Alaska Hatchery Research Program Synthesis, 2022

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With Review by the Alaska Department of Fish and Game

Cover photo: Pink Salmon in Vanishing Creek in Northern Prince William Sound, Alaska. September 2015. Photo By Benjamin Americus

Glossary of Terms

- ADF&G: Alaska Department of Fish and Game
- AHRP: Alaska Hatchery Research Program

- PWS: Prince William Sound
- PWSAC: Prince William Sound Aquaculture Corporation
    - AFK: Armin F. Koernig Hatchery
    - CCH: Cannery Creek Hatchery
    - WNH: Wally Noerenberg Hatchery
- VFDA: Valdez Fisheries Development Association
    - SGH: Solomon Gulch Hatchery
- NSRAA: Northern Southeast Regional Aquaculture Association
- SSRAA: Southern Southeast Regional Aquaculture Association
- DIPAC: Douglas Island Pink and Chum Incorporated
- AKI: Armstrong-Keta Incorporated

- pHOS: Proportion of hatchery-origin strays
- RS: Reproductive success
- RRS: Relative reproductive success
- F_{ST}: Fixation index. A metric of genetic differentiation between populations
- SNP: Single nucleotide polymorphism.
- Stray: A fish that returns as an adult to a different location from where it was born. In this document we use "strays" to describe recipient strays that add to the population of a stream rather than donor strays that are lost to other populations.
- Wild origin fish: A fish that is born in a wild/natural stream, not a hatchery. We use this term irrespective of the hatchery/wild status of preceding generations.

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Abstract

In Alaska, most hatchery salmon production occurs with Pink Salmon in Prince William Sound and Chum Salmon in Southeast Alaska. These hatcheries are operated by private non-profit organizations and follow state regulations to minimize impact to wild populations. State law requires use of local broodstock and selection of release sites away from significant wild populations, among other measures. In both Prince William Sound (PWS) and Southeast Alaska (SEAK), hatchery-origin strays have been observed in wild populations. Straying is a natural component of salmon biology but straying of hatchery-origin fish raises concerns of potential introgression of maladapted traits into wild populations. To address these concerns, the Alaska Department of Fish and Game and hatchery operators began the Alaska Hatchery Research Program (AHRP) in 2011. The AHRP seeks to understand the impact of straying hatchery fish on wild populations by assessing (1) the baseline genetic stock structures and evidence of introgression, (2) the extent of and variability of straying, and (3) the effect of straying on salmon fitness. This document synthesizes and contextualizes the findings of the AHRP and is organized by these three research questions.

The AHRP found significant, but shallow genetic differences among wild populations of Pink Salmon in PWS and Pink and Chum Salmon in SEAK, consistent with patterns found for these species in other areas of similar geographic size. Hatchery-origin strays were found at variable proportions among streams (with highest proportions near release sites) in both regions, with regional averages ranging from 0.05 to 0.15 for Pink Salmon and 0.03 to 0.09 for Chum Salmon in PWS and 0.03 to 0.06 for Chum Salmon in SEAK. Finally, hatchery-origin Pink Salmon strays produced, on average, about half as many offspring that returned to the stream as wild-origin fish did, with high variability among streams, sexes, and years. We discuss potential mechanisms that may explain this fitness discrepancy and potential management strategies to reduce the extent and negative impacts of straying hatchery-origin fish. The AHRP is an ongoing work, thus the conclusions made here are preliminary.

Introduction

History of Hatcheries in Alaska

The first salmon hatchery in Alaska was constructed for Sockeye Salmon enhancement at Kutlakoo Creek on Kuiu Island in 1892 (Hunt, 1976). This site, independently run and short-lived, was followed by a dozen federally and territorially operated hatcheries in the early 1900s. Poor hatchery practices and infrastructure failure kept returns low, and all Alaskan hatchery work was discontinued by the late 1930s (Roppel, 1982). Between the late 1940s and 1960s, there were small hatchery releases by territorial/state hatcheries and federal research hatcheries (Roppel, 1982). Following historically low commercial salmon harvests in the 1950s and 1960s, the Alaska Legislature established the Division of Fisheries Rehabilitation, Enhance and Development (FRED) within Alaska Department of Fish and Game (ADF&G) in 1971 to revisit fish culture practices. The overarching goal of the program was to enhance salmon fisheries while minimizing adverse impacts on wild stock production. In the 1974 Private Non-Profit Hatchery Act, the Alaska legislature stated that “the program shall be operated without adversely affecting natural stocks of fish in the state and under a policy of management which allows reasonable segregation of returning hatchery-reared salmon from naturally occurring stocks” (Snow, 1991).

Along with ADF&G biologists, a broad consortium of experts from other regulatory agencies, the University of Alaska, and fishermen's associations collaborated to formulate guidelines and policies for the development of Alaska’s modern hatchery program throughout the 1970s and 1980s. Above all else, this consortium was charged with the development of a program that intended to supplement and not replace wild salmon fisheries (McGee, 2004). Policies and regulations were enacted to specifically protect wild stocks from potential negative effects of hatchery activities. According to McGee (2004), the protection of wild salmon stocks in Alaska is accomplished through (1) a rigorous hatchery permitting process that includes review by experts in the fields of genetics, fish pathology, and fishery management; (2) policies that require the placement of hatcheries away from significant wild stocks; (3) use of local brood stocks; (4) legal mandates requiring wild stock prioritization in fishery management; (5) requirements for the tagging and marking of hatchery-produced fish; and (6) requirements for special studies on interactions between hatchery and wild fish, as necessary.

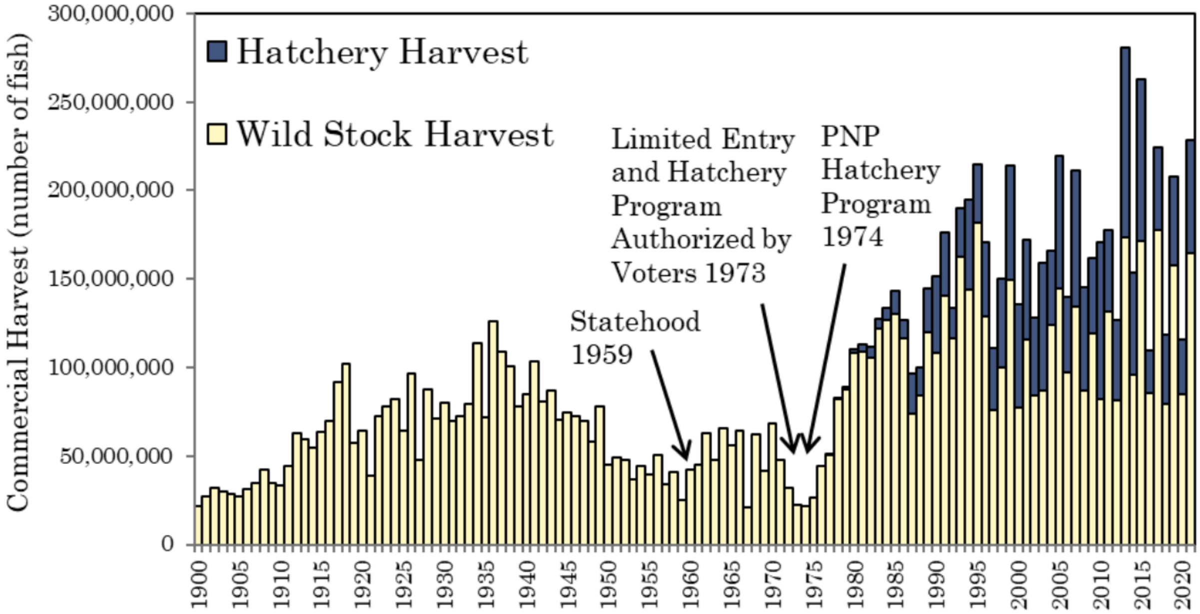


Figure 1. Commercial salmon harvest in Alaska, 1900–2021. From Wilson, 2022.

The State of Alaska funded and oversaw the construction of 18 hatcheries between 1969 and 1983. Starting in 1974, the legislature allowed hatcheries to be operated by private, non-profit (PNP) corporations with State permitting and oversight (Fig. 1). As of 2021, there were 30 production hatcheries operating in Alaska, 26 of which were operated by PNPs. Non-PNP hatcheries include two sport fish hatcheries operated by ADF&G, one research hatchery at Little Port Walter operated by the National Marine Fisheries Service, and one production hatchery operated by the Metlakatla Indian Community. Statewide annual hatchery releases from 1995 to 2021 range from 1.3–1.8 billion fish, mostly consisting of Pink Salmon (*Oncorhynchus gorbuscha)* from Prince William Sound (0.5–0.8 billion) and Chum Salmon (*Oncorhynchus keta*) from Southeast Alaska (0.3–0.6 billion) (NPAFC, 2022; Fig. 2; Table 1; Table 2). Canada, Japan, Korea, and Russia also operate production salmon hatcheries, with the largest contributions coming from Japanese and Russian Chum Salmon (1.4–2.0 billion fish) and (0.2–1.0 billion), respectively, since 1995 (NPAFC, 2022).

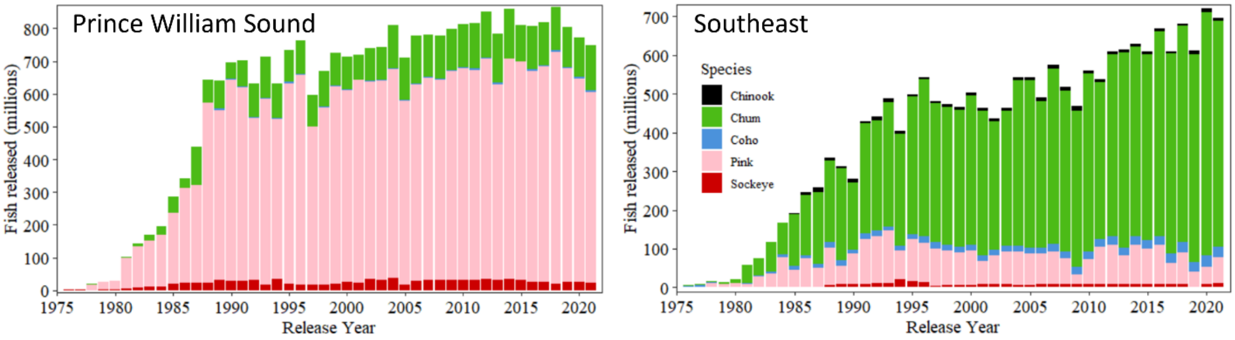


Figure 2. Hatchery salmon releases from Prince William Sound and Southeast Alaska from 1975 to 2021. From Wilson, 2022.

Prince William Sound Pink and Chum Salmon Hatcheries

In response to poor salmon returns to PWS during the late 1960s and early 1970s, which can be tied in part to losses in productivity stemming from the 1964 Great Alaskan Earthquake, the Prince William Sound Aquaculture Corporation (PWSAC) was founded in 1974. The goal of PWSAC was to develop hatcheries in the area, and to stabilize Pink and Chum Salmon runs at levels similar to those which occurred from 1920–1950 (Stopha, 2013). According to Stopha (2013), PWSAC's founders also viewed salmon hatcheries as safeguards against potential impacts from oil development in the region, including the construction of the Trans-Alaska Pipeline System (TAPS) terminus in Port Valdez. The State of Alaska commenced PWS hatchery construction in the mid-1970s at Cannery Creek Hatchery, with PWSAC building its first hatchery simultaneously at a former cannery site in Port San Juan in southwestern PWS, a facility that is now known as the Armin F. Koernig Hatchery.

