

OCEAN AND STREAM ECOLOGY OF ADULT HATCHERY AND WILD PINK
SALMON

By

Julia McMahon, B. A.

A Thesis Submitted in Partial Fulfillment of the Requirements

for the Degree of

Master of Science

in

Fisheries

University of Alaska Fairbanks

August 2021

Peter Westley, Ph.D., Committee Chair
Kristen Gorman, Ph.D., Committee Member
Megan McPhee, Ph.D., Committee Member
Peter Rand, Ph.D., Committee Member
Andrew Seitz, Ph.D., Chair
Department of Fisheries
S. Bradley Moran, Ph.D., Dean
College of Fisheries and Ocean Sciences
Richard Collins, Ph.D.,
Director of the Graduate School

Abstract

In this thesis I investigate potential interactions of hatchery and wild pink salmon (*Oncorhynchus gorbuscha*) at sea and on the spawning grounds, in the context of the ecological and economic importance of modern Alaskan hatcheries. Although hatchery and wild salmon are known to interact, the nature and outcome of those interactions remain unclear. Here, I identify potential mechanisms of competition and hatchery salmon fitness with two datasets from Prince William Sound, Alaska, home to the largest pink salmon hatchery program in the world. First, I compared fitness-related traits such as body length, return timing, instream lifespan, and egg retention between straying hatchery and homing wild pink salmon to identify potential barriers or bridges to gene flow with over 120,000 individuals sampled over six years (2013–2018). Predicted lengths of hatchery and wild fish depended on the even or odd year lineage, return timing, and sex. Odd year pink salmon were smaller on average than even year pink salmon, odd year hatchery fish were smaller than wild fish, odd year length decreased over the season, and odd year males tended to be larger than females. In even years, hatchery pink salmon were larger on average than wild pink salmon, length increased over the season, and hatchery females were larger on average than any other group. I found no statistically significant differences in instream lifespan (2017: t-test_(20,54), P = 0.41; 2018: t-test_(6,26), P = 0.556) or egg retention ($\chi^2_{(2)} = 4.5$, p = 0.11; 2017 and 2018 combined) between hatchery and wild fish. In contrast, I detected significant differences in stream life of the wild fish between two different sized streams in a manner consistent with observed black bear (*Ursus americanus*) predation; specifically stream life was shorter in the smaller stream with markedly higher predation. Second, I used stable carbon and nitrogen isotope analysis to test the hypothesis that hatchery and wild pink salmon have distinct foraging niches during their last months at sea, which could underpin observed

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Acknowledgments

First, I thank the Rasmuson Fisheries Research Center for their Rasmuson Fellowship award that supported my academic research in Fairbanks, Alaska (AK) and made this work possible. I also thank the Northern Gulf of Alaska Applied Research Award that made it possible to have a full 2018 field season in Prince William Sound (PWS), AK. I am incredibly grateful to have been selected for the Alvin G. Ott Fish and Wildlife Scholarship award during the last year of my degree. Additionally, I thank the Prince William Sound Science Center, of Cordova, AK, for their logistical support and for sharing a field camp station in PWS during 2017 and 2018.

Second, I extend the most profound thanks to my advisor Dr. Peter Westley, who supported me through the trials of this academic journey at every turn and provided me with the tools to grow as a scientist and a professional. I thank my committee members Dr. Kristen Gorman, Dr. Megan McPhee, and Dr. Pete Rand for their guidance and patience as I navigated the writing process; this document and numerous presentations have benefitted from their insights and contributions throughout. A special thanks to the otolith reading experts of the Cordova Otolith Lab for reading the hundreds of pink salmon otoliths collected during my field seasons, I am in constant awe of their otolith reading accuracy and speed. I thank the Alaska Hatchery Research Project and the National Fish and Wildlife Foundation for supporting the science that made this project a reality and for generously providing access to the data. A very special and personal thanks to all of the field and lab technicians from the Prince William Sound Science Center involved in collecting and processing all of the hundreds of thousands of pink salmon carcasses with dedication and enthusiasm. Finally, I extend my eternal gratitude to my family, friends, and Salmonid Evolution Ecology and Conservation (SEEC) lab mates for their unwavering support and friendship during the pursuit of my goals.

