On Hatcheries and Wild Salmon[1]

Summary

Anadromous salmonid fisheries add over $500 million to Oregon's economy each year on runs that average about 10% of historical levels. ODFW is charged with managing this resource for the benefit of present and future generations, presumably with the intention of returning harvest to something approaching historical potential. Instead, tremendous effort is being spent on measures that are actually reducing fish numbers and fisheries in an effort to protect wild runs deemed to be of particular genetic importance. Despite over 40 years of these efforts, salmon populations are not rebounding as predicted. Public opinion and lawyers have been enlisted to blame hatcheries for this failure based on adaptive gene theory, which predicts declining reproductive success when populations adapted to a particular river system are mixed with fish subjected to domestication selection in hatchery supplementation programs. In reality, salmon originating from hatcheries are successfully establishing self-sustaining runs in rivers where historical runs have been extirpated and elsewhere around the world. At the population level, there is scant evidence that removing hatcheries does anything other than reduce fish density. New biology suggests that, rather than 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 early in response to the ever-changing stream habitats that define riverine ecology in this region. Under a phenotypic plasticity model, hatcheries are not predicted to represent a threat to wild salmon, consistent with observations from the field. To be successful, salmon management policy needs to better integrate empirical data, ecology and up-to-date biology or risk losing the important fisheries economy while gaining little in terms of biodiversity.

Introduction

The reputation that salmon hatcheries in the Pacific Northwest have earned in the public mind as an "ecological disaster" (c.f. Taytor III, 1999) is unjustified, and 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.

There is no doubt that much of the massive effort that the government put into hatcheries in the 1930s, '40s and '50s 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 were the hatchery programs in Oregon, scattering billions of salmon smolts throughout the state and around the world in a rather haphazard and opportunistic fashion largely necessitated by getting a late start on the problem (major issues with salmon were publicly recognized as early as 1852; Leitritz 1970, Traylor 2009) compounded by the effort wasting issues mentioned above.

Also clear from the history of hatcheries is that when done correctly and in places where salmon are able to find suitable habitat, they work to both supplement existing runs (Koch et al. 2022) and establish new runs. Large and economically important, naturally sustaining salmon populations based on hatchery fish have been established in the US Great Lakes, New Zealand, Chile and Argentina (Groot & Margolis 1991, Riva-Rossi et al. 2012, Jonas 2022). Some 68% of fish caught by recreational anglers and 75% of commercial fishers in Oregon and 65-75% of salmon captured in Washington fisheries come from hatcheries (Highland Economics 2022).

Proportion of Catch of Hatchery Origin[2]		
Recreational	Oregon	Washington
Freshwater Salmon/Steelhead	68%	65%
Saltwater salmon	68%	70%
Commercial		
Salmon	75%	75%

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[1] Randall Brummett, Jim Muck, Jim Pex, Lyle Curtis, Reese Bender & Joe Watkins.

[2] Highland Economics' (2022) analysis of sport angler catch card raw data provided by Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife.

Note that the public is paying[3] our state agencies to manage fisheries, not just fish. A salmon fishery is an ecosystem that includes birds, insects, 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 an estimated 42 million pounds of salmon, some 50% of the runs[4]. The modern economy likewise interacts with and is mutually dependent upon salmon. Maybe less so, tragically less so[5], than before the dams, irrigation, pollution, gravel and woody debris removal, logging, mining, poldering and draining of wetlands and rampant over-fishing, the impacts of which continue in some form to this day, but still contributing half a billion dollars per annum to Oregon's economy.

Based to a large extent upon a fishing ethos described by transcendentalist author Henry David Thoreau and the Hudson River School (of landscape artists) in the 1800's, US hatchery programs have long come under fire from wild fish purists for producing "inferior" fish (US Department of Commerce 1934). Since 1967, under pressure from wild fish advocacy lawyers, 43 salmon and trout populations (no species of salmonid is in danger of extinction) have been listed as threatened or endangered under the Endangered Species Act with hatchery activity on these runs consequently curtailed; only one has been delisted, and that was due to a taxonomic revision rather than improvement in stock status.

This review and analysis is intended to help readers understand why the theory driving Oregon's salmon hatchery management policy is not generally reflected in observations from the field, and propose some actions that could help managers avoid the pitfalls of the past so as to enjoy a greater bounty of salmon in the future.