In 2021, Prince William Sound Pink Salmon accounted for 34% of all statewide hatchery releases, totaling 583 million fish (Wilson, 2022). Presently, four Pink Salmon hatcheries operate in Prince William Sound: (1) Armin F. Koernig (AFK), (2) Cannery Creek (CCH) and (3) Wally Noerenberg (WNH) hatcheries operated by PWSAC, and (4) Solomon Gulch Hatchery (SGH) operated by the Valdez Fisheries Development Association (VFDA). Original broodstock for these hatcheries came from multiple sources in Eastern and Western Prince William Sound in the 1970s and 1980s (Fig. 3; Habicht et al., Seeb, 2000). Annual broodstock is collected during historical peak run timing by voluntary entry into brood holding ponds. This timing varies between hatcheries, with SGH broodstock collection beginning in late July and ending mid-August (VFDA, 2022) and PWSAC hatchery collection beginning in late August/early September and running until mid-September (PWSAC, 2022a; 2022b; 2022c). PWSAC hatcheries have periodically employed barrier seines with closable openings to restrict the escape of hatchery returns. In the late 1980s through the mid-1990s at AFK and WNH, fish outside the barrier nets were collected via purse seine and moved inside for broodstock (Habicht et al., 2000). This may have inadvertently introduced wild origin broodstock from mixed populations (Sharr et al., 1996; Seeb et al., 1999). Since the late 1990s, fish have voluntarily entered brood holding areas to be harvested irrespective of hatchery or wild origin. Under the modern sampling program (volitional entry) >99% of all fish are likely of hatchery-origin (Smoker, 2009).

While 78% of hatchery releases in Prince William Sound are Pink Salmon, PWSAC does operate large Chum and Sockeye Salmon programs. In 2021, Main Bay and Gulkana hatcheries collectively released 23 million Sockeye Salmon fry, and AFK and WNH collectively released 137 million Chum Salmon (Wilson, 2022). In 2021, 41 million of these Chum Salmon were raised at WNH and transported to net pens at Port Chalmers near Montague Island for imprinting and remote release.

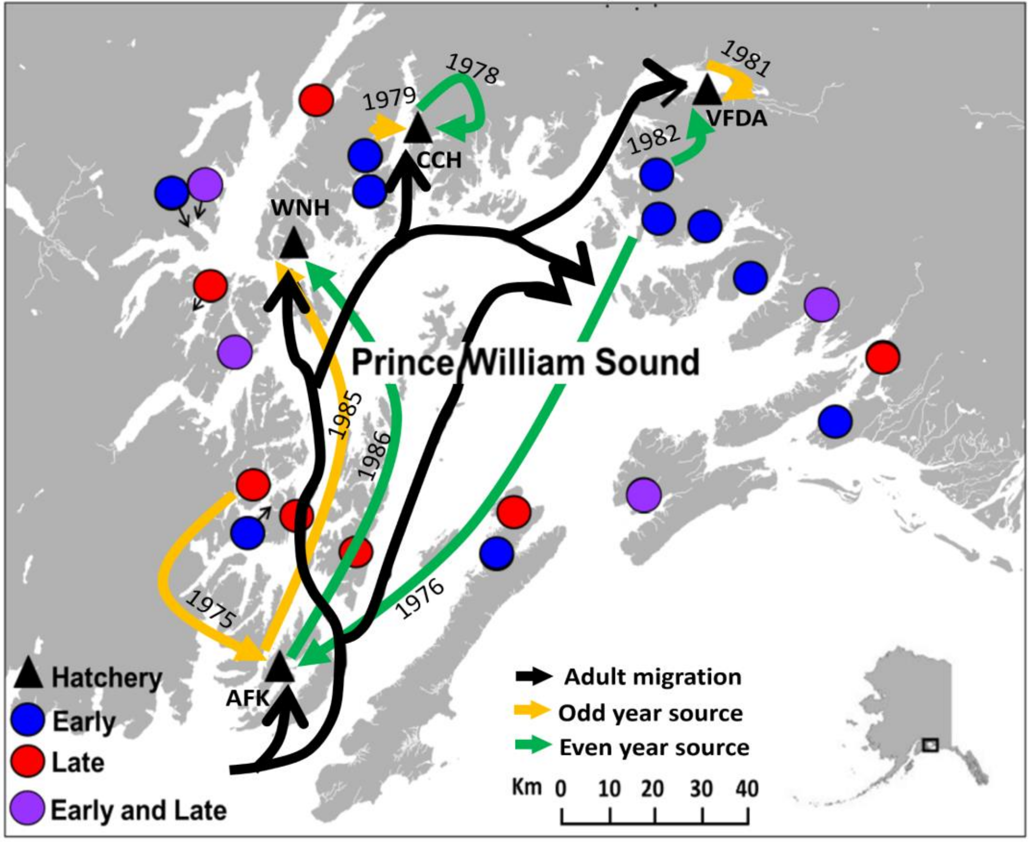


Figure 3. Adult migration routes (black arrow) and movement of ancestral sources of Pink Salmon broodstock for Prince William Sound Hatcheries (colored arrows). Only the largest contributors are included here. For a more detailed review see Habicht et al., (2000).

During broodstock harvest, for both Pink and Chum Salmon, eggs and milt are collected in a common trough that feeds into buckets. Water is added to the buckets to induce fertilization, and eggs are gently poured into incubation trays (PWSAC, 2022d). In dark rooms, eggs are incubated in artificial plastic substrate with constant upwelling of fresh water. Fish are thermally marked in October, as eyed eggs (Volk et al., 1994). By March, fry emerge from incubation substrate and are moved to saltwater rearing net pens in front of the hatchery. In the net pens, fish are fed commercially manufactured feed and then released as smolts to feed on April zooplankton blooms (PWSAC, 2022d).

Table 1. 2021 Prince William Sound Pink and Chum Salmon releases as reported by operators. From Wilson, 2022.

Operator	**District**	**Hatchery**	**Release Site**	**Pink (millions)**	**Chum (millions)**
PWSAC	Southwestern	A F Koernig	Sawmill Bay	131.1	18.8
	Northern	Cannery Creek	Unakwik Inlet	114.6	0
	Coghill	Wally Noerenberg	Lake Bay	88.3	77.3
			Port Chalmers	0	41.1
VFDA	Eastern	Solomon Gulch	Solomon Gulch	249.1	0
Total				**583.2**	**127.2**

Southeast Chum Salmon Hatcheries

In 1976, two years after the formation of the PNP Hatchery Program, Douglas Island Pink and Chum Incorporated (DIPAC) and Southern Southeast Regional Aquaculture Association (SSRAA) were founded. These regional organizations were modeled after PWSAC (DIPAC, 2022; Roppel, 1986), however, unlike PWSAC, SSRAA propagated mostly Chum Salmon from the start, DIPAC propagated Pink and Chum Salmon initially but focused on propagating Chum Salmon in 1991, and both operators developed strategies of a central incubation facility with remote release sites. Release sites were selected near anadromous water sources to imprint juveniles but away from large wild populations (Heard, 2012). In the early part of the following decade, more PNPs were founded using this model including the Northern Southeast Regional Aquaculture Association (NSRAA) in 1978 (NSRAA, 2020), and Armstrong-Keta Incorporated (AKI) in 1980 (AKI, 2022).

In 2021, Southeast Alaska hatchery Chum Salmon accounted for 34% of all statewide hatchery releases, totaling 583 million fish (SSRAA, 2022; Wilson, 2022). In Southeast Alaska, 10 Chum Salmon-producing hatcheries presently operate, with 16 separate remote release sites. SSRAA operates Burnett Inlet, Neets Bay, and Whitman Lake hatcheries. NSRAA operates Hidden Falls, Medvejie, and Sawmill Creek hatcheries. DIPAC operates the Macaulay Hatchery, and the Sitka Sound Science Center operates the Sheldon Jackson Hatchery. The Metlakatla Indian Community operates the Tamgas Creek Hatchery, and AKI operates Port Armstrong Hatchery. Original broodstock for the three largest Southeast Alaska Chum Salmon producers, SSRAA, NSRAA, and DIPAC, came from local stocks (within 40 miles) in the 1970 and 1980s (Roppel, 1986; Josephson et al., 2021). Approximately half the parr reared in Southeast Alaska are released at remote sites (Table 2; Wilson, 2022). Annual broodstock is primarily collected at the hatcheries, however in cases of shortage, remote egg-take and transfers from remote release sites occur (SRAA, 2022; Wilson, 2022).

Table 2. Southeast Chum Salmon as reported by Operators. From Wilson, 2022.

Operator	**Region**	**Hatchery**	**Release Site**	**Chum (millions)**
SSRAA	Southern Southeast	Burnett Inlet	Burnett Inlet	32.4
			Anita Bay	22.8
			Nakat Inlet	14.7
			Port Asumcion	18.2
	Southern Southeast	Neets Bay	Neets Bay	67.2
			Nakat Inlet	1.2
	Southern Southeast	Whitman Lake	Kendrick Bay	22.2
			McLean Arm	11.0
Metlakatla Indian Community	Southern Southeast	Tamgas Creek	Tamgas	20.0
			Port Chester	10.0
NSRAA	Northern Southeast Inside	Hidden Falls	Thomas Bay	11.7

			Kasnyku Bay	48.9
			Southeast Cove	35.4
	Northern Southeast Inside	Gunnuk Creek	Gunnuk Creek	17.6
	Northern Southeast Outside	Medvejie	Bear Cove	37.4
			Deep Inlet	34.1
	Northern Southeast Outside	Sawmill Creek	Deep Inlet	16.0
			Crawfish Inlet	25.9
AKI	Northern Southeast Outside	Port Armstrong	Port Armstrong	13.2
DIPAC	Northern Southeast Inside	Macaulay	Gastineau Channel	11.7
			Amalga Harbor	46.3
			Boat Harbor	23.5
			Limestone Inlet	11.8
			Sheep Creek	21.3
SSSC	Northern Southeast Outside	Sheldon Jackson	Crescent Bay	3.0
			Deep Inlet	6.1
Total				**583.3**

Introduction to Straying

Straying is a necessary component of salmon biology, supporting genetic resilience, population stability, and range expansion (Keefer & Caudill, 2014). In western Prince William Sound, straying may have allowed population recovery after major habitat disturbance events like the 1964 Earthquake and the 1989 Exxon Valdez Oil Spill. Many factors are suspected to drive straying including interrupted juvenile imprinting, adult homing failure, and attraction to non-natal streams (Keefer & Caudill, 2014). Pink and Chum Salmon may have higher stray rates than other Pacific Salmon due to their limited reliance on fresh water for early growth and imprinting, lack of variation in intertidal spawning habitats, and for Pink Salmon, the lack of overlapping age cohorts (Beacham et al., 2012; Bett et al., 2016; Quinn, 2018). Pink Salmon in particular have lower olfactory selectivity during upstream migration, contributing to their lower stream fidelity (Ueda 2011; Ueda 2012). Higher stray rates of Pink Salmon may be adaptive, allowing for their wide and abundant distribution in the North Pacific and elsewhere (Ueda 2012). Additionally, within species, there may be population-specific dispersal (i.e., straying) plasticity, as found for Chinook Salmon (Westley et al., 2015).

While staying between wild populations is useful for long term survival, straying of hatchery-origin fish into wild systems may have negative consequences. Several mechanisms are discussed below and reviewed in detail in Naish et al., (2007): (1) Hatchery-origin strays may interbreed with wild fish, thereby introducing maladapted traits, (2) hatchery fish may transmit or amplify disease, (3) hatchery fish may displace wild fish on the spawning grounds, and (4) harvests of mixed wild and hatchery populations may overfish small wild populations. The focus for most of this synthesis is on the first mechanism.

In fisheries management, it has been proposed that a 2% incidence of pre-spawning hatchery strays in a neighboring wild stock population could serve as a trigger point for action, and for consideration of hatchery reform to reduce straying. This “2% rule” is based on the theoretical rate of loss of alleles in a wild salmon population as described by Withler (1997). According to Withler’s (1997) research, at a 1.5% influx of hatchery genes in each generation, a 2.5% effective stray rate, and alleles with an intermediate difference in fitness between the wild genotype with the highest level of survival and the hatchery genotype (selection coefficient= 0.025), the replacement of 50% of alleles in a wild population could occur in 25 generations. It is proposed by some that replacement of dissimilar alleles would accompany a decrease in population fitness and a resulting decrease in productivity of the wild population (Hilborn & Eggers, 2000).