Introduction

Captive breeding has long been seen as a solution to declines in economically important fisheries, such as those for Pacific salmon (*Oncorhynchus* spp.), yet hatchery practices can have far-reaching and unintended ecological consequences. For example, interspecific competitive interactions for resources in the open ocean are important for growth, which in turn influences biomass available for commercial fisheries harvests (Ruggerone et al. 2007; Ruggerone and Connors 2015). Pacific salmon are renowned for their ability to return to spawn in natal sites, termed ‘homing’; but dispersal to new sites, termed ‘straying,’ is equally important to gene flow and colonization in natural systems (Hanski 1998; Pess 2009; Yeakel et al. 2018). With the addition of numerically abundant hatchery-reared salmonids (Brenner et al. 2012) that may have been unintentionally selected for traits unsuited to wild spawning (Reisenbichler and Rubin 1999; Mclean et al. 2004; Tillotson et al. 2019), straying is usually referred to in a negative light for introducing potential spawning competition and maladapted alleles (Araki et al. 2008; Laikre et al. 2010; McConnell et al. 2018). However, the genetic effects of hatchery straying depend on the opportunity for reproduction. In Pacific salmon, reproductive potential can be mediated by a variety of life-history traits such as body size, run timing, instream lifespan, and egg retention (Quinn and Foote 1994; Bigler et al. 1996; Fleming and Petersson 2001; Dickerson et al. 2002; Quinn 2018). Despite the volume of literature surrounding these frequently studied life-history traits, relatively little is known about the traits of strays (but see Lin et al. 2008 and McConnell et al. 2018). Since these life-history traits are heritable to varying degrees, trait differences between stray hatchery and wild Pacific salmon may indicate mechanisms that reduce or enable gene flow and influence fitness (Bolnick et al. 2003; McConnell et al. 2018).

Body size, or length, directly and indirectly contributes to reproductive potential of salmonids through fecundity and egg size, as well as dominance and mate choice (Quinn and Foote 1994; Bigler et al. 1996; Fleming and Petersson 2001; Dickerson et al. 2002; Quinn 2018) and is a cornerstone of ecological studies of fitness (Garcia De Leaniz et al. 2007). Pacific salmon gain over 90% of their length at sea (Quinn 2018), where inter- and intraspecific competition among species may limit total growth (Ruggerone and Connors 2015) and reproductive potential (Essington et al. 1999). Currently, the abundance of sockeye (*O. nerka*), chum (*O. keta*) and pink (*O. gorbuscha*) salmon is particularly high, and hatchery production accounts for 40% of the total biomass in the North Pacific Ocean (Ruggerone and Irvine 2018). Pink salmon are the most abundant of these three species (Ruggerone and Irvine 2018) and their increasing numbers have coincided with declines in size and age at maturity for all species of Pacific salmon (Kendall et al. 2020; Oke et al. 2020). Although pink salmon appear to play a key role shaping North Pacific food webs (Springer and van Vliet 2014), and 29% of hatchery supplementation in the North Pacific Ocean is pink salmon (Ruggerone and Irvine 2018), most studies investigating foraging interactions among hatchery and wild Pacific salmon at sea are conducted on juveniles (Armstrong et al. 2008; Moss et al. 2009) or are concerned with interspecific interactions that do not identify hatchery or wild origin (Davis 2003; Kaeriyama and Qin 2014).

Prince William Sound (PWS), Alaska is an ideal ecosystem for investigating relationships between hatchery and wild Pacific salmon because it supports the largest pink salmon hatchery program in the world (NPAFC 2020), which overlaps with a substantial wild population. For the last three decades, hatcheries in PWS have released an average of 650 million juvenile pink salmon each spring (Stopha 2018). From 1990 through 2017, hatchery pink

salmon in PWS accounted for an average of 85% of the total pink salmon harvest, or 32 million fish annually (Evenson et al. 2018). Pink salmon have an obligatory two-year life cycle that reproductively isolates even- and odd-year populations in time (Aspinwall 1974; Beacham et al. 2012). Due to this short generation time and temporally isolated reproductive cycle between years, hatcheries might cause higher rates of genetic and phenotypic divergence in pink salmon compared to other salmon species, especially in hatchery systems that do not routinely introduce wild broodstock (Araki et al. 2008). Additionally, studies suggest that pink salmon stray to non-natal areas at higher rates than other species (Hendry and Stearns 2003), and hatchery Pacific salmon may stray more often than their wild conspecifics (Keefer and Caudill 2014; Bett et al. 2017). The parent stock for hatchery practice in PWS is locally sourced from within the region (Habicht et al. 2000), yet some domestication is likely because hatcheries have been cultivating the same brood line without intentional input of wild stock (i.e., segregated; Naish et al. 2007) for approximately 15 pink salmon generations (Evenson et al. 2018).

