating Selection.” *Science* 384: 688–693.

Hughes, A. L. 2008. “Near Neutrality: Leading Edge of the Neutral Theory of Molecular Evolution.” *Annals of the New York Academy of Sciences* 1133: 162–179. https://doi.org/10.1196/annals.1438.001.

Hume, R. D. 1893. *Salmon of the Pacific Coast*, 73. Western World Publishers.

Hutchings, J. A. 2011. “Old Wine in New Bottles: Reaction Norms in Salmonid Fishes.” *Heredity* 106: 421–437.

Islam, S. S., X. Xue, A. Caballero-Solares, I. R. Bradbury, M. L. Rise, and I. A. Fleming. 2022. “Distinct Early Life Stage Gene Expression Effects of Hybridization Among European and North American Farmed and Wild Atlantic Salmon Populations.” *Molecular Ecology* 31, no. 9: 2712–2729.

IUCN (International Union for the Conservation of Nature). 2025. “IUCN Redlist of Threatened Species.” https://www.iucnredlist.org/search?query=Salmon&searchType=species.

Jabbur, M. L., B. P. Bratton, and C. H. Johnson. 2024. “Bacteria Can Anticipate the Seasons: Photoperiodism in Cyanobacteria.” *Science* 385: 1105–1111.

Jaeger, W. K., and M. D. Scheuerell. 2023. “Return(s) on Investment: Restoration Spending in the Columbia River Basin and Increased Abundance of Salmon and Steelhead.” *PLoS One* 18: e0289246. https://doi.org/10.1371/journal.pone.0289246.

Janowitz-Koch, I., C. Rabe, R. Kinzer, D. Nelson, M. A. Hess, and S. R. Narum. 2019. “Long-Term Evaluation of Fitness and Demographic Effects of a Chinook Salmon Supplementation Program.” *Evolutionary Applications* 12: 456–469. https://doi.org/10.1111/eva.12725.

Jonas, J. 2022. “Stocked and Naturalized Steelhead in Lake Michigan. NRC Meeting, Fisheries Division, Lansing, MI.” https://www.michigan.gov.

Jones, K. K., T. J. Cornwell, D. L. Bottom, S. Stein, and K. J. Anlauf-Dunn. 2018. “Population Viability Improves Following Termination of Coho Salmon Hatchery Releases.” *North American Journal of Fisheries Management* 38: 39–55.

Kause, A., O. Ritola, T. Paananen, H. Wahlroos, and E. A. Mäntysaari. 2005. “Genetic Trends in Growth, Sexual Maturity and Skeletal Deformations, and Rate of Inbreeding in a Breeding Programme for Rainbow Trout (*Oncorhynchus mykiss*).” *Aquaculture* 247: 177–187.

Kaylor, M. J., S. M. White, E. R. Sedell, and D. R. Warren. 2019. “Carcass Additions Increase Juvenile Salmonid Growth, Condition, and Size in an Interior Columbia River Basin Tributary.” *Canadian Journal of Fisheries and Aquatic Sciences* 77: 703–715. https://doi.org/10.1139/cjfas-2019-0215.

Kimura, M. 1968. “Evolutionary Rate at the Molecular Level.” *Nature* 217: 624–626.

Koch, I. J., N. M. Nuetzel, and S. R. Narum. 2023. “Epigenetic Effects Associated With Salmonid Supplementation and Domestication.” *Environmental Biology of Fishes* 106: 1093–1111.

Koch, I. J., T. R. Seamons, P. F. Galbreath, et al. 2022. “Effects of Supplementation in Upper Yakima River Chinook Salmon.” *Transactions of the American Fisheries Society* 151: 373–388. https://doi.org/10.1002/tafs.10354373.

Krabbe, S. 2024. “Epigenetic Control of Memory Formation.” *Science* 385, no. 6707: 367–368.

Lansing, W. A. 2017. *It Takes a River to Make a Fish*, 182. Bridgeview Publishing.

Larsen, D. A., B. R. Beckman, K. A. Cooper, et al. 2004. “Assessment of High Rates of Precocious Male Maturation in a Spring Chinook Salmon Supplementation Hatchery Program.” *Transactions of the American Fisheries Society* 133: 98–120.

Leeds, T., R. L. Valllejo, G. M. Weber, D. Gonzalez-Pena, and J. T. Silverstein. 2016. “Response to Five Generations of Selection for Growth Performance Traits in Rainbow Trout (*Oncorhynchus mykiss*).” *Aquaculture* 465: 341–351.