To address these concerns, the extent of hatchery straying has been widely studied. In Alaska, hatchery straying was first assessed in Prince William Sound in 1991 using coded wire tags applied to Pink Salmon fry from the 1989 brood year (Sharp et al., 1994). Strays from all four PWS Pink Salmon hatcheries were identified in wild systems, with the most strays coming from WNH and AFK. Thermal marking was employed to replace coded wire tags in 1995 (Joyce et al., 1996), and all PWS hatchery Pink Salmon were marked in 1996 (Joyce & Evans, 2000). Thermally marked strays were found in wild systems in 1997 (Joyce & Evans, 2000). The largest contributors to straying were WNH and AFK, confirming the earlier studies with coded wire tags. In Southeast Alaska, thermal marking was implemented in 1991 and thermally marked strays were first identified in wild streams in 1995 (Josephson, 2010).

Whereas the extent of hatchery straying has been widely studied in Alaska, the physiology of hatchery-origin fish relative to their wild-origin counterparts is less known. We can draw inference from hatchery programs with other species. In a study of Skagit River, both male and female hatchery-origin Chinook Salmon had earlier spawn timing than wild-origin fish, an important fitness trait (Austin et al., 2022). In the Yakima River, after one generation of hatchery rearing, male and female Chinook Salmon were significantly shorter and lighter than their wild-origin counterparts (Knudsen et al., 2006). When accounting for size differences, hatchery-origin females were 8% less fecund than wild-origin females (Knudsen et al., 2008). Some, but not all studies found reduced egg-fry survival in offspring of hatchery-origin fish (Schroder et al., 2008; Knudsen et al., 2008).

Reduced fitness (reproductive success) of hatchery-origin fish in wild systems has been observed in three of six species of anadromous Pacific Salmon: Coho (*Oncorhynchus kisutch*), steelhead

(*O. mykiss*), and Chinook (*O. tshawytscha*), although results can be mixed (Araki et al., 2008; Williamson et al., 2010). Male but not female hatchery-origin Chinook Salmon had consistently lower reproductive success than wild-origin Chinook colonizing new habitat (Anderson et al., 2013). Hatchery-origin Chinook Salmon returns can have slightly less offspring than wild-origin females (Fast et al., 2015). The fitness of hatchery-origin strays relative to natural-origin fish they spawn alongside has been rarely studied prior to the project synthesized here.

Goals of Alaska Hatchery Research Program

In order to address concerns over straying, the Alaska Department of Fish and Game (ADF&G) began the Alaska Hatchery Research Program (AHRP) in 2011. Funding for the program was provided by the State of Alaska, hatchery operators, fish processors, and external grants. The goals of the program are detailed in Box 1. Field sampling was contracted to the Prince William Sound Science Center and Sitka Sound Science Center. Hatchery or wild origin and pedigree reconstructions were determined by the Alaska Department of Fish and Game. In this report we summarize the findings of the ongoing work by ADF&G and contextualize their findings.

Box 1. Priority Questions of the Alaska Hatchery Research Project

- What is the genetic stock structure of pink and chum salmon in each region?
- What is the extent and annual variability in straying of hatchery pink salmon in Prince William Sound (PWS) and chum salmon in PWS and Southeast Alaska (SEAK)?
- What is the impact on fitness (productivity) of wild pink and chum salmon stocks due to straying of hatchery pink and chum salmon?

Genetic Stock Structure

Prince William Sound Pink Salmon

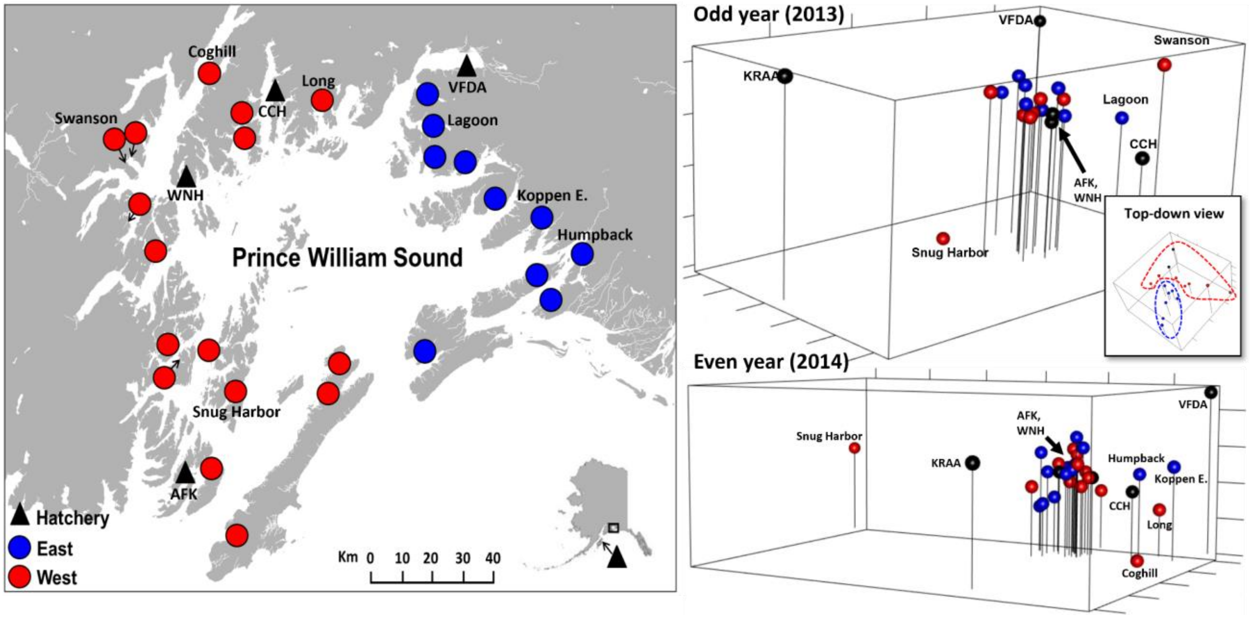


Figure 4. Non-metric Multidimensional Scaling plot of Prince William Sound Pink Salmon collected as adults 2013 and 2014 and genotyped with 16 microsatellite loci. From Cheng et al., 2022a.

The most recent genetic stock assessment of Prince William Sound Pink Salmon in Alaska was carried out in 2013 and 2014. There were 3,000 adult Pink Salmon samples collected from 23 sites in 2013 and 6,554 samples collected from 26 sites in 2014 (Fig 4; Cheng et al., 2015). In both years, samples from Kitoi Bay Hatchery on Kodiak Island were included as an outgroup. For Prince William Sound, Cheng et al (2015) genotyped 16 microsatellite loci and calculated a fixation index (F_{ST}, a metric of genetic differentiation among populations) of 0.002 among spawning groups in 2013, and 0.001 in 2014. These F_{ST} values align with prior work on Pink Salmon populations from other regions in Northern America that lack large scale hatchery programs (Churikov & Gharrett, 2002; Beacham et al., 2012).

The relatively low genetic diversity in Pink Salmon may be due to their intertidal spawning, the proximity of potential spawning areas within and between streams, and low diversity of habitat that they depend on for their life history (Quinn, 2018; Waples et al., 2001). Despite the relatively low natural genetic diversity of Pink Salmon and potential homogenization from straying, statistically significant differences were detected among natural and hatchery collections. WNH and AFK were genetically similar to each other and some wild populations. WNH was originally sourced from AFK broodstock. There are two potential explanations for the similarity between AFK and wild populations: (1) wild broodstock were introduced during the late 1980s to mid 1990s era of purse seining to collect broodstock and (2) AFK fish are more commonly found among wild populations than Pink Salmon from other hatcheries (Brenner et al., 2012).

In an ongoing study, Cheng et al., compared the 2013 and 2014 genotypes of samples from AFK, CCH, and SGH to historical samples from the same sites collected in the 1990s (Cheng, 2022). No significant differences were detected across time within hatcheries. To ascertain whether wild systems had become more similar to their hatchery donors over time, Cheng compared historical (1990s) and contemporary (2013 and 2014) hatchery broodstock samples to contemporary wild-origin samples from Prince William Sound streams (Fig. 5).

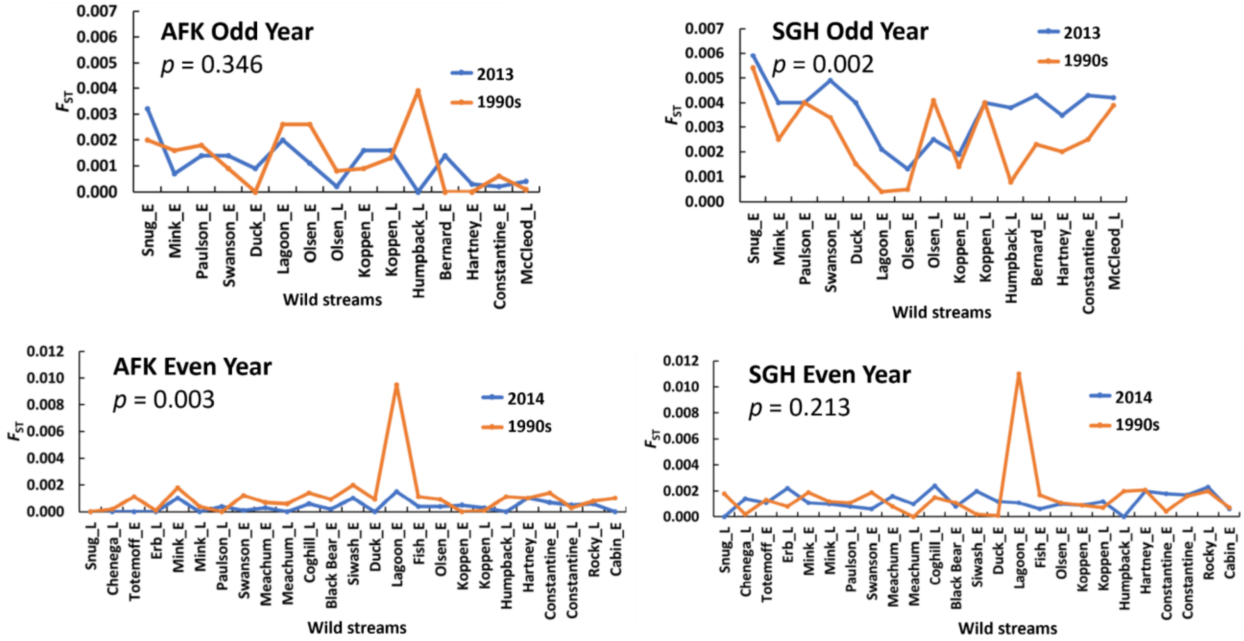


Figure 5. F_{ST} values of genetic differentiation for Pink Salmon at Armin F. Koernig and Solomon Gulch hatcheries when comparing contemporary samples (2013 and 2014) to historical samples from the 1990s. From Cheng et al., 2022b.

For AFK, in the even lineage, wild fish had become significantly more similar to AFK broodstock over time ($p = 0.003$) suggesting introgression of hatchery fish to wild populations. This relationship had not significantly changed in the odd year lineage. For SGH, the even year lineage had not changed in its relationship to wild fish, but the odd year lineage had become significantly less similar to SGH broodstock ($p = 0.002$), suggesting genetic isolation and drift. These results align with straying studies that found AFK to contribute the largest proportion of strays to wild streams, and SGH to contribute relatively few strays (Brenner et al., 2012; Knudsen et al., 2021).