Generally, the extent of straying in PWS varies across spatial scales; streams closer to hatcheries (i.e., southwestern PWS streams) tend to have more hatchery strays, yet individual streams experience highly variable recipient straying rates within seasons and among years (Sharr et al. 1995; Joyce and Evans 1999; Brenner et al. 2012; Knudsen et al. 2021). Using coded-wire tagging, Sharr et al. (1995) found that 3 – 32% of sampled pink salmon from six wild salmon streams in PWS were hatchery strays, although coded-wire tag placement may have interfered with olfactory sensing and artificially increased straying (Habicht et al. 1998). Thermal marking of hatchery-reared Pacific salmon in Alaska (Volk et al. 1990) eliminated this complication and provided a new method to quantify the occurrence and distribution of hatchery strays. In 1997, average hatchery contribution to 13 southwestern streams in PWS was 65%

(Joyce and Evans 1999) and more recently, Brenner et al. (2012) reported hatchery contributions in streams across PWS ranged from 0 to 98% (mean 18%). Ongoing work of the Alaska Hatchery Research Project (AHRP), a stakeholder-involved inter-agency project led by the Alaska Department of Fish and Game, found that the average hatchery presence in streams sampled from 2013 to 2015 was 10%, but was highly variable among streams (0% – 92%; Knudsen et al. 2021). While the ongoing AHRP is testing for differences in fitness between hatchery and wild pink salmon in PWS with genetic analysis, differences in reproductively associated life-history traits of hatchery and wild pink salmon that could provide a mechanistic basis driving any fitness differences have not been thoroughly assessed.

The first chapter of this thesis quantifies differences in length, a key fitness trait, between hatchery and wild pink salmon from the extensive AHRP dataset that encompasses six years (2013 – 2018) and over 120,000 samples and quantifies life-history differences in freshwater instream lifespan and egg retention with a mark-recapture experiment in two streams over two years to assess these traits as potential barriers or bridges to hybridization.

The second chapter of this thesis focuses on whether foraging history as inferred from carbon and nitrogen stable isotope analysis provides evidence for a potential mechanism of decreased hatchery pink salmon length as compared to wild salmon using a unique dataset collected during 2015. This was assessed by 1) comparing the relative broad-scale spatial foraging niche of hatchery and wild pink salmon with stable carbon isotope values and 2) comparing the relative trophic position of hatchery and wild pink salmon with stable nitrogen isotope values.

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Chapter 1 Do fitness-associated reproductive traits differ between hatchery strays and wild pink salmon (*Oncorhynchus gorbuscha*)? A large-scale empirical test in Prince William Sound, Alaska¹

Abstract

Mounting evidence indicates that hatchery Pacific salmon (*Oncorhynchus* spp.) spawning in the wild are less fit than their wild counterparts, but the ecological mechanisms underpinning fitness variability among conspecifics are not well understood. Because body size often mediates reproductive performance and fitness, we quantified differences in body length between hatchery and wild pink salmon (*Oncorhynchus gorbuscha*) using a dataset of over 112,000 individuals sampled from 29 streams over six years (2013 – 2018) throughout Prince William Sound, Alaska. Additionally, we quantified instream lifespan and egg retention by females in two representative streams by tagging adults upon freshwater entry and tracking their fate. In odd years, when pink salmon returns were high, hatchery fish were 3.6% shorter (14.5 mm on average) than wild fish, but in even years when returns were low, hatchery fish were 1.0% longer (4.5 mm on average) than wild fish, revealing important between-lineage variability in body size. Body length of returning hatchery and wild pink salmon depended on timing, lineage, and sex. Hatchery and wild fish differed more in length early in a season and were similar-sized towards the end of a season, but comparative size of hatchery and wild pink salmon depended on lineage (even or odd year). In even years, hatchery fish were slightly larger on average and length increased over a season but in odd years, wild fish were larger and length decreased over a

¹ McMahon, J., P. Rand, K. B. Gorman, M. McPhee, and P.A.H. Westley. *In prep.* Do fitness-associated reproductive traits differ between hatchery strays and wild pink salmon (*Oncorhynchus gorbuscha*)? A large-scale empirical test from Prince William Sound. Canadian Journal of Fisheries and Aquatic Sciences.

season. Additionally, in both even and odd years, the size of hatchery fish varied less over a season compared to wild fish, especially for hatchery females. This suggests that hatchery fish may have reduced length-associated fitness early in the season during odd years, but greater length-associated fitness towards the end of a season in even years. Lifespan of hatchery fish on the spawning grounds was two days shorter than wild fish regardless of year (2017: t-test_(20.54), P = 0.41; 2018: t-test_(6.26), P = 0.556), although this was not statistically significantly different. We observed no differences in egg retention between hatchery and wild fish ($\chi^2_{(2)} = 4.5$, p = 0.11) and rates of egg retention were low overall (~10%). While this study was not able to detect significant differences in two related components of reproductive fitness (stream life and egg retention), the reported differences in size at time of spawning for hatchery and wild pink salmon may have fitness implications that should be explored further.