Population Genetics

The debate over the importance of having a particular type of salmon in a river revolves around the concept of adaptive gene complexes. An adaptive gene complex is a set of genes and their expression machinery that makes a salmon run particularly well adapted to the ecology and hydrology of a specific stream. 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). Under this model, interbreeding with hatchery fish that are not carriers of adaptive genes would tend to dilute the level of adaptation in resultant offspring. On the downside of adaptive gene complexes are: 1) inbreeding and, 2) environmental instability, both of which mean that if a population becomes too well adapted to a particular stream, they can become vulnerable to change in the ecosystem. According to population genetics theory, it takes at least 4,000 breeding individuals (~20,000 fish in the case of salmon) at least 40 generations (200 years for chinook, *Oncorhynchus tshawytscha*) with no external gene flow for a population of any organism to achieve measurable differentiation from a generic parental population (Altukov et al. 2000). Over this period of isolation, null alleles (those genes not actively under natural selection) will drift to fixation, reducing genetic diversity (Hart 1980). Genes under selection that are essential to survival are conserved over many generations and maintained in the population by epistasis at more or less constant frequencies (Couce et al. 2024).

A number of studies have focused on the extent to which wild salmon genomes can be negatively affected by introgression of hatchery genotypes. An early and typical example is Reisenbichler & 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 in four streams and a hatchery pond, these authors documented highly variable outcomes, but managed to demonstrate survival of 10 more fish per wild clutch than per hatchery clutch (out of an average of 329), and a 1 mm difference in growth (hatchery x wild hybrids being larger). The authors concede that the results were inconsistent and differences in survival and growth were not clear, but proceeded anyway to build a

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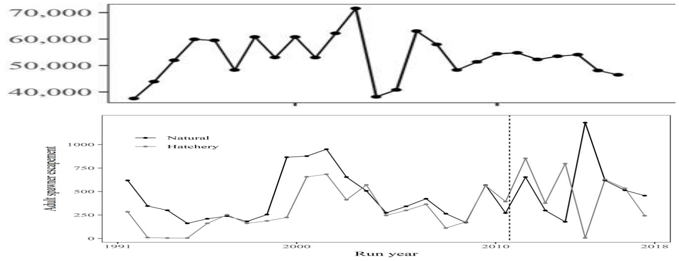
[3] Approximately half of ODFW's budget comes from fishing and hunting licenses and commercial fishing fees (https://www.dfw.state.or.us/agency/budget/docs/21-23_LAB/E.%20Revenues.pdf).

[4] Equal to 4.5-6.3 million fish out of an estimated total of 11-16 million (Taytor III, 1999, page 23, citing work from Randall Schalk and Robert Boyd in the late 1980's).

[5] Oregon's commercial salmon harvest in 2019 was only 1.2 million pounds according to TRC (2021).

hypothetical model to show what could theoretically happen to wild steelhead populations in the long term. Sampling error resulting from small broodstock numbers (4-13 pairs of adults) alone is more than enough to account for the minor differences measured.

A series of studies on the Hood River has been influential in shaping salmon hatchery policy. Studying differences between hatchery and wild steelhead (*Oncorhynchus mykiss*) broodstock, Blouin (2003) found that brooders domesticated over numerous generations in the hatchery produce an F_1 generation that is relatively less "fit" than wild fish, but also showed that offspring of wild captured broodstock compare favorably with native fish, out-competing them in two out of three 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) and no difference in 2000 (133 returning fish).



Number of hatchery juveniles planted into the Hood River (top) 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 (from Courter et al. 2022).

The winter run of wild steelhead in the Hood River averages around 500 fish (figure right, lower graph). Given that the documented number of effective breeders in wild salmonid populations rarely exceeds 20% of mature returning fish (Altukhov et al. 2000) and in the available empirical literature is much lower: Bartley et al (1992) (4.3%); Altukov et al. 2000 (3.6%), the likely number of fish actually contributing to subsequent generations is well under 100 fish, a value not large enough to contain the genetic diversity needed to say that the wild fish in this run are anything special or better adapted to the particular stream ecology than any other stock (McElhany et al. 2000). A recent review of Hood River winter steelhead by Courter et al. (2022) used a long-term (1992-2010) dataset to show that the presence of hatchery fish had no negative effect on wild fish abundance, but in most years nearly doubled the number of fish in the river. Based on the findings of Araki et al. (2007) and subsequent work, hatchery stocking of winter steelhead was stopped in 2021, along with the fishing (except for some residuals).