Prince William Sound Chum Salmon

To look for genetic introgression between hatchery and wild Prince William Sound Chum Salmon, ADF&G compared SNP allele panels in samples from four wild streams collected in the years 1964–1982 and 2008–2010 and broodstock from WNH collected 2008–2010 (Jasper et al., 2013). The degree of differentiation in 2008–2010 samples was slightly less than that of the historical samples (F_{ST}=0.0161 vs F_{ST}=0.0158). The authors used a source-sink model to quantify changes in allele frequencies due to introgression from straying WNH fish. In all four study streams, there was a convergence of wild allele frequencies towards hatchery frequencies, suggesting introgression from hatchery strays. In some cases, the rate of introgression was more closely tied to the degree of temporal overlap between hatchery and wild fish than proximity to WNH or the intensity to straying.

Southeast Chum Salmon

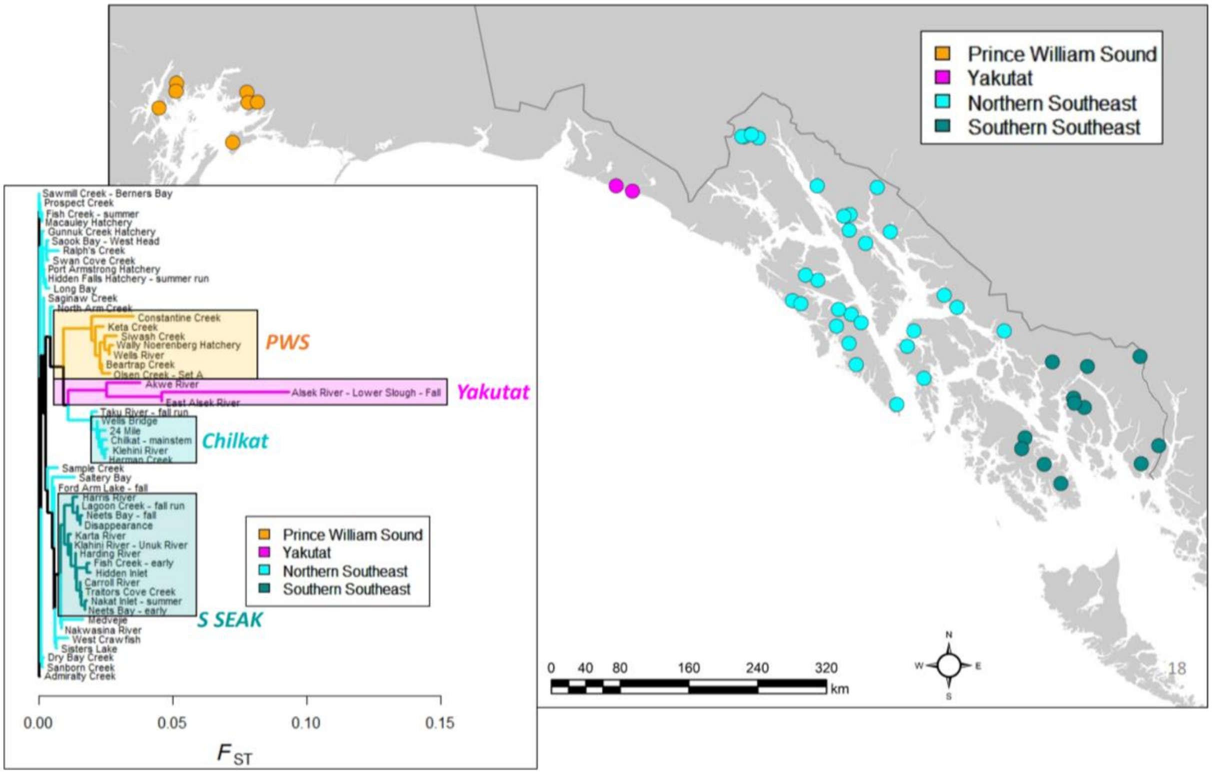


Figure 6. Stock structure of Southeast and Southcentral Alaska Chum Salmon from a 2014 survey. From Habicht et al., 2022.

ADF&G is currently performing a genetic stock assessment of Chum Salmon in Southeast Alaska, and some preliminary results are available (Habicht et al., 2022). Results from 52 stream sites using 93 microsatellite loci suggest that stocks partition by geography and run timing (Fig. 6). Southern Southeast Chum Salmon are genetically distinct from Northern Southeast Chum Salmon, and fish from Yakutat and Prince William Sound. Fall-run Chum Salmon are also genetically distinct from spring and summer-run fish from the same region. This is the case in both Northern and Southern Southeast Alaska. These trends align with a previous study on Chum Salmon in Southeast Alaska (Kondzela et al., 1994).

Straying extent and interannual variability

Prince William Sound Pink Salmon

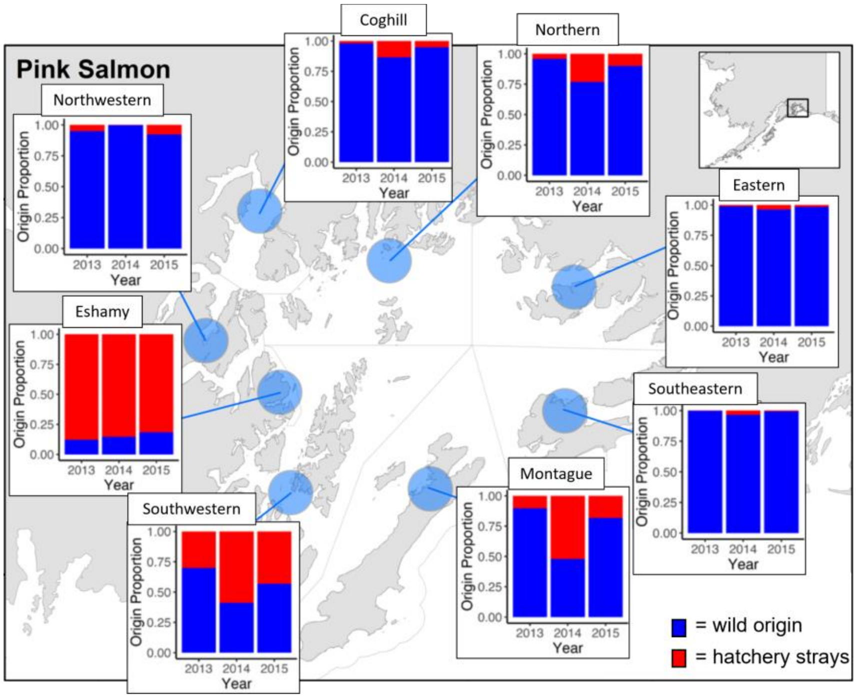


Figure 7. Pink Salmon proportion of hatchery-origin spawners (red; pHOS) in Prince William Sound fishing districts in 2013–2015. From Knudsen et al., 2021.

The most recent and comprehensive survey of Prince William Sound Pink Salmon straying was performed from 2013–2015. Across all regions, the estimated proportion of hatchery-origin spawners (pHOS) in streams was 0.05 in 2013, 0.15 in 2014, and 0.11 in 2015. pHOS was highly variable across streams among the eight fishing districts (Fig. 7), with the higher proportions near hatcheries, as noted in a 2008–2010 survey (Brenner et al., 2012). The Eshamy district had the highest proportion of hatchery strays across all years (average of 0.86), though only one stream (Comstock Creek) was sampled. Eshamy District contributed less than 1% of estimated Prince William Sound Pink escapement across the three years surveyed (Knudsen et al., 2016).

The Southwestern district had the second highest pHOS (0.37) and accounted for 9% of PWS escapement. The Eastern and Southeastern districts, the two largest contributors to total PWS Pink escapement (27% each), consistently had the lowest hatchery pHOS in the survey years (0.026 and 0.016 respectively). When comparing streams surveyed in both studies, 2008–2010 (Brenner et al., 2012) and 2013–2015 (Knudsen et al., 2021), Pink Salmon pHOS increased in all districts surveyed, though not in all streams within districts. During this time hatchery releases remained consistent. pHOS is highly dependent on interannual survival rates, run size, and harvest patterns. These factors caveat interannual comparisons (Knudsen et al., 2021).

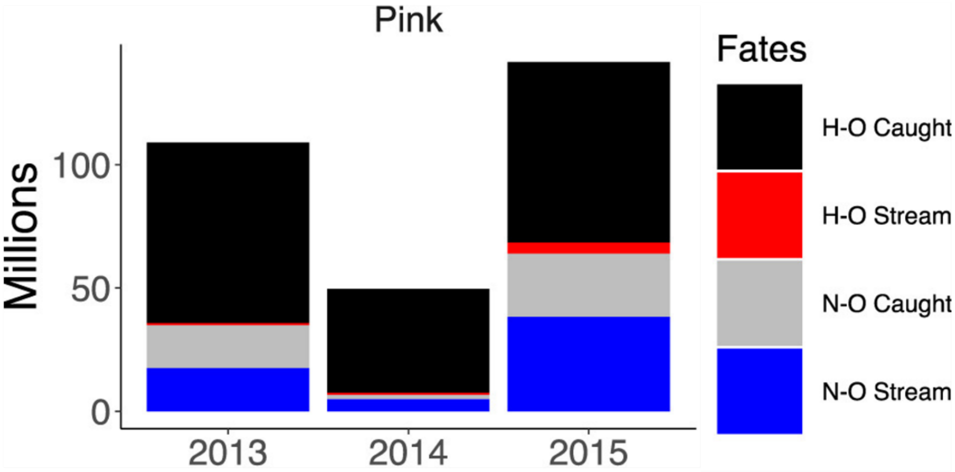


Figure 8. Estimations of escapement to streams and catch for hatchery-origin (H–O) and natural-origin (N–O) Pink Salmon in Prince William Sound during 2013–2015. From Knudsen et al., 2021.

In 2013–2015, counts from aerial and ground surveys and hatchery-wild proportions from stream and ocean sampling were combined to estimate the hatchery, natural, and total run size of Pink Salmon in Prince William Sound (Fig 8; Knudsen et al., 2021). The total run size ranged from 49.6–141.8 million fish, with hatcheries contributing 55–86%. Across PWS, fisheries harvested 70–88% of the total run. This included 94–99% of all hatchery fish returning to PWS, and 27–50% of returning natural-origin fish.

Prince William Sound Chum Salmon

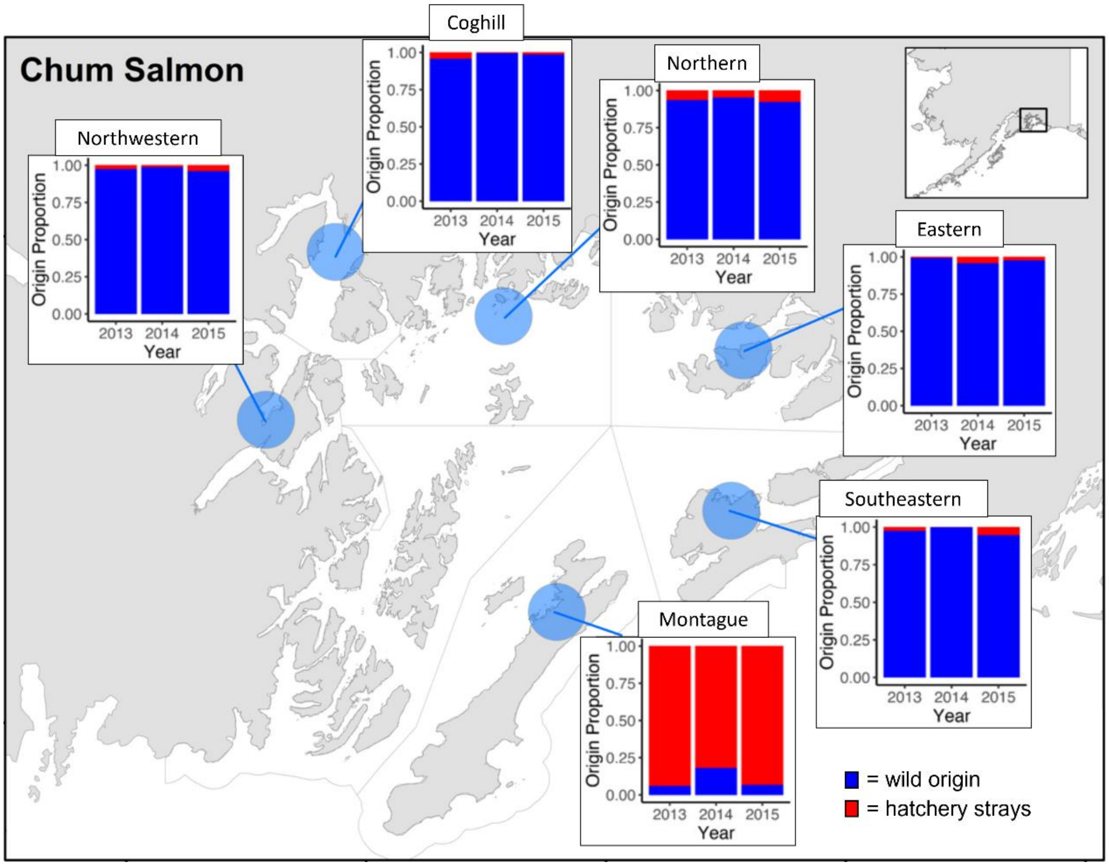


Figure 9. Chum Salmon proportion of hatchery-origin spawners (red; pHOS) in Prince William Sound fishing districts in 2013–2015. From Knudsen et al., 2021.