Introduction

Many captive-bred organisms have highly mobile life stages, can disperse to unintended locations, and interact with wild conspecifics (Clobert et al. 2001; Barbour et al. 2008). Dispersing captive-bred individuals can introduce traits that may have increased the success of individuals in captivity but are maladapted in the wild (Laikre et al. 2010; Gering et al. 2019). Captive breeding (i.e., hatchery production or sea-ranching) is frequently used to enhance commercially important fish species, such as Pacific salmon (Molony et al. 2003; *Oncorhynchus* spp., hereafter salmon), which are an anadromous group of semelparous fishes that return from the ocean to natal streams where they reproduce before dying (Quinn 2018). In natural systems, this ‘homing’ behavior reproductively isolates breeding populations, facilitating local adaptation (Hendry and Stearns 2003; Kawecki and Ebert 2004; Fraser et al. 2011). Pacific salmon enhancement strategies frequently rely on these homing abilities to replenish hatchery broodstocks and focus fishery harvest effort near hatchery release locations, yet some hatchery fish disperse to non-natal breeding sites (Keefer and Caudill 2014; Quinn 2018). Such dispersal, or ‘straying,’ is a fundamental and unavoidable phenomenon of salmon biology that mediates the demographic connection among populations (Hanski 1998) and can facilitate the recolonization of habitat following disturbance (Pess 2009; Yeakel et al. 2018). However, large-scale salmon hatcheries can dramatically increase the numbers and proportions of hatchery strays in wild breeding areas (Brenner et al. 2012; Bett et al. 2017; Knudsen et al. 2021), raising concerns over the genetic and ecological integrity of wild, locally adapted populations (Reisenbichler and Rubin 1999; Ford 2002; Anderson et al. 2012).

Mounting evidence suggests that there are substantial risks to the productivity of wild salmon populations based on the extent of interaction with captive-reared individuals (Christie et al. 2014). In salmon hatcheries, as few as two generations of breeding can alter patterns of

natural selection and decrease fitness (Araki et al. 2007), and many generations of hatchery breeding can further decrease fitness and create measurable phenotypic differences between captive-bred and wild individuals (Araki et al. 2008; Ford et al. 2016). Large body size and early return timing among salmon is often associated with increased fecundity and reproductive success (Dickerson et al. 2005), yet hatchery-produced salmonids tend to be smaller and less variable in size than wild fish upon return (Mclean et al. 2004; Knudsen et al. 2006). Earlier arriving fish tend to have longer instream lifespans and greater reproductive success (Hendry et al. 2003), and intentional and unintentional hatchery stock selection can alter return timing, creating a mismatch between hatchery strays and the wild spawning environment (Tillotson et al. 2019). Longer instream lifespans and lower rates of egg retention are associated with higher reproductive success (Dickerson et al. 2002), but in some systems hatchery fish have shorter in stream lifespans and retain more eggs post-mortem (McConnell et al. 2018). Quantifying differences in fitness-related life-history traits between captive-reared and wild individuals is an important step towards elucidating mechanisms that mediate gene flow (Bolnick et al. 2003), and can aid in assessing and developing management strategies focused on mitigating any negative impacts due to interactions between hatchery and wild salmon.

The majority of hatchery programs in Alaska were established to support commercial fisheries and have a deliberately conservative set of regulations that aim to guard against risks associated with hatchery and wild interactions (McGee 2005, Evenson et al. 2018). Hatchery programs in Prince William Sound (PWS), Alaska, are the largest pink salmon enhancement effort in the world (NPAFC 2020), providing a natural experiment for investigating hatchery and wild spawning interactions of this ecologically and economically influential species. Hatcheries in PWS use thermal otolith marking to differentiate between other hatcheries, brood years, and

wild fish (Volk et al. 1990). To clarify terminology used in this paper, ‘hatchery’ refers to an adult fish that was sampled and identified as hatchery origin by a thermally marked otolith, thus was bred and raised in a hatchery until the fry stage (~2 cm long). ‘Wild’ refers to an adult fish that was sampled and observed without a thermal mark, and therefore developed in a stream without human intervention.