Similar findings were reported by Janowitz-Koch et al. (2019) and Hess et al. (2012) who evaluated the effects of a Chinook Salmon supplementation program 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), 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 program with 100% natural-origin broodstock provided a long-term demographic boost to the population (mean of 4.56 times in the first generation and mean of 2.52 times in the second generation). Overall, when spawning in nature, hatchery-origin fish demonstrated a trend toward 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 & 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 17-year period exhibited stable or decreasing trends in redd abundance. Expected heterozygosity in the supplemented population increased significantly. Allelic richness increased, but to a lesser (non-significant) degree. Estimates of the effective number of breeders increased from a harmonic mean of 24.4 in the generation before supplementation to 38.9 after supplementation.

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 standard deviations are large. Overall, the literature on salmon genetics and hatchery management reveals very high 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 can suffer catastrophic run failures due to drought, fire, floods, landslides, etc.[6] Although there is no reported study that identifies adaptive gene complexes in salmon, Rougement et al. (2022) found single nucleotide polymorphisms related to spawning migration distance that have evolved over the last 20,000 years. Vøllestad & Primmer (2019) documented small differences in grayling (*Thymallus thymallus*) populations isolated in stable conditions for 30 generations that might eventually evolve to be adaptive. No studies have identified gene complexes adaptive enough to create a run with characteristics that would make it particularly well-suited to a particular stream. For chinook, 30 generations is 150 years, over which time in Oregon's recent past few if any riverine habitats have been stable. 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.

Taken together, these findings suggest that an alternative to adaptive gene complexes might be at play. Rather than incrementally adapting to stable stream habitats, the theory of phenotypic plasticity (Fusco & Minelli 2010) describes how Genotype x 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). 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 & Primmer 2019, Stankowski et al. 2024). Willoughby et al. (2018) and Sparks et al. (2023) studying the naturalization of hatchery steelhead in the Great Lakes identified such mechanisms, allowing these fish to overcome low genetic diversity in founding populations. The phenomenon of "jacking" is further evidence for GxE in Pacific salmon (see below) and GxE effects have been demonstrated under controlled conditions in Atlantic salmon (Gonzalez et al. 2022) among other species (Dunham et al. 1990).

Authors focused on advising management are often tempted to jump to conclusions justified by the "precautionary principle" (i.e., if hatchery fish are a problem, then getting rid of them is good, and even if they are not a problem then removing them doesn't hurt anyone and keeping them isn't worth the risk; c.f. Araki et al. (2007)4 online supporting material). Instead of seeking to understand how the extremely complicated life history of salmonids actually works, a considerable amount of salmon research and, subsequent management policy seems to be driven by the felt need to find something to blame for the continuing demise of salmon that doesn't involve a major change in lifestyle for urban populations (Lackey 2000). Rather than science and economics, much of the public opposition to hatcheries seems to derive from a romantic notion of prehistoric nature (Taylor III 1999) that attributes spiritual superiority to wild fish (c.f., House 1999, Lichatowich 2013).

An Ecosystems Perspective

The freshwater ecosystems of this state are heavily dependent on salmon abundance. 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). And it is

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[6] See Leitritz (1970) for a stream-by-stream review of the California experience with ecosystem variability.

not just the salmon that benefit from these marine nutrients. Between 25 and 90% of the nitrogen in bones and fur of bears in the Columbia River Basin come 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 & Reynolds 2011). In SE 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 & Margolis 1991) supporting a complex food web that includes many charismatic species such as eagles, bears, seals and orcas. Our coastal ecosystems need salmon and it doesn't matter in the least whether these are hatchery or wild fish. Oke et al. (2020) in a study of the ecological impacts of reduced size of migrating chinook salmon since 2010 estimated average per-fish reductions in egg production (−16%), nutrient transport (−28%), fisheries value (−21%), and meals for rural people (−26%).