Across all Prince William Sound wild Chum Salmon populations, the estimated proportion of hatchery-origin spawners (pHOS) in streams was 0.03 in 2013, 0.03 in 2014, and 0.09 in 2015 (Knudsen et al., 2021). Of the six fishing districts surveyed, Montague District had the highest pHOS (0.78–0.85). For contrast, the Northern District had the next highest pHOS with 0.05–0.10. These findings align with results from surveys in 2008–2010 (Brenner et al., 2012), which found the Chalmers River in Montague District to have a pHOS greater than 0.90. Strays sampled in the 2013–2015 surveys in Montague District mostly came from the WNH remote release site in Port Chalmers (Knudsen et al., 2021). Port Chalmers was originally selected as a remote release site due to the limited wild Chum Salmon production in nearby streams, possibly due to uplift from the 1964 earthquake (Roys, 1965) and separation from the main migratory path (Knudsen et al., 2021). In Coho Salmon (Labelle 1992) and Chinook Salmon (Candy & Beacham, 2000), remote rearing and release increases straying by disrupting imprinting.

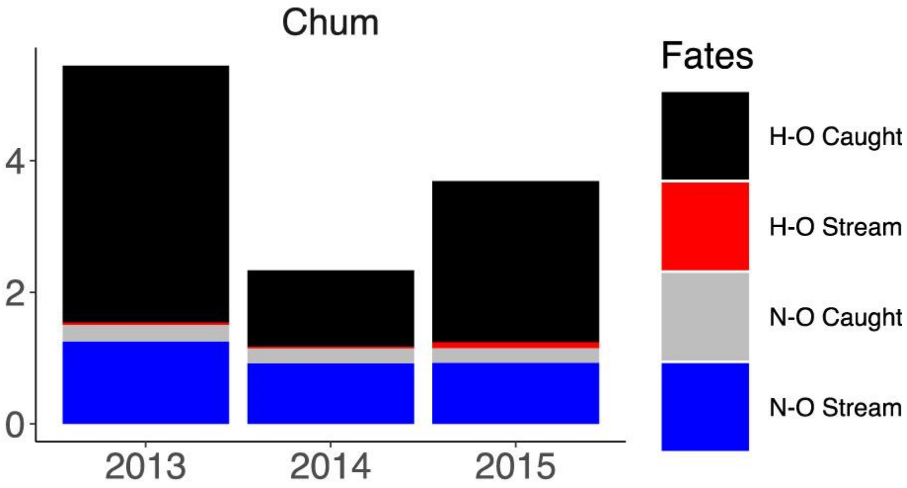


Figure 10. Estimations of escapement to streams and catch for hatchery-origin (H–O) and natural-origin (N–O) Chum Salmon in Prince William Sound during 2013–2015. From Knudsen et al., 2021.

The sampling and survey techniques used to estimate the total Pink Salmon run in 2013–2015 were simultaneously applied to Chum Salmon. The total run size ranged from 2.3–5.4 million, with hatchery fish contributing 51–72%. Across PWS, fisheries harvested 59–76% of the total run. This consisted of 96–99% of all hatchery fish returning to PWS, and 17–20% of all natural-origin fish.

Southeast Chum Salmon

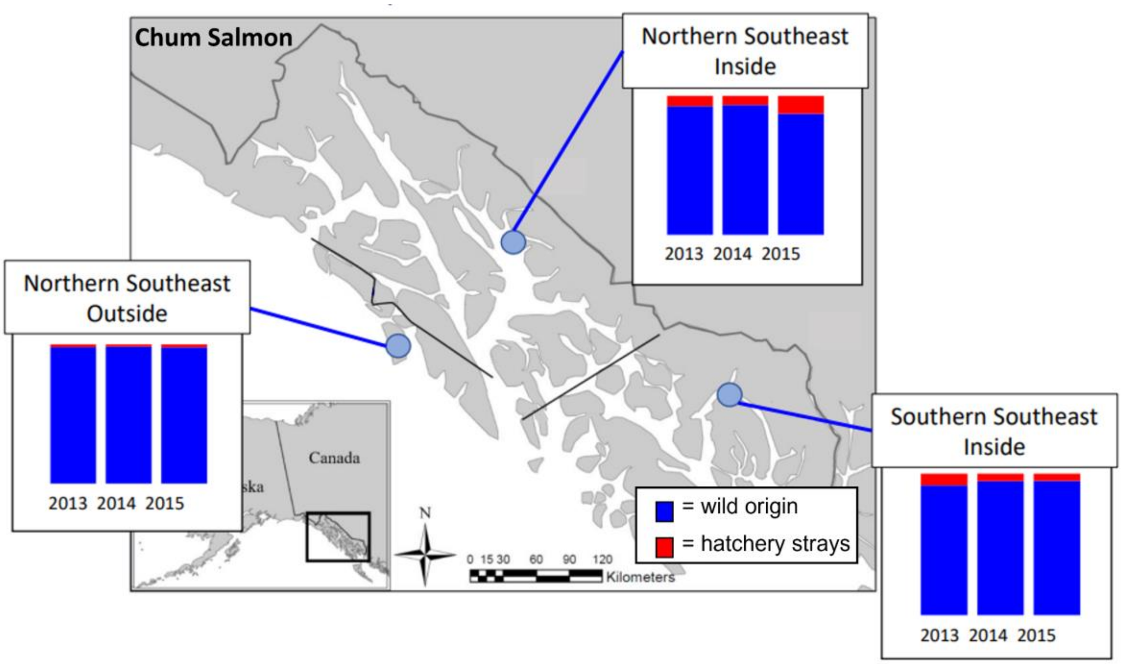


Figure 11. Chum Salmon proportion of hatchery-origin spawners (red; pHOS) in Southeast Alaska regions in 2013–2015. From Josephson et al., 2021.

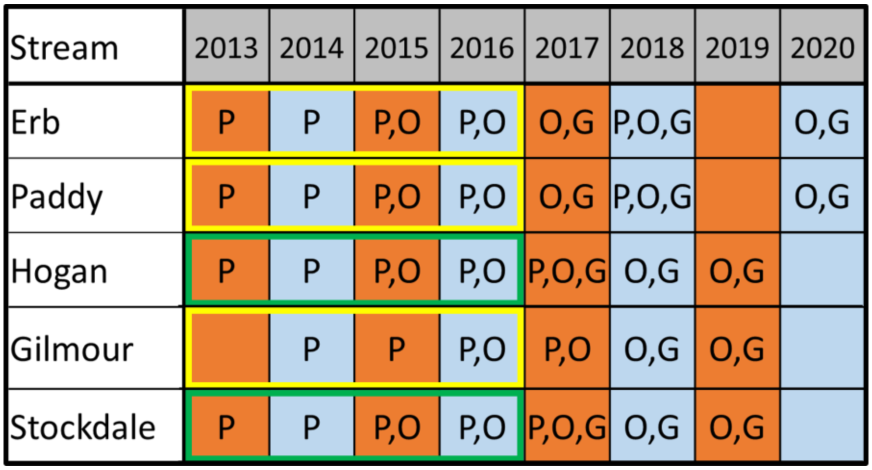
A comprehensive survey of Chum Salmon in Southeast Alaska spawning streams (Josephson et al., 2021) was completed during the same years as the Pink and Chum Salmon surveys in Prince William Sound (2013–2015). Across Southeast Alaska regions, the pHOS was 0.03 in 2013, 0.03 in 2014, and 0.06 in 2015. Of the three management areas, Southern Southeast had the highest 2013–2015 average pHOS at 0.05 and accounted for 30% of estimated total Southeast Chum escapement during these years (Fig. 11.). The Northern Southeast Inside (NSI) region had an average pHOS of 0.04 and accounted for the majority of total Southeast escapement at 59%, and the Northern Southeast Outside (NSO) had the lowest pHOS of 0.02 and accounted for the remaining 11% of escapement. As with PWS Chum Salmon, pHOS was highly variable between streams and regions, with the highest pHOS in streams near hatcheries and remote release sites. The pHOS estimates from NSO align with results from 2008–2011 surveys (Piston & Heinl 2012a, 2012b. NSI previously had higher pHOS values (0.13 in 2010), though this may be reflective of high variability between years and sampling differences between studies.

In 2018 and 2019, hatchery Chum Salmon returned in unprecedented numbers to a new (2015) remote release site in Crawfish Inlet (Piston & Heinl, 2020). In both years, many fish were observed straying into West Crawfish Inlet rather than returning directly to the release site. This caused an increase in pHOS in several nearby streams, including West Crawfish NE Arm, an AHRP index stream. In 2013–2015 surveys, this stream had a pHOS of 0.01–0.02 (Josephson et al., 2021). In 2018 and 2019, the stream was surveyed after the peak of wild returns, typically mid-August (Piston & Heinl, 2020). In 2018, the pHOS of West Crawfish NE Arm Head was 0.62 on August 27th, then 0.99 on September 28th. In 2019, the pHOS was 0.08 on August 27, 2019, and then 0.94 on September 4th, (Piston & Heinl, 2020). These findings suggest that the unprecedented hatchery Chum returns to Crawfish Inlet did result in increased pHOS in nearby streams. In the case of West Crawfish NE, this occurred after the peak of wild spawning, so hatchery and wild-origin spawners were temporally segregated, possibly limiting introgression.

Impact on Fitness

Prince William Sound Pink Salmon

Since the implementation of wide scale hatchery Pink Salmon releases in 1989 (15+ Pink Salmon generations), extensive hatchery straying has occurred, yet wild productivity in Prince William Sound has remained strong, with three of the four highest wild returns on record occurring in the last 10 years. The environmental factors driving these returns are complex, and population-level changes in reproductive success are overshadowed by broader environmental changes (Ohlberger et al., 2022).



Stream	2013	2014	2015	2016	2017	2018	2019	2020
Erb	P	P	P,O	P,O	O,G	P,O,G		O,G
Paddy	P	P	P,O	P,O	O,G	P,O,G		O,G
Hogan	P	P	P,O	P,O	P,O,G	O,G	O,G	
Gilmour		P	P	P,O	P,O	O,G	O,G	
Stockdale	P	P	P,O	P,O	P,O,G	O,G	O,G	

Figure 12. Sampling of Prince William Sound Pink Salmon for pedigree analysis. P=parent, O=offspring, G=grand offspring. Green boxes=published results (Shedd et al., 2022a). Yellow boxes=preliminary results. Modified from Shedd et al., 2022b.