To date, studies comparing hatchery and wild salmonids have focused on species associated with extended freshwater rearing such as steelhead trout (*O. mykiss*) and coho salmon (*O. kisutch*; Araki et al. 2008). Few studies on hatchery and wild pink salmon (*O. gorbuscha*) have been conducted despite pink salmon being the numerically dominant salmon species (Ruggerone and Irvine 2018), with a strong hatchery presence in some regions. Hatcheries in PWS have cultivated pink salmon over 15 generations, which is sufficient time for the relaxation of natural selection to result in measurable phenotypic divergence that might interfere with their reproductive success in the wild. Furthermore, pink salmon’s obligatory two-year life cycle isolates even- and odd-year populations (Aspinwall 1974; Beacham et al. 2012), meaning that the process of divergence between hatchery and wild pink salmon in PWS has been replicated independently. While the presence of hatchery pink salmon in wild salmon streams of PWS has been documented for decades (Sharr et al. 1995; Joyce and Evans 1999; Brenner et al. 2012, Knudsen et al. 2021), little attention has been given to the potential mechanisms underlying the ecological and evolutionary impacts of stay hatchery fish.

The purpose of this study was to quantify phenotypic traits related to reproduction of stray hatchery and wild pink salmon on a regional and within-stream scale in PWS, Alaska. To achieve this, 257,353 pink salmon were sampled from 29 streams over six years (2013–2018), and 1,199 pink salmon were tracked from freshwater entry until death in two streams in two

years (2017–2018). On a regional scale (objective 1), we hypothesized that the body length of hatchery and wild pink salmon would differ and the extent to which differences varied would depend on fish origin, lineage (even vs. odd), sampling date, and sex. Our hypotheses were based on previous studies showing that salmon of hatchery origin tend to be smaller than their wild conspecifics (McClean et al. 2004; Knudsen et al. 2006; McConnell et al. 2018); commercial catch records of PWS indicate that pink salmon weigh less (and thus are probably shorter) in odd years of high abundance than in even years of low abundance (Wiese et al. 2015; Haught et al. 2017; Russell et al. 2017; Vega et al. 2019); pink salmon size and arrival date can have negative (Skud 1958), positive (Pritchard 1937; Beacham et al. 1988), or neutral (Pritchard 1937; Dickerson et al. 2002) relationships primarily depending on sex, and year; and finally, male pink salmon tend to be larger than females (Pritchard 1937; Quinn 2018). The second objective of this paper is focused on investigating two traits linked to reproductive fitness in two streams in two years (objective 2). In this second objective, we hypothesize that instream lifespan is lower and egg retention is higher in stray hatchery than wild pink salmon, as seen in hatchery and wild chum salmon (Berejikian et al. 2009; McConnell et al. 2018).

Methods

Study system

Prince William Sound (Figure 1.1) is located in southcentral Alaska and supports five species of Pacific salmon, but is numerically dominated by pink salmon, chum salmon, and to a lesser extent sockeye salmon (Clark and Thiessen-Bock 2018). The study area encompasses roughly 9,000 km² and receives around 350 cm of precipitation annually (Kibele and Jones 2018). There are over 1,000 documented salmon streams in PWS; they are characteristically small, short, and steep, with rain dominated hydrology and minimal yet productive salmon

spawning habitat (Moffitt et al. 2014). Spawning habitat is restricted to lower stream reaches and intertidal zones where gravel substrate supports hundreds of thousands of spawning salmon annually from June through October. Pink salmon returning to eastern PWS have historically arrived and spawned two weeks earlier (approximately mid-July) than western PWS populations (Helle et al. 1964; Fukushima and Smoker 1997). Pink salmon in western PWS generally spawn from early August through mid-September. Upstream migrations are generally short and limited by suitable spawning habitat, and as many as 75% of PWS pink salmon spawn intertidally (Helle et al. 1964; Sharp et al. 1994).

Regional scale field methods

To determine if body length differed by lineage, within-season arrival timing, origin, or sex, we used a multi-year pink salmon dataset collected by the Alaska Hatchery Research Project (AHRP) from 2013 to 2018. The AHRP is a collaborative effort between the Alaska Department of Fish and Game (ADF&G) and commercial salmon fishing industry partners in aquaculture; it was designed and is managed by scientists and industry partners and is expected to continue through 2021. In PWS, data were collected by the Prince William Sound Science Center following protocols and sampling collection procedures described by Knudsen (2021), and are briefly outlined below.

The majority of samples were collected during mid to late August and early September each year, reflecting the peak spawning season. Upon collection in the field, each carcass was measured (mid-eye to hypural plate; mm), sex was recorded (based on external and/or internal inspection), evidence of failure to spawn or predation marks were noted, and GPS coordinates were documented. Finally, sagittal otoliths were removed, placed individually into 48- or 96-well plates (hereafter “tray”) and stored for post-season processing to determine origin. All thermally

marked (hatchery) and unmarked (wild) otoliths were identified by ADF&G's Cordova, Alaska Otolith Lab (Fernandez & Moffitt 2016).