Unlike the debate over the adaptive value of particular salmon genotypes, there is little argument about the futility of over-stocking juvenile salmon into streams. These ecosystems are partitioned among a number of salmon and other species. Too many of any particular species can be bad for some or all of these at certain stages of their life cycle. Accepted ecological theory predicts that if fish populations that exceed some carrying capacity that optimizes both size and abundance don't crash due to oxygen depletion 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. However, given that current runs are, in the best years, still <20% of pre-industrial salmon abundance (Hume 1893, Meengs & Lackey 2005) and spawning habitat has declined by 40% (Taylor III 1999, Lichatowich 2013), it is reasonable to assume that salmon carrying capacity could be significantly boosted if hatchery fish were available to enrich both the gene pool and the nutrient profile of salmon nursing habitats.

What is being discounted by those who would close all hatcheries and thus reduce the numbers of fish in streams over some unknown number of years in hopes that they might eventually rebound is that the entire ecosystem would be damaged for a long time, perhaps forever. If closures and regular environmental catastrophes 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, Stokes & 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 PNW are not stable and neither are salmon runs. The gravel essential to spawning success comes from landslides that regularly block streams for a period of years. This gravel moves down stream; a baseball sized rock can move up to 7 km during heavy rains (Underwood 2012), meaning that without another landslide, all the gravel essential for salmon spawning eventually washes out to sea. The salmon need landslides that destroy salmon runs. Salmon are adapted to this Catch-22 situation.

These stream ecosystems interact with the life-history and genetics of fish (Koch et al. 2022). To adapt to the wildly variable ecosystems in which they have thrived for millions of years, 2/3 to 3/4 of a salmon population is at any given time, out at sea so that when a landslide dams up their natal stream and erases the run this year, there is still a chance that things will work out better next year. Under a phenotypic plasticity model, the occurrence of jacks is an expected phenological response to abundant food and high early growth rates, which is why hatchery populations tend to produce more of them (Larson et al. 2004). Ford et al. (2012) evaluated a large three-generation pedigree of an artificially supplemented population[7] of 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 vs hatchery fish. The

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[7] The hatchery program produced ∼50%–80% of the individuals spawning naturally in the river each year.

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).

Conclusions

Review of the literature indicates that salmon are tough and designed to survive in the harsh environment of the PNW. Over 40,000 naturally spawned non-indigenous coho salmon (*Oncorhynchus kisutch*) swam through the fish ladder at Willamette Falls in 2023 (ODFW 2023), meaning that some 3500 adult hatchery fish managed to complete their life cycle in a totally new environment. If we don't completely ruin their rivers and destroy the oceans, salmon will survive and could even thrive and restore totally wild runs. Without help, however, that isn't going to happen for a very long time. Stray rates for wild fish are usually in the range of 4-10% per generation (Groot & Margolis 1991). If the habitat is intact, a depopulated stream might bounce back quickly if a strong population of salmon resides close at hand. That is not the current state of affairs. What we are facing is a future of depopulated streams that have been deprived of spawning beds and stripped of their nutrients by the absence of salmon and only small populations in a similar state of disrepair are 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 (Groot & Margolis 1991), putting small populations into a death spiral.

The prevailing system of managing "evolutionarily significant units" for specific genetic diversity and adaptive gene complexes under the Endangered Species Act (ESA) is not restoring native runs or improving fishing (Smith 2014), the two pillars of the Oregon Department of Fish and Wildlife (ODFW) mission. Runs have been listed for decades with no sign of improvement. The practice of basing hatchery release numbers on the Proportion of Hatchery Origin fish on the Spawning grounds (pHOS) so as to minimize gene flow is actually accentuating any minor differences between wild and hatchery genotypes. Discounting arguments that there are political/economic incentives to maintain ESA listing, it appears that something is wrong with the model. We think it's unlikely to work because the basic assumptions that genetic purity and high levels of dependence upon adaptive gene complexes aligned to a specific spawning location are not the dominant driver of differentiation in salmon because of their complicated life histories (Primmer 2011). In fact, the basic biology behind the assumption that speciation in salmonids is adaptive and key to survival in variable and diverse habitats has recently been challenged by Anderson & Weir (2022) who found that the vast majority of speciation in vertebrates is driven by genetic drift rather than evolutionary adaptation. What the data from field studies show is high variability among populations and between years, which is exactly what one would expect from a group of species, almost a "species flock", like salmon, that are adapted to violent environmental change.