To understand the effects of straying on population fitness, the AHRP investigated five streams in western Prince William Sound. A genetic-based parentage analysis was used to estimate relative reproductive success (RSS) across multiple generations of even and odd year lineages. ADF&G used thermally marked otoliths and genetic parentage analyses to identify hatchery strays and natural-origin donor fish in 2013–2018, and then quantified their adult returning progeny in 2015–2020 (Fig. 12). Presently, results from two generations (2013–2016) of even and odd year fish from two streams (Hogan and Stockdale) have been published (Shedd et al., 2022a). Hogan Creek on Knight Island and Stockdale Creek on Montague Island both have high pHOS (0.59 and 0.31 respectively, across the study period), with potentially 16 generations of introgression prior to the study. In all years, most hatchery strays in both streams came from the nearby AFK hatchery (Knudsen et al., 2016).

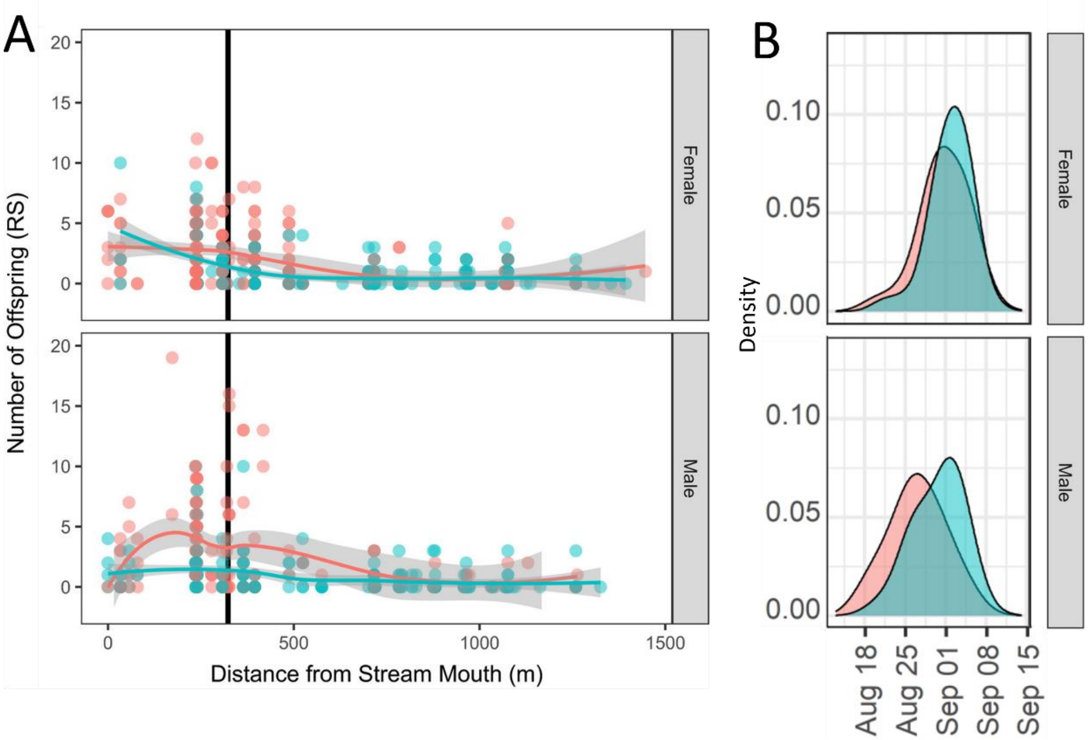


Figure 13. Phenotypic difference between 2014 brood year hatchery and wild fish at Stockdale Creek. A: The association between spawning location and reproductive success, B: relative density of hatchery and wild fish at Stockdale creek across time in 2014. From Shedd et al., 2022a and 2022b.

Reproductive success (RS) was highly variable between years and streams. In both Hogan Creek and Stockdale River, body size, spawning date, and spawning location were significantly associated with RS (Shedd et al., 2022a). Hatchery-origin spawners were generally bigger than wild origin fish, spawned later in the season and further upstream (Figs. 13 & 14). When not correcting for these morphological and behavioral differences, RRS ranged from 0.05–0.86 for males, and 0.03 to 0.47 for females (Table 3). When accounting for these factors, the RRS of the even year lineage was 0.42–0.60 (excluding Hogan males with ah RRS that was not different by origin). However, these models explained < 10% of the variation in RS of Hogan Bay (6% for females and 4% for males) and < 40% of variation in RS in Stockdale (25% for females and 36% of males). This suggests some other fitness-determining factors are at play besides body size, spawning time, spawning location.

The effect of origin on reproductive success was also observed among different types of matings. Two hatchery-origin parents produced fewer returning spawners than two wild origin parents (origin was significant for Stockdale but not Hogan). The number of returning spawners from one hatchery and one wild origin parent was intermediate between two hatchery and two wild spawners.

Table 3. Proportion of hatchery-origin strays and relative reproductive success (RRS) of hatchery-origin Pink Salmon in five streams in Prince William Sound. From Shedd et al., 2022a, 2022b.

Stream	**Lineage**	**Brood year pHOS**	**Male parent RRS (95% CI)**	**Female parent RRS (95% CI)**
Hogan	2013/2015	0.64	0.05 (0.01–0.17)	0.03 (0.01–0.08)
	2014/2016	0.92	0.80 (0.68–0.94)	0.62 (0.52–0.74)
Stockdale	2013/2015	0.16	0.69 (0.31–1.35)	0.17 (0.03–0.55)
	2014/2016	0.74	0.29 (0.25–0.34)	0.43 (0.37–0.50)
Gilmore	2013/2015	NA	NA	NA
	2014/2016	0.56	0.82 (0.69–0.96)	0.88 (0.76–1.01)
Paddy	2013/2015	0.15	NA	NA
	2014/2016	0.60	0.96 (0.78–1.19)	0.63 (0.53–0.76)
Erb	2013/2015	0.11	NA	NA
	2014/2016	0.23	0.33 (0.28–0.39)	0.34 (0.30–0.39)

Preliminary results from the 2014–2016 lineage for three additional streams in Prince William Sound are available (Shedd, 2022b; Table 3). These streams vary in brood year pHOS: Erb Creek 0.23, Gilmour Creek 0.56, Paddy Creek 0.60 (Gorman et al., 2017). At all three sites, hatchery-origin fish were found later in the season and further upstream than natural-origin fish, as was observed at Hogan and Stockdale. Similarly, body length was generally greater in hatchery-origin fish than wild origin fish (Fig. 14). Hatchery-origin RRS was lowest at Erb Creek, which had the lowest brood year pHOS. RRS was similar between Gilmour and Paddy, which had similar brood year pHOS.

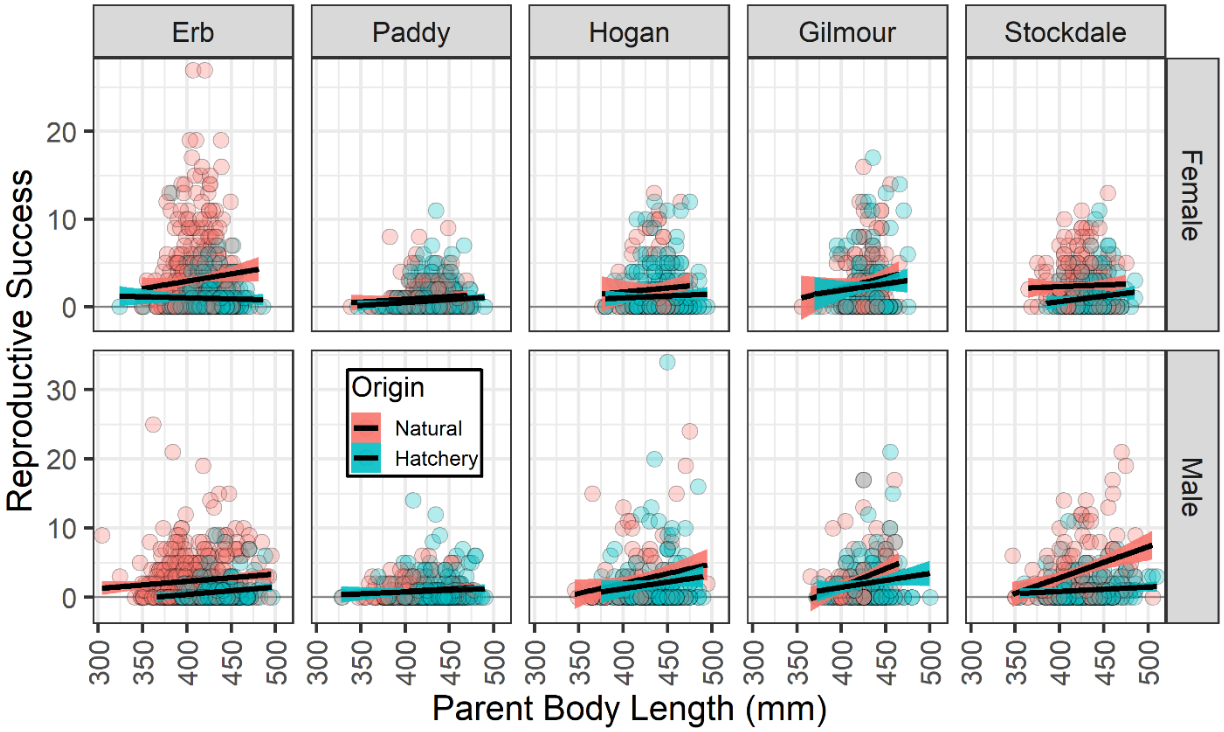


Figure 14. Relationship between parent body length and reproductive success in five Prince William Sound Pink Salmon streams in 2014. From Shedd, 2022b.

Southeast Chum Salmon

Mirroring the work in Prince William Sound, Chum Salmon from four streams in Southeast Alaska were sampled for pedigree reconstruction beginning in 2013 (Fig. 15). Due to low sampling proportion and variable age at spawning, Chum Salmon fitness information could not be ascertained from samples collected in Southeast Alaska streams from brood years 2013–2016. ADF&G sampled three of the four streams more intensively in 2017–2022, and there are tentative plans to continue sampling in 2023. RRS data from these years are expected to be available in 2024.

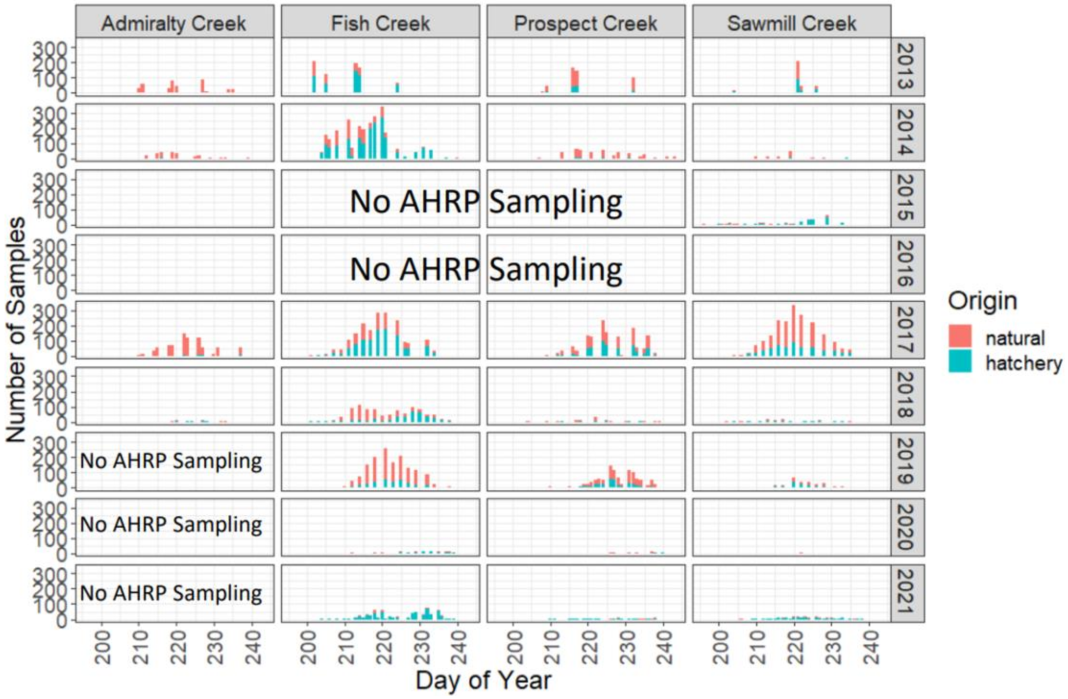


Figure 15. Sampling of Southeast Chum Salmon for pedigree analysis. 2022 samples are currently being processed to determine origin. From Shedd 2022.