For the majority of creeks, the number of otoliths collected each year exceeded the minimum number of otoliths specified in the sampling protocol. Thus, subsets of otoliths from each stream were selected for analyses in the following fashion: every n^{th} full tray of otoliths was selected where $n = \text{the number of trays per stream divided by eight}$ (Kyle Shed, ADF&G, pers. comm.). This process of sub-setting the collected otoliths was applied to all streams regardless of sampling frequency except for those from Hogan Bay and Stockdale creeks, which were almost entirely sampled because they were assigned as priority streams by the AHRP. Of the 257,323 samples collected from the 29 streams (Figure 1.1), 112,180 samples had otolith readings as well as other necessary information at the time of analysis. These data were archived by the AHRP, and used here to compare body length of hatchery and wild individuals (Table 1.1).

Regional scale analytical approach

To determine if there were body-length differences between hatchery and wild pink salmon, linear mixed-effects models (Bates et al. 2015) were used to test our hypothesis that body length was influenced by the fixed effects of run-timing, lineage, sex, and/or origin while accounting for the random effect of stream and within-stream sampling order (upstream to downstream or vice versa). Run-timing was represented by carcass sample date within spawning seasons, 'lineage' was the even- or odd-year of sampling, origin was assigned from otolith readings as hatchery or wild, and sex was assigned based on external and internal traits. All statistical analyses were conducted using the R language environment (version 3.6.1, R Core Team 2019).

Streams were selected with a stratified random sampling design (Knudsen et al. 2021), so stream identity was included as a random effect to account for unbalanced sample numbers and uneven proportions of hatchery and wild fish among streams (Bennington & Thayne 1994). Additionally, because sample collection in the field (up or downstream) and tray selection in the lab were non-random we included ‘tray’ as a random effect nested within the random effect of stream. Effectively, this acknowledges that the selected streams ($n = 29$) and trays ($n = 2,735$) in this dataset are only a small amount of the total number of possible trays and streams in PWS (which follow the “true” mean, with normally distributed variance; Harrison et al. 2018). We used a likelihood ratio test to confirm that the model performed better with the nested random intercept compared to a non-nested stream-only design ($\chi^2_{(1)} = 12,731, p < 2.2e^{-16}$), and a linear model without any random effects ($\chi^2_{(2)} = 14,382, p < 2.2e^{-16}$).

After determining the appropriate model structure, we used two methods for developing specific models to test combinations of lineage, timing, origin, and sex to predict mid-eye-hypural length of pink salmon. First, we developed hypotheses based on existing knowledge of differences between hatchery and wild salmon. For example, hatchery fish tend to arrive later than wild fish in PWS (Brenner et al. 2012) because they were selected from later arriving broodstock (Habicht et al. 2000); hence an interaction between sample date and origin was predicted. Second, since pink salmon have distinct abundance, age, and timing patterns compared to other species it was also necessary to visually assess the data to determine the extent of biologically plausible interactions. For example, we assumed that males would be more abundant in the creeks at earlier dates than females (Nickerson 1979); however, this applied to hatchery fish but not wild fish, so we included an interaction between origin and sex. We gauged model success by comparing the model with the lowest Akaike's Information Criterion corrected

for small sample size (AICc) value to that of the next best model (Δ AICc) where models more than 2 AICc units lower were considered significantly better than the next (Burnham and Anderson 2002). All models were fit using the lmer function in the R package ‘lme4’ (Bates et al. 2015) and model selection was done using the R package ‘AICcmodavg’ (Mazerolle 2019).

Local scale field methods

We conducted a mark-recapture study in Paddy and Erb creeks (Figure 1.1) to compare the instream lifespan, egg retention by females, and changes in these traits over the 2017 and 2018 spawning seasons for hatchery and wild pink salmon. For each tagging event, the goal was to tag 100 or 200 fish depending on the run timing (Table 1.2). In 2017 there were two tag groups at Paddy Creek for a total of 200 fish tagged. In 2018, there were three tag groups at each creek for a total of 999 fish tagged. Based on results in 2017, we weighted tagging events in 2018 towards the latter half of the run in an attempt to tag enough hatchery fish to have sufficient statistical power to make comparisons between hatchery and wild fish. Over the two years 1,199 individuals were caught prior to spawning (see below), anesthetized, externally marked with a unique tag color coded by release group, and released. Subsequently, exhaustive effort was made to re-sight tagged live fish and recover tagged carcasses.