Leitriz, E. 1970. “A History of California's Fish Hatcheries 1870–1960.” In *Fish Bulletin*, vol. 150. California Department of Fish and Game.

Lichatowich, J. 2013. *Salmon, People and Place: A Biologist's Search for Salmon Recovery*, 242. Oregon State University Press.

Lorenzen, K. 2008. “Understanding and Managing Enhancement Fisheries Systems.” *Reviews in Fisheries Science* 16, no. 1–3: 10–23.

Lorenzen, K. 2014. “Understanding and Managing Enhancements: Why Fisheries Scientists Should Care.” *Journal of Fish Biology* 85: 1807–1829.

Lorenzen, K., M. C. M. Beveridge, and M. Mangel. 2012. “Cultured Fish: Integrative Biology and Management of Domestication and Interactions With Wild Fish.” *Biological Reviews* 87: 639–660.

Lorenzen, K., K. M. Leber, and H. L. Blankenship. 2010. “Responsible Approach to Marine Stock Enhancement: An Update.” *Reviews in Fisheries Science* 18: 189–210. https://doi.org/10.1080/10641262.2010.491564.

Macqueen, D. J., and I. A. Johnston. 2014. “A Well-Constrained Estimate for the Timing of the Salmonid Whole Genome Duplication Reveals Major Decoupling From Species Diversification.” *Proceedings of the Royal Society B* 281: 20132881. https://doi.org/10.1098/rspb.2013.2881.

McElhany, P., M. H. Ruckelshaus, M. J. Ford, T. C. Wainwright, and E. P. Bjorkstedt. 2000. “Viable Salmonid Populations and the Recovery of Evolutionarily Significant Units. NOAA Technical Memorandum NMFS-NWFSC-42.”

McGinnity, P., P. Prodöhl, N. Ó. Maoiléidigh, et al. 2004. “Differential Lifetime Success and Performance of Native and Non-Native Atlantic Salmon Examined Under Communal Natural Conditions.” *Journal of Fish Biology* 65, no. Suppl. A: 173–187.

McMillan, J. R., B. Morrison, N. Chambers, et al. 2023. “A Global Synthesis of Peer-Reviewed Research on the Effects of Hatchery Salmonids on Wild Salmonids.” *Fisheries Management and Ecology* 30: 1–18. https://doi.org/10.1111/fme.12643.

Mederos, S., P. Blakely, N. Vissers, C. Clopath, and S. B. Hofer. 2025. “Overwriting an Instinct: Visual Cortex Instructs Learning to Suppress Fear Responses.” *Science* 387: 682–688.

Meengs, C. C., and R. T. Lackey. 2005. “Estimating the Size of Historical Oregon Salmon Runs.” *Reviews in Fisheries Science* 13: 51–66.

Molony, B. W., R. Lenanton, G. Jackson, and J. Norriss. 2005. “Stock Enhancement as a Fisheries Management Tool.” *Reviews in Fish Biology and Fisheries* 13: 409–432.

Momigliano, P., H. Jokinen, A. Fraimout, A.-B. Florin, A. Norkko, and J. Merilä. 2017. “Extraordinarily Rapid Speciation in a Marine Fish.” *Proceedings of the National Academy of Sciences* 114: 6074–6079. https://doi.org/10.1073/pnas.1615109114.

Montgomery, D. R. 2004. *King of Fish: The Thousand-Year Run of Salmon*, 290. Basic Books.

Myers, R. A., S. A. Levin, R. Lande, F. C. James, W. W. Murdoch, and R. T. Paine. 2004. “Hatcheries and Endangered Salmon.” *Science* 303: 1980.

Nei, M., Y. Suzuki, and M. Nozawa. 2010. “The Neutral Theory of Molecular Evolution in the Genomic Era.” *Annual Review of Genomics and Human Genetics* 11: 265–289. https://doi.org/10.1146/annurev-genom-082908-150129.

Neira, R., F. N. Díaz, G. A. E. Gal, J. A. Gallardo, J. P. Lhorente, and R. Manterola. 2006. “Genetic Improvement in Coho Salmon (*Oncorhynchus kisutch*). I: Selection Response and Inbreeding Depression on Harvest Weight.” *Aquaculture* 257: 9–17.