In an AHRP-associated study on Sawmill Creek in 2015, differences in fitness-associated traits were observed between hatchery and wild Chum Salmon (McConnell et al., 2018). As of 2015, hatchery releases had occurred in nearby waters for 28 years (5 to 8 generations) using mixed broodstock originally sourced from Sawmill Creek and four other locations. Sawmill Creek has evidence of long-term immigration of hatchery fish, with strays recorded as early as 1995, and a pHOS of 0.152–0.512 from 2013–2015. In 2015, hatchery strays entered the creek later, were younger, and smaller than their wild counterparts. Hatchery-origin females lived shorter duration in-stream than wild origin females, and retained 28% more eggs, though this was linked to arrival timing and not necessarily origin (Fig. 16).

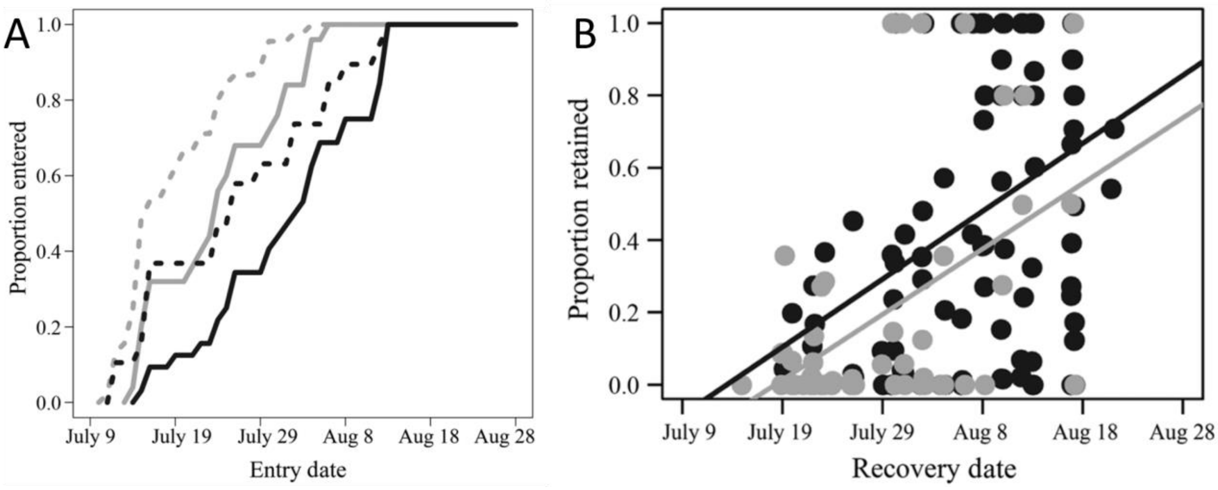


Figure 16. 2015 brood year characteristics for Chum Salmon in Sawmill Creek, Southeast Alaska. A: Cumulative proportion of Chum Salmon entering Sawmill Creek. B: Proportion of eggs retained by natural and hatchery-origin female Chum Salmon. Dashed lines: male, solid lines: female. Grey: natural-origin, black: hatchery-origin. From McConnell et al., 2018.

Given the extent of hatchery straying that has occurred, the phenotypic differences between hatchery and wild Chum Salmon in Sawmill Creek are surprising. One explanation is that hatchery and wild spawners are segregated, thereby unable to interbreed. McConnell et al., (2018) observed hatchery-wild temporal overlap in 92% of visits to Sawmill Creek, and all spawning occurred within a 300m reach, suggesting extensive spatial and temporal overlap. Both male and female hatchery fish arrived to the stream 10 days later than wild-origin fish and had to displace natural fish to spawn. This, alongside smaller body sizes for competition and redd building, put hatchery fish at a competitive disadvantage that may be reflected in greater egg retention. In Sawmill Creek, hatchery Chum Salmon spawning also coincides with high Pink Salmon abundance and periodic hypoxic conditions (Sergeant et al., 2017), which may further contribute to reduced reproductive success and limited gene flow to wild populations.

Potential mechanisms for reduced reproductive success in hatchery fish

Domestication selection/relaxation of natural selection

Domestication selection is the process by which a wild-origin population genetically adapts to captivity. This occurs simultaneously with the relaxation of selective pressures imposed in natural systems. These pressures are applied to hatchery fish due to differences in their life histories to wild fish. In hatcheries, unfertilized egg to fry survival is approximately 90% for Pink and Chum Salmon, (PWSAC, 2022a; NSRAA 2022), whereas in wild systems this value is 7–9% (Bradford, 1995). Environmental factors contributing to this difference include regulation of temperature, oxygenation, substrate quality, egg density, and egg disinfection in hatcheries. Hatchery-origin Pink and Chum Salmon are held in saltwater net-pens for 6 and 12 weeks respectively (PWSAC, 2022a) and fed fishmeal. Net pen rearing alters their early marine experience relative to wild-origin fish, that experience high size-specific mortality (Beamish & Mahnken 2001). Once released, hatchery and wild-origin fish share a common marine-phase life history, although annual growth patterns sometimes differ by stock, suggesting different environments or feeding behavior (Beauchamp et al., 2007; Cross et al., 2009). As returning adults, hatchery fish that school at, and most commonly swim up fish ladders at hatchery sites are selected for broodstock, regardless of success in selecting suitable mates, or spawning sites. In Table 4, we summarize potential sources of domestication selection and relaxation of natural selection on hatchery fish.

Table 4. Potential sources of domestication selection and relaxation of natural selection and potential impacts on fitness.

Domestication selection	**Relaxation of natural selection**
Juvenile - Feeding on fishmeal - Volitional movement to net pens - Higher egg density Adult - Schooling outside of hatchery	Juvenile - Temperature and oxygen stress - Egg surface pathogens - Prey avoidance Adult - Mate selection - Spawning site selection

The effects of domestication selection and the relaxation of natural selection can be observed at several levels: germline, transcription, phenotype, and reproductive success. The AHRP identified differences between hatchery-origin strays and wild fish in terms of phenotype (body size, run timing, spawning location) and reproductive success, but the germline and/or transcriptional drivers of these processes remain poorly understood. To explore possible drivers for RRS and body size differences, we can make inferences from other Pacific Salmon species.

The reduction in fitness of hatchery-origin Prince William Sound Pink Salmon aligns with similar studies on other Pacific Salmon. Several studies compared the genetics (DNA sequences) and epigenetics (DNA-methylation) of wild-origin and hatchery-origin Steelhead and Coho. In hatchery-origin Coho, Le Luyer et al., (2017) identified differentially methylated regions in genes relating to osmoregulatory processes (smoltification), and swimming performance, corresponding with previously noted deficiencies in hatchery fish (Brauner et al., 1994; Shrimpton et al., 1994). In another study on Coho Salmon, hatchery rearing was associated with epigenetic modifications in the germline DNA of adult salmon that persisted in their offspring, even after 1.5 years in the ocean (Leitwein et al., 2021).

In Steelhead, changes in gene expression (Christie et al., 2016) and fitness (Christie et al., 2012) can be induced within a single generation of hatchery rearing. In a separate study on Steelhead, no hatchery or wild-origin specific differences were identified in DNA, however differentially methylated regions were identified in somatic cell DNA (non-heritable) and germ-cell DNA (heritable) (Gavery et al., 2018). Taken together with the Coho Salmon results, this suggests selective pressures from hatchery rearing induce changes at the epigenetic level, but not in terms of allele frequency. Epigenetic changes occur rapidly and are heritable for hatchery fish that return to the hatchery. The persistence of these modifications in the wild, in the case of staying fish, remains unknown. In zebrafish, epigenetic changes inherited from the mother undergo resetting during early development whereas epigenetic modifications from the father are stably inherited (Jiang et al., 2013). This may explain why the RRS was lower for hatchery-stray females than males in 3 of the 4 lineages examined (Shedd et al., 2022b). To quantitatively assess the persistence of epigenetic modifications brought about by hatchery rearing, it will be necessary to examine the survival of grand-offspring of hatchery strays.

Run Timing

In Pink Salmon, run timing is a heritable trait with much genetic variation (Smoker et al., 1998). Interannual variation in freshwater environments (temperature) allows genetic variation in run timing within populations to persist. Even and odd year Pink Salmon lineages from the same river systems consistently evolve the same run timing in the absence of interbreeding, suggesting environmental conditions can shape the run timing of populations (Oke et al., 2019). Parallel evolution between lineages is observed in streams with less than 40 years of data. In Chinook and Steelhead Salmon, run timing has been linked to a single locus containing two genes: GREB1L and ROCK1 (Hess et al., 2016; Waples et al., 2022). Fish with early run timing consistently display different GREB1L/ROCK1 genotypes than fish with late run timing (Narum et al., 2018; Willis et al., 2020; Thompson et al., 2020). It is unknown whether the heritability of run timing in Pink Salmon is also mediated by GREB1L/ROCK1. The placement of Pink Salmon in the Salmonid phylogeny suggests they inherited these genes, however Pink Salmon run timing varies little relative to Chinook and Steelhead Salmon (a few weeks versus between seasons).

Prince William Sound hatchery strays generally return later than wild-origin fish. Late run timing in a wild system may reduce reproductive success by a variety of mechanisms discussed below.

1. **Differential fishing pressure**: In Prince William Sound, commercial harvest is highly spatially and temporally variable during the months of Pink Salmon returns. Across PWS, 94–99% of hatchery fish are harvested, whereas only 27–50% of natural-origin fish are harvested (Knudsen et al., 2021). In a natural stream, the offspring of hatchery strays may inherit the late run-timing of its parents and be exposed to fishing pressures for hatchery fish, whereas the offspring of wild fish, born in the same river, may inherit the early run timing of their wild-origin parents and be exposed to less fishing pressure. In 2016, little fishing pressure was applied to western Prince William Sound, and Hogan and Stockdale hatchery stray RRS remained low, suggesting commercial harvest is not the sole driver of RRS.
2. **Straying fish delays**: It may be the case that hatchery strays take longer to find and utilize a suitable spawning location than wild fish. In a survey of hatchery and wild fish from 2017 and 2018 in Paddy and Erb Creek, hatchery strays spent on average 2 days longer in spawning streams than wild-origin fish, though few hatchery strays were collected and this difference was not statistically significant (McMahon 2021 Thesis).
3. **Spawning ground competition**: When hatchery fish do escape commercial harvests and stray into wild streams, they face more spawning ground competition than wild-origin fish that arrive on average, 5 days earlier for males and 2 days earlier for females (Shedd et al., 2022). This later spawning time may place the hatchery fish at a disadvantage for competing for prime spawning habitat.
4. **Egg incubation temperature:** Timing of spawning is correlated to temperature regimes experienced by juveniles, with earlier spawning in colder systems (Sheridan, 1962; Hogson & Quinn, 2002). In the Auke Lake System in Southeast Alaska, early spawning fish utilized cooler upstream waters and late spawning fish used warmer downstream waters (Fukushima & Smoker, 1997). The two groups were expected to have synchronous fry emergence. The late season, upstream spawning of strays observed in Shedd et al., 2022 may result in too low of incubation temperatures for their progeny and suboptimal emergence time.