Evolution is not goal oriented. Natural selection works across a maze of structural variability in both protein-coding DNA (codons) and non-coding epigenetic DNA that influences how, how many, and how much codons produce. In the "adapted allele" 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 streams that wind through pristine forests are highly variable, short lived ecosystems and anyway are not presently the same as they were when salmon evolved and diversified. The way nature deals with this problem is through phenotypic plasticity[8], driven by disruptive natural selection and enabled by variability in gene expression modified by epigenetic interactions among genes and with the internal cell environment. Extraordinarily complicated combinations of traits can evolve in this way (Chomicki et al. 2024, Stankowski et al. 2024). These fish 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 decommission 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

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[8] See Fusco & Minelli (2010) for a full discussion of phenotypic plasticity.

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 (Rougement et al. 2020).

Recommendations

Oregon's natural resources belong to all of us and it is the government's responsibility to manage these in the interest of the public. Optimizing the contributions of resource exploitation to the State's economy and ensuring that private vested interests do not degrade these resources to the detriment of future generations of resource users are central to this mandate. Recreational angling in Oregon is a $1 billion industry (L Phillips, American Sport Fishing Association, pers comm, 19 July 2023). Hatchery operations over 2021-2023 cost government about $36 million per annum, but angler expenditures on licenses, gear and fishing trips alone approach $400 million, a return on investment that should be applauded as a success rather than denigrated as an environmental catastrophe. We propose several straightforward and scientifically sound steps that could reduce conflict and maximize the likelihood that ODFW can achieve its twin goals:

1. Using whole genome DNA, identify those rivers with viable runs that are identifiable as distinct to that particular ecosystem (in terms of selected genes, not null DNA that is under drift rather than selection), and design specific interventions to protect those runs and watersheds.
2. Compare locations where hatchery activity has been discontinued or reduced to evaluate impact on run size and calculate the cost/benefit of efforts to keep hatchery salmon off spawning beds.
3. Evaluate the factors limiting productivity of streams and oceanic feeding areas targeted for supplementation, and scale hatchery, habitat and nutrient density interventions to grow the population to the extent feasible.

Everyone in the PNW wants to have healthy streams and robust salmon populations. Essential to any workable solution to the current impasse between fisheries managers and wild fish advocates, as with other issues that are dividing the American body politic, will be a commitment to stick to all the facts (not just those that conform to prior held beliefs), and avoid hyperbole whether motivated by economics or some idealized notion of wilderness.

References

Altukhov YP, EA Salmenkova & VT Omelchenko. 2000. Salmonid fishes; population biology, genetics and management. Blackwell, Oxford, UK (354 pp).

Anderson SAS & JT Weir. 2022. The role of divergent ecological adaptation during allopatric speciation in vertebrates. Science 378 (issue 6625): 1214-1218.

Araki H, B Cooper & MS Blouin. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science 318:100-103.

Bartley DM, M Bagley, GAE Gall & B Bentley. 1992. Use of linkage disequilibrium data to estimate effective size of hatchery and natural fish populations. Conservation Biology 6:365-371.

Berejikian BA & DM 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(1): e0190799.

Bigler BS, DW Welch & JH Helle. 1996. A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). Can. J. Fish. Aquat. Sci. 53: 455–465.

Blouin M. 2003. Relative reproductive success of hatchery and wild steelhead in the Hood River. Bonneville Power Administration Final Project Report DOE/BP-00009245-1.

Chomicki, G, G Burin, L Busta, J Gozdzik, R Jetter, B Mortimer & U Bauer. 2024. Convergence in carnivorous pitcher plants reveals a mechanism for composite trait evolution. Science 383: 108-113.

Couce A, A Limdi, M Magnan, SV Owen, CM Herren, RE Lenski, O Tenaillon & M Baym. 2024. Changing fitness effects of mutations through long-term bacterial evolution. Science 383: 383.