Netboy, A. 1974. *Salmon; Their Fight for Survival*, 613. Houghton Mifflin.

NOAA (National Oceanographic and Atmospheric Agency). 2024. “Pacific Salmon and Steelhead: ESA Protected Species.” Accessed 2 Nov 2024. https://www.fisheries.noaa.gov/national/endangered-species-conservation/delisting-species-under-endangered-species-act.

NPCC (Northwest Power and Conservation Council). 2023. “ISRP Review of the Lower Snake River Compensation Plan Spring/Summer Chinook Program, 2022–2023. Council Document Number: ISRP 2023–1.” https://www.nwcouncil.org/reports/isrp2023-01/.

Nuetzel, H. M., P. F. Galbreath, B. A. Staton, C. A. Crump, L. M. Naylor, and G. E. Shippentower. 2023. “Improved Productivity of Naturalized Spring Chinook Salmon Following Reintroduction From a Hatchery Stock in Lookingglass Creek, Oregon.” *Canadian Journal of Fisheries and Aquatic Sciences* 80: 375–392. https://doi.org/10.1139/cjfas-2022-0110.

ODFW (Oregon Department of Fish and Wildlife). 2021–2023. “Biennium Governor's Recommended Budget.” https://www.dfw.state.or.us/agency/budget/docs/21-23_GRB/_Complete%202021-2023%20Governors%20Recommended%20Budget.pdf.

ODFW (Oregon Department of Fish and Wildlife). 2024. “Willamette Falls Fish Counts.” https://myodfw.com/willamette-falls-fish-counts.

O'Donnell, J. A., M. P. Carey, J. C. Koch, et al. 2024. “Metal Mobilization From Thawing Permafrost to Aquatic Ecosystems Is Driving Rusting of Arctic Streams.” *Communications Earth & Environment* 5: 268.

Ohta, T. 2011. “Near-Neutrality, Robustness, and Epigenetics.” *Genome Biology and Evolution* 3: 1034–1038.

Oke, K. B., C. J. Cunningham, P. A. H. Westley, et al. 2020. “Recent Declines in Salmon Body Size Impact Ecosystems and Fisheries.” *Nature Communications* 11: 4155. https://doi.org/10.1038/s41467-020-17726-z.

Phillips, T. 2008. “The Role of Methylation in Gene Expression.” *Nature Education* 1, no. 1: 116.

Primmer, C. R. 2011. “Genetics of Local Adaptation in Salmonid Fishes.” *Heredity* 106: 401–403.

Quinn, T. P., and K. Fresh. 1984. “Homing and Straying in Chinook Salmon (*Oncorhynchus tshawytscha*) From Cowlitz River Hatchery, Washington.” *Canadian Journal of Fisheries and Aquatic Sciences* 41: 1078–1082.

Rand, P. S., B. A. Berejikian, A. Bidlack, et al. 2012. “Ecological Interactions Between Wild and Hatchery Salmonids and Key Recommendations for Research and Management Actions in Selected Regions of the North Pacific.” *Environmental Biology of Fishes* 94: 343–358.

Reisenbichler, R. R., and J. D. McIntyre. 1977. “Genetic Differences in Growth and Survival of Juvenile Hatchery and Wild Steelhead Trout (*Salmo Gairdneri*).” *Journal of the Fisheries Research Board of Canada* 34, no. 1: 123–128.

Riddell, B. E., I. Pearsall, and A. Rosenberger. 2024. “A Review of Pacific Salmon Hatcheries in British Columbia, Canada, and Interactions With Wild Populations.” *Fisheries* 49: 303–318.

Riva Rossi, C. M., M. A. Pascual, E. Aedo Marchant, et al. 2012. “The Invasion of Patagonia by Chinook Salmon (*Oncorhynchus tshawytscha*): Inferences From Mitochondrial DNA Patterns.” *Genetica* 140: 439–453. https://doi.org/10.1007/s10709-012-9692-3.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, et al. 2019. “Decline of the North American Avifauna.” *Science* 366: 120–124.

Rougemont, Q., J.-S. Moore, T. Leroy, et al. 2020. “Demographic History Shaped Geographical Patterns of Deleterious Mutation Load in a Broadly Distributed Pacific Salmon.” *PLoS Genetics* 16: e1008348.

Santoni, G., S. Astori, M. Lelleu, et al. 2024. “Chromatin Plasticity Predetermines Neuronal Eligibility for Memory Trace Formation.” *Science* 385: 408.