5. **Temporal sampling bias**: Finally, sampling efforts in Prince William Sound were biased towards the beginning of the run, and the tail ends of the run were not always captured (Shedd et al., 2022a). Perhaps late-returning progeny of hatchery strays were excluded from sampling efforts.

Spawning ground familiarity

A final, non-heritable driver of RRS in hatchery strays may be a lack of familiarity for spawning grounds. Wild fish chemically imprint to highly specific areas within a stream as juveniles and return to the same location to spawn as adults (Bentzen et al., 2001; Neville et al., 2006; Barnett et al., 2019). Sockeye Salmon in particular, can return to spawn within 50 meters of their natal site (Quinn et al., 2006). Sockeye Salmon that spawn further from their natal site have lower reproductive success, even if spawning occurs within 500 meters of their natal site (May, 2022). A similar, though less fine-scale relationship between natal homing and fitness was identified in Atlantic Salmon (Mobley et al., 2019). Fitness associated with precise homing is an example of microgeographic adaptation (Richardson et al., 2014). These results in sockeye and Atlantic Salmon suggest that straying fish, regardless of hatchery or wild origin, are at an inherent fitness disadvantage due to maladaptation. In Prince William Sound Pink Salmon, it may be that the reduced RRS observed in hatchery strays is indicative of all fish that stray from their natal stream, regardless of hatchery or wild origin (Ueda 2012).

Strays, regardless of origin, may have maladapted immunological profiles for their spawning environment. Anadromous Pacific Salmon heavily express the stress hormone cortisol during the return to freshwater. Cortisol assists in freshwater adaptation but inhibits B cell development and proliferation, leaving spawners vulnerable to infections (Zwollo, 2018). In mammals, long-lived plasma cells (LLPCs) secrete pathogen specific-antibodies and survive years in bone marrow without the replenishment of new memory B cells (Slifka et al., 1998). In teleost fish, which lack bone marrow, LLPCs are stored in the interior kidney and perform a similar function (Schouten et al., 2013).

The “immunological imprinting hypothesis” (Zwollo, 2012) proposes that juvenile salmon develop immunological profiles specific to the pathogen fingerprint of their natal site. This early adaptive immunity is stored in the “immunological memory” of LLPCs, which later defend returning spawners from the pathogens of their natal streams. More broadly, this may explain some of the fitness advantage of returning to the natal site, and the disadvantage of straying.

In testing the hypothesis, Sockeye Salmon were found to secrete IgM from LLPCs constitutively though spawning in parallel with depletion of developing B cells (Schouten et al., 2013). Sockeye Salmon from geographically distant sites in Alaska expressed varying levels IgM, with unique compositions of Immunoglobin V_H gene families for each site. V_H gene expression was also correlated to the presence of fish pathogens in the natal streams (Chappell et al., 2017). Altogether, these results align with the “immunological imprinting hypothesis.” By this mechanism, straying fish arrive in wild systems immunologically ill-prepared, which may contribute to reduced fitness.

Considerations for Management

In future years, hatcheries may adapt practices to mitigate potential negative consequences of hatchery-origin fish straying into wild systems. These changes should aim to increase hatchery salmon homing or reduce hatchery salmon straying. A third possible approach to “rewild” hatchery fish has been explored in conservation hatcheries with natural rearing (Tave et al., 2019; Sheller & Bruchs, 2020) or by integrating wild broodstock (Hayes et al., 2013). Integration of wild broodstock has been employed with success in Chinook Salmon conservation hatcheries outside of Alaska (Fast et al., 2015; Waters et al., 2020). However, the large broodstock requirements of production hatcheries and potential to deplete wild stocks makes this strategy problematic for Alaska. Given the scale of Alaskan production hatcheries, and difficulty in unraveling the source of fitness discrepancy between hatchery strays and wild fish, we only propose methods to address homing and straying.

Strategies to increase homing

Adult salmon use magnetic fields to navigate from the open ocean to their natal coastal range (Putman et al., 2013) and then olfactory cues to identify their natal river and spawning site (Hasler & Scholz, 2012; Keefer & Caudill, 2014b). Amino acids are a signal for olfactory homing of Pacific Salmon (Yamamoto et al., 2013) and are released in natural rivers by biofilms (Ishizawa et al., 2010) and sediment (Thomas & Eaton, 1996).

Artificial imprinting odors

Potential for artificial imprinting odors to boost homing has long been speculated (Hasler & Scholz, 2012), but has been explored little in recent years. Early efforts had mixed success in boosting homing (Cooper et al., 1976; Rehnberg et al., 1985; Hassler & Kucas, 1988). These experiments utilized an artificial compound, morpholine, rather than amino acids as a homing signal and only imprinted fish at the smolt life stage. More recent work suggests imprinting occurs while fish are embryonic and during parr-smolt transformation (Dittman et al., 2015). An experiment currently ongoing at the Oregon Hatchery Research Center (OHRC) imprinted embryonic and parr Chinook Salmon with a cocktail of amino acids, released the imprinted and tagged fish as smolt in 2020, 2021, and 2022. In 2024, adult fish will begin to return to a spawning ladder also releasing the amino acid cocktail (OHRC, 2022). In Alaska, potential applications of this research may include adding porous, solute-releasing sediment to rearing waters, adding biofilm-covered organic substrates like macroalgae to hatchery sites (Weigel et al., 2022), or the addition of unique chemical cocktails to rearing waters and hatchery discharge similar to the OHRC.

Strategies to reduce straying

Temporal segregation

In Prince William Sound, hatchery broodstock were selected to provide diverse fishing opportunities across the entire season, not necessarily for maximal temporal and spatial separation from wild fish (Fig. 3). Presently, broodstock is harvested during historical run peaks to preserve run timing. To enhance temporal separation, hatchery broodstock may be intentionally taken further from the peak of wild returns, e.g. earlier at SGH, and later at AFK. A consequence of this strategy is that hatchery strays will become more divergent in run timing from wild fish, spawning at a highly suboptimal time. This will decrease their overlap with wild fish and also decrease the relative survival of their offspring. This presents a "double-edged sword" that conflicts with Alaska's strategy of minimal stock manipulation. Limited temporal overlap would limit introgression, but in the case of hatchery-wild hybridization, reduced fitness could exacerbate the consequences of introgression.

New broodstock

As an alternative to manipulating current broodstock, the hatcheries that produce the most strays (AFK, WNH) could source more suitable broodstock from current wild PWS populations. Different Pink Salmon populations may stray more or less than others, as has been found with Chinook Salmon (Westley et al., 2015). Whereas SGH and CCH acquired ancestral broodstock from individual sources, the ancestral AFK broodstock, which was later propagated at WNH, came from multiple wild populations (Habicht et al., 2000). This may have inadvertently introduced fish with inherently higher stray rates. For new broodstock, a source population could be selected with a low natural stray rate and limited temporal overlap with wild fish.

Spatial segregation

Spatial overlap of hatchery and wild fish is dependent on run timing; however, management strategies may reduce spatial overlap without changing run timing. The fishery in the Eastern district of Prince William Sound may currently serve as a model of this. SGH in the Eastern district is the largest single producer of Pink Salmon fry in the state of Alaska, and its early run timing coincides with wild stocks in the region. Despite this overlap, the pHOS of the Eastern district is the second lowest in the Prince William Sound. This may be due to the relatively aggressive harvest of the fishery in the early season, with pressure on Jack Bay along the migratory path of incoming adults. Perhaps aggressive and early harvest of hatchery fish, at the expense of increased wild fish harvest, may reduce hatchery fish residence time in Prince William Sound and reduce straying. At AFK a barrier net was historically used to reduce hatchery fish residence time and potential to leave the bay, however private lodges in the area and fish crowding concerns prevent similar redeployment today.

Reduced hatchery production

The current management strategy in PWS is informed by in-season sampling (Russell et al., 2021) and successfully captures 94–99% of hatchery Pink Salmon that enter PWS (Knudsen et al., 2021). However, given the large abundance of hatchery returns (43.8–77.3 million Pink Salmon), this donor rate of 1–6% can represent a major source of introgression, particularly in small streams near hatcheries. It remains unknown whether hatchery strays are augmenting or replacing wild-origin fish, however reducing total hatchery releases may reduce pHOS. Reductions in production may be particularly effective at the AFK Hatchery in Southwest PWS where the wild runs are relatively small and where most hatchery and wild fish pass nearby on their migratory path into Prince William Sound.

Conclusions

Below, we revisit the priority questions of the Alaska Hatchery Research Program:

1. What is the genetic stock structure of Pink and Chum Salmon in each region?

Within Prince William Sound, Pink Salmon have similar genetic differentiation to Pink Salmon from other similarly sized regions (Cheng et al., 2015). Of the four contemporary hatchery Pink Salmon stocks in PWS, fish from AFK Hatchery were the most similar to wild fish in streams. Since the 1990s, even-year wild fish in streams had become more similar to AFK fish. A similar result was observed in PWS Chum Salmon, though rates of introgression were driven more by temporal overlap with wild fish than pHOS (Jasper et al., 2013). Odd-year wild fish had become less similar to SGH, potential due isolation and genetic drift of the hatchery broodstock. Like PWS Pink and Chum Salmon, Southeast Chum Salmon show genetic differentiation corresponding to geography and run timing (Habicht et al., 2022). Genetic introgression by hatchery strays into wild Southeast Chum Salmon populations remains to be tested.

2. What is the extent and annual variability in straying of hatchery Pink Salmon in Prince William Sound (PWS) and Chum Salmon in PWS and Southeast Alaska (SEAK)?

In PWS between 2013 and 2015, the total proportion of hatchery-origin straying Pink Salmon ranged from 0.05 to 0.15 (Knudsen et al., 2021). This proportion is highly variable between streams, with the highest pHOS found near hatcheries. Excluding Eshamy District, which contributes less than 1% of Pink Salmon escapement, the largest district-wide pHOS consistently occurred in the Southwestern district. Southwestern District contains the AFK Hatchery and the predominant migratory pathway for all Pink Salmon entering PWS. For PWS Chum Salmon, the total proportion of hatchery-origin strays in PWS ranged from 0.03 to 0.06 with the highest proportion of hatchery-origin strays in Montague District, which contains the Port Chalmers remote release site Knudsen et al., 2021). The pHOS of Southeast Chum Salmon ranged from 0.03 to 0.09 between 2013 and 2015 (Josephson et al., 2021). As was the case in PWS Pink and Chum Salmon, pHOS was highest near hatcheries and remote release sites.

3. What is the impact on fitness (productivity) of wild Pink and Chum Salmon stocks due to straying of hatchery Pink and Chum Salmon?

This component of the AHRP is still ongoing with additional results expected in 2023 and 2024. Presently, fitness data is available for Prince William Sound Pink Salmon from 2013 and 2014 brood years from two streams (Shedd et al., 2022a). Preliminary data is available from 2014 brood year fish from three other streams Shedd et al., 2022b. RS for hatchery-origin strays relative to their natural origin counterparts is highly variable between brood year, stream, and sex, with values ranging from 0.03–0.96. In all streams, hatchery-origin fish spawned later in the season and further upstream than their wild-origin counterparts. Body length was generally greater in hatchery-origin fish. When accounting for these differences, RRS for the 2014-year broodstock of hatchery strays was 0.42–0.60. This suggests additional factors besides spawning date, spawning location, and body size are contributing to reduced fitness. It remains unknown whether hatchery strays convey a heritable, lasting fitness disadvantage to wild populations, or the reduced RRS observed is ephemeral, and caused by other factors. We summarize possible mechanisms driving RRS in the section *Potential mechanisms for reduced RRS in hatchery fish*. Further, hatchery straying may impact wild populations in a manner irrespective of reproductive success, for example genetic homogenization might be detrimental to the resilience (e.g. portfolio effect (Schindler et al., 2010)). Future studies should seek to identify the most likely mechanism at play and recommend adjustments to management accordingly.

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