Pink salmon were captured from the nexus of the tide line and the mouth of the creek by beach seine (30 x 3 m, 2-mm mesh), and any captured fish that showed signs of spawning activity (identified by scarring or wear on snout, dorsal hump, and/or fins) were immediately released so that only individuals that had not started spawning were tagged (hereafter noted as ‘pre-spawned’). Individuals selected for tagging (Peterson disc, 1.25 in) were sedated with Aquis 20E® (30 ppm). Fish were released and monitored as they recovered. No mortalities associated

with tagging were observed. Once a tag group was established, daily surveys were conducted to re-sight tagged individuals and recover tagged carcasses that died, by senescence, stranding, or predation by black bears, *Ursus americanus*, since the previous survey. Surveys included exhaustive searches of stream banks up to 20 m into adjacent woods to recover bear-killed fish. Additionally, surveys coincided with low tide every day to re-sight intertidally spawning tagged individuals. All carcass data were collected in accordance with the AHRP sampling protocols. Carcasses of females showing no signs of predation were dissected and egg retention was qualified visually as ‘spawned’ (less than 20 remaining eggs), ‘partially spawned’ (20 or more remaining eggs), or ‘pre-spawned’ (females with complete gonads). Any female showing evidence of predation was excluded from egg retention analysis due to likely egg loss during a predation event. Any whole tag (two discs still attached to the pin) recovered from adjacent woods or stream bank without a fish was presumed to be bear-killed. Tag surveys were conducted until the last living tagged fish senesced.

Local scale analytical approach

We used t-tests to determine whether body length of hatchery and wild pink salmon tagged in 2017 and 2019 were different within each year. Differences in seasonal run timing were described by the minimum and mean carcass-recovery dates of hatchery and wild pink salmon. Instream lifespan was defined as the number of days from first re-sight in freshwater to carcass recovery. Egg retention was categorized as spawned, partially spawned, or pre-spawned. Specimens were not included in the instream lifespan analyses if they were missing both otoliths, were recovered as carcasses without re-sighting events, or were preyed upon. Specimens were not included in the egg retention analysis if they were missing both otoliths or were preyed upon.

After excluding such specimens, 36 and 202 individuals with otoliths were used in analysis for 2017 and 2018, respectively.

Results

Regional differences in fitness-associated traits

At the regional scale, the best-supported model for body length included a four-way interaction between lineage, sampling date, origin, and sex (Table 1.3). Hatchery and wild pink salmon differed in average length, but the direction and magnitude of the difference depended on the interaction of lineage, timing, origin, and sex (Figure 1.2). Body length of hatchery and wild fish was greater in even than odd years, had different slopes by lineage (even- or odd-year) within a season, and the difference in average body length within an even- or odd-year season was different between sexes (Table 1.4). Pooled across all years, model predictions indicated the average wild pink salmon was 0.9% longer (3.8 mm) than the average hatchery fish; however, this minimal overall difference masked variation due to the contradictory influences of lineage (even-year and odd-year), timing, origin, and sex. Regardless of origin, even-year fish were 4.6% longer (18.9 mm) on average than odd-year fish. Including origin, body length depended on lineage; in even-years, average hatchery fish were 1.2% longer (5.1 mm) than wild fish, but in odd-years, average hatchery fish were 3.1% shorter (12.7 mm) than wild fish. This contrasting length and lineage pattern also had contrasting within-season patterns. The magnitude of change in average body length over a season differed between hatchery and wild fish of different sexes and between lineages (Figure 1.2). Consistent with length and sex patterns in other salmonids, we found that males were larger than females in odd years; however, even-year hatchery females were 1.8% longer (7.7 mm) than all other even-year males and wild females. This difference was most apparent early in the season when early arrival timing was coupled with longer length.

Based on the date of first carcass recovery, as averaged over three even and three odd years, hatchery presence in spawning streams was documented five days later than initial wild presence in even years and eight days later than wild presence in odd years (Figure 1.3). Hatchery and wild fish had relatively equal sex ratios over the season, and as expected, male wild fish arrived slightly earlier than female wild fish. However, early in the season, female hatchery fish tended to be sampled in greater numbers than male wild fish, indicating that female hatchery fish arrive, spawn and die earlier on average than male hatchery fish.