Courter I, R Gerstenberger, M Roes, S Gibbs & 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 https://doi.org/10.1139/cjfas-2021-0351

Dunham, RA, RE Brummett, MO Ella & RO Smitherman. 1990. Genotype-environment interactions for growth of blue, channel and hybrid catfish in ponds and cages at varying densities. Aquaculture 85:143-151.

Ford M, A Murdoch & S 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 DJ, MW Jones, TL McParland & JA Hutchings. 2007. Loss of historical immigration and the unsuccessful rehabilitation of extirpated salmon populations. Conservation Genetics 8:527–546.

Fusco G & A Minelli. 2010. Phenotypic plasticity in development and evolution: facts and concepts. Philos Trans R Soc Lond B Biol Sci. 365(1540): 547–556.doi: 10.1098/rstb.2009.0267

Gonzalez C, J Gallardo-Hidalgo & JM Yáñez. 2022. Genotype-by-environment interaction for growth in seawater and freshwater in Atlantic salmon (*Salmo salar*). Aquaculture (Vol 548, Part 2). https://doi.org/10.1016/j.aquaculture.2021.737674

Groot C & L Margolis. 1991. Life histories of Pacific salmon. UBC Press, Vancouver (564 pp).

Hankin, D.G., Nicholas J.W. & Downey T.W. (1993) Evidence for inheritance of age of maturity in Chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences, 50; 347-358.

Hart, D. 1980. Principles of population genetics. Sinauer Associates, Sunderland, MA, USA. 488 pp.

Hess M A, CD Rabe, JL Vogel, JJ Stephenson, DD Nelson & SR Narum. 2012. Supportive breeding boosts natural population abundance with minimal negative impacts on fitness of a wild population of Chinook Salmon. Molecular Ecology 21:5236–550.

Highland Economics, LLC . 2022. Economic contribution & value of hatcheries in Oregon & Washington. https://hatchery-wild-coexist.com/wp-content/uploads/2022/11/HWCEconomicStudy.pdf

Hocking MD & JD Reynolds. 2011. Impacts of salmon on riparian plant diversity. Science 331:1609-1612.

Horn RL & SR Narum. 2023. Going the distance to test local adaptation in Coho salmon. Molecular Ecology 32:539–541.

House F. 1999. Totem Salmon; life lessons from another species. Beacon Press, Boston. 228 pp.

Hume RD. 1893. Salmon of the Pacific coast. Western World Publishers, Bandon, Oregon. 73 pp.

Hutchings JA. 2011. Old wine in new bottles: reaction norms in salmonid fishes. Heredity 106; 421–437.

Ilana Janowitz-Koch I, C Rabe, R Kinzer, D Nelson, MA Hess & SR Narum. 2019. Long-term evaluation of fitness and demographic effects of a Chinook Salmon supplementation program. Evolutionary Applications 12(3): pp 456-469. https://doi.org/10.1111/eva.12725.

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

Kaylor MJ, SM White, ER Sedell & DR 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*, https://doi.org/10.1139/cjfas-2019-0215.

Kaylor MJ, SM White, ER Sedell, AM Sanders & DR Warren. 2020. Carcass additions influence food webs through bottom-up and direct consumption pathways along a fish species assemblage gradient. *Ecosystems*, https://doi.org/10.1007/s10021-020-00510-x.

Koch IJ, TR Seamons, PF Galbreath, HM Nuetzel, AP Matala, KI Warheit, DE Fast, MV Johnston, CR Strom, SR Narum & WJ Bosch. 2022. Effects of Supplementation in Upper Yakima River Chinook Salmon. Transactions of the American Fisheries Society 151:373–388. DOI: 10.1002/tafs.10354373

Lackey RT. 2000. Restoring wild salmon to the Pacific Northwest: chasing an illusion? In: P Koss & M Katz (eds) *What We Don't Know about Pacific Northwest Fish Runs; An Inquiry into Decision-Making*., Portland State University, Portland, Oregon, pp. 91 - 143.

Larsen D.A., Beckman, B.R., Cooper, K.A. et al. (2004) Assessment of high rates of precocious male maturation in a spring Chinook salmon supplementation hatchery program. Trans. Am. Fish. Soc., 133, 98-120.

Leitriz E. 1970. A history of California's fish hatcheries 1870-1960. Fish Bulletin 150. California Department of Fish and Game, Sacremento.