Schalk, R. F. 1986. “Estimating Salmon and Steelhead Usage in the Columbia Basin Before 1850: The Anthropological Perspective.” *Northwest Environmental Journal* 2: 1–29.

Smith, C. 2014. *Salmon Abundance and Diversity in Oregon; Are We Making Progress?* Oregon State University.

Snyder, R. E., S. P. Ellner, and G. Hooker. 2021. “Time and Chance: Using Age Partitioning to Understand How Luck Drives Variation in Reproductive Success.” *American Naturalist* 197: E110–E128.

Stankowski, S., Z. B. Zagrodzka, M. D. Garlovsky, et al. 2024. “The Genetic Basis of a Recent Transition to Live-Bearing in Marine Snails.” *Science* 383: 114–119.

Stokes, M. D., and D. White. 2014. *The Fish in the Forest: Salmon and the Web of Life*, 159. University of California Press.

Subramanian, S., and M. Kumar. 2023. “Genomic Footprints of Bottleneck in Landlocked Salmon Population.” *Scientific Reports* 13: 6706. https://doi.org/10.1038/s41598-023-34076-0.

Takahashi, K. H. 2019. “Multiple Modes of Canalization: Links Between Genetic, Environmental Canalizations and Developmental Stability, and Their Trait Specificity.” *Seminars in Cell & Developmental Biology* 88: 14–20.

Tave, D. 2024. *Conservation Aquaculture: An Evolution-Based Approach for the Production of Fish for Aquaculture-Assisted Fisheries Programs*, 167. Springer International Publishing.

Taylor, J. E., III. 1999. *Making Salmon: An Environmental History of the Northwest Salmon Crisis*, 421. University of Washington Press.

Thompson, N. F., E. C. Anderson, A. J. Clemento, et al. 2020. “A Complex Phenotype in Salmon Controlled by a Simple Change in Migratory Timing.” *Science* 370: 609–613.

Thompson, T. Q., M. R. Bellinger, S. M. O'Rourke, et al. 2019. “Anthropogenic Habitat Alteration Leads to Rapid Loss of Adaptive

Variation and Restoration Potential in Wild Salmon Populations." *Proceedings of the National Academy of Sciences* 116: 177–186.

Tian, S., Y. Asano, T. D. Banejee, et al. 2024. "A microRNA Is the Effector Gene of a Classic Evolutionary Hotspot Locus." *Science* 386: 1135–1140.

Traylor, E. 2009. *A Bridge Back; the Early Days of Florence, Oregon*, 110. Port Hole Publications.

TRC (The Research Group LLC). 2021. "Oregon Commercial and Recreational Fishing Industry Economic Activity Coastwide and in Proximity to Marine Reserve Sites for Years 2018 and 2019, Technical Report. Oregon Department of Fish and Wildlife, Marine Reserve Program and Marine Resource Program." (76 pp).

Underwood, E. 2012. "How to Build a Smarter Rock." *Science* 338, no. 6113: 1412–1413.

US Department of Commerce. 1934. *Report of the Commissioner of Fisheries*, 484. Government Printing Office.

Venditti, D. A., R. N. Kinzer, K. A. Apperson, et al. 2018. "Effects of Hatchery Supplementation on Abundance and Productivity of Natural-Origin Chinook Salmon." *Canadian Journal of Fisheries and Aquatic Sciences* 75, no. 9: 1495–1510.

Vøllestad, L. A., and C. R. Primmer. 2019. "Understanding Local Adaptation in a Freshwater Salmonid Fish: Evolution of a Research Programme." *ICES Journal of Marine Science* 76, no. 6: 1404–1414.

Waples, R. S., G. R. Pess, and T. Beechie. 2008. "Evolutionary History of Pacific Salmon in Dynamic Environments." *Evolutionary Applications* 1: 189–206.

Wilder, A. P., D. M. Shier, S. N. D. King, et al. 2025. "Fitness Benefits of Genetic Rescue Despite Chromosomal Differences in an Endangered Pocket Mouse." *Science* 389, no. 6762: 835–839.

Zabel, R. W., M. D. Scheuerell, M. M. McClure, and J. G. Williams. 2006. "The Interplay Between Climate Variability and Density Dependence in the Population Viability of Chinook Salmon." *Conservation Biology* 20, no. 1: 190–200.