Local differences in fitness-associated traits

Of the 200 tags deployed in 2017, 99 tags were recovered, but due to black bear predation, only 74 carcasses had otoliths that were identified to origin. In 2018 we had a 72% tag recovery rate from both creeks (719 tags), yet only 117 and 327 tagged carcasses were recovered with otoliths from Paddy and Erb creeks, respectively. Bear predation was 75% higher at Paddy Creek than Erb Creek. We expected 15–40% of tagged fish would be of hatchery origin in each year (Sharr et al. 1995; Brenner et al. 2012; Knudsen et al. 2021); but cumulatively, only 7% (37) of the 527 specimens recovered were identified as hatchery fish.

The body lengths of recovered hatchery and wild pink salmon in Paddy and Erb creeks were not statistically different ($t_{42} = 0.82$, $p = 0.41$), and fell within the expected length range based on the greater PWS model in 2017 and 2018. In 2017, the average body length (\pm sd) of female hatchery fish (398 ± 14 mm) tended to be smaller than wild (416 ± 25 mm), while hatchery and wild males had similar body lengths (435 ± 37 mm and 431 ± 53 mm, respectively). In 2018, the average length of hatchery females (434 ± 19 mm) and males (431 ± 15 mm) was larger than that of wild origin females (423 ± 20 mm) and males (418 ± 35 mm).

Tagged hatchery and wild pink salmon overlapped in space and time in Paddy and Erb creeks (Figure 1.4), but the earliest date of recovery for hatchery origin fish was two weeks later than that of wild fish. Tagged wild fish were recovered as early as 8 August and as late as 11 September, while tagged hatchery fish were recovered from 20 August through 11 September in both tagging years. This trend of later-arriving hatchery fish in Paddy Creek and Erb Creek corresponded with the greater PWS trends we observed.

In 2017, Paddy Creek pink salmon from the early release group lived an average of two days longer than fish in the late release group. The average instream lifespan (\pm sd) of wild fish recovered from the early release group was 8.1 ± 4.7 days; there were no hatchery fish recovered from this release group. The instream lifespan for the late release group was 6.7 ± 3.1 days for wild fish and 6.4 ± 1.7 days for hatchery fish. Although this two-day difference was not significantly different by origin (t-test $(_{20,54})$, $P = 0.41$), it represented ~30–50% of total time on the spawning grounds and is valuable time for post-spawning nest defense (McPhee and Quinn 1998).

In 2018, fish recovered from Erb Creek were senescent an average of two days longer than fish recovered at Paddy Creek (Figure 1.4). In both creeks, fish recovered from the early release groups were senescent about two and five days longer than fish recovered from mid or late release groups, respectively. Mean instream lifespan (\pm sd) of recovered fish in the early release group was 9.6 ± 4.3 days at Erb Creek and 7.5 ± 1.9 days at Paddy Creek. The mid release group had instream lifespans 7.2 ± 3.2 at Erb Creek and 6.3 ± 2.9 days at Paddy Creek, while the late tag group were senescent approximately 6.0 ± 2.1 days in Erb Creek and 2.3 ± 1.5 days in Paddy Creek. A paucity of hatchery samples made it difficult to detect differences between hatchery and wild instream lifespans between release groups (Figure 1.5). Overall in

2018, hatchery pink salmon ($n = 7$) had an average instream lifespan of 6.4 ± 4.6 days and wild origin pink salmon ($n = 195$) had an average instream lifespan of 7.5 ± 3.5 ($t\text{-test}_{(6,26)}$, $P = 0.556$) regardless of release group or stream, and this was not a statically significant difference.

Discussion

Using a dataset of over 128,000 individual pink salmon sampled from wild spawning streams, we show repeated differences in body length between hatchery and wild pink salmon, which may contribute to reduced reproductive success of hatchery fish in the wild (Lescak et al. 2019). Stray hatchery pink salmon of Prince William Sound (PWS) were longer on average than wild fish in even years and shorter in odd years. Stray hatchery fish had later average run timing and shorter reproductive lifespans (although not statistically significant) than their wild counterparts. We did not detect differences in egg retention between hatchery and wild fish monitored in two streams in two years. Body size and timing are known to be associated with fitness in salmon and are thus likely to affect differences in potential reproductive success (Gilk et al. 2004; Garcia De Leaniz et al. 2007; Peterson et al. 2014).

Body size is heritable, can be influenced by environmental conditions, and has allometric relationships with many fitness-related traits (Garcia De Leaniz et al. 2007). For fishes, increased body size is generally predicted to increase reproductive success either as more and larger eggs in females, or competitive dominance in males (Fleming and Petersson 2001; Hendry 2001; Dickerson et al. 2002). However, the environment mediates the relative costs and benefits of attaining large size (DiBattista et al. 2007). In spawning salmonids, greater size can