Lichatowich J. 2013. Salmon, People and Place; a biologist's search for salmon recovery. Oregon State University Press, Corvallis. 242 pp.

McElhany P, MH Rucklelshaus, MJ Ford, TC Wainwright & EP Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. NOAA Technical Memorandum NMFS-NWFSC-42. (http://www.nwfsc.noaa.gov).

Meengs CC & RT Lackey. 2005. Estimating the size of historical Oregon salmon runs. Reviews in Fisheries Science 13:51-66.

Montgomery, DR. 2004. King of fish: the thousand yar run of salmon. Basic Books. 290 pp.

Myers RA, SA Levin, R Lande, FC James, WW Murdoch & RT Paine. 2004. Hatcheries and endangered salmon. Science 303: 1980.

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). 2023. Willamette Falls fishway counts. www.dfw.state.or.us/fish/fish_counts/willamette/2023/2023%20Monthly%20Counts.pdf

Oke KB, CJ Cunningham, PAH Westley, ML Baskett, SM Carlson, J Clark, AP Hendry, VA Karatayev, NW Kendall, J Kibele, HK Kindsvater, KM Kobayashi, B Lewis, S Munch, JD Reynolds, GK Vick & EP Palkovacs. 2020. Recent declines in salmon body size impact ecosystems and fisheries. Nature Communications https://doi.org/10.1038/s41467-020-17726-z.

Primmer CR. 2011. Genetics of local adaptation in salmonid fishes Heredity 106; 401–403. doi:10.1038/hdy.2010.158.

Riva Rossi, CM, MA Pascual, E Aedo Marchant, N Basso, JE Ciancio, B Mezga, DA Ferna´ndez & B Ernst-Elizalde. 2012. The invasion of Patagonia by Chinook salmon (*Oncorhynchus tshawytscha*): inferences from mitochondrial DNA patterns. Genetica 140:439–453. DOI 10.1007/s10709-012-9692-3

Rougemont Q, J-S Moore, T Leroy, E Normandeau, EB Rondeau, RE Withler et al. 2020. Demographic history shaped geographical patterns of deleterious mutation load in a broadly distributed Pacific Salmon. PLoS Genetics 16(8): e1008348.

Rougemont, Q., Xuereb, A., Dallaire, X., Moore, J.-S., Normandeau, E., Perreault-Payette, A., Bougas, B., Rondeau, E. B., Withler, R. E., Van Doornik, D. M., Crane, P. A., Naish, K. A., Garza, J. C., Beacham, T. D., Koop, B. F., & Bernatchez, L. (2022). Long-distance migration is a major factor driving local adaptation at continental scale in Coho salmon. *Molecular Ecology*, *32*, 542–559.

Smith C. 2014. Salmon abundance and diversity in Oregon; are we making progress? ORESU-S-14-002, Oregon State University, Corvallis.

Sparks MM, CE Schraidt, X Yin, LW Seeb & MR Christie. 2023. Rapid genetic adaptation to a novel ecosystem despite a large founder event. Molecular Ecology. doi: 10.1111/mec.17121. Epub ahead of print.

Stankowski S, ZB Zagrodzka, MD Garlovsky, A Pal, D Shipilina, et al. 2024. The genetic basis of a recent transition to live-bearing in marine snails. Science 383: 114-119.

Stokes, MD & D White. The fish in the forest; salmon and the web of life. University of California Press, 159 pp.

Taylor III, JE. 1999. Making salmon, an environmental history of the northwest salmon crisis. University of Washington Press, Seattle (421 pp).

Traylor E. 2009. A bridge back; the early days of Florence, Oregon. Port Hole Publications, Florence. 110 pp.

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 (6113): 1412-1413.

US Department of Commerce. 1934. Report of the Commissioner of Fisheries. Government Printing Office, Washington, DC. 484 pp.

Vøllestad LA & CR Primmer. 2019. Understanding local adaptation in a freshwater salmonid fish: evolution of a research programme. ICES Journal of Marine Science 76(6): 1404–1414.

Willoughby JR, AM Harder, JA Tennessen, KT Scribner & MR Christie. 2018. Rapid genetic adaptation to a novel environment despite a genome-wide reduction in genetic diversity. Molecular Ecology 27(20): 4041-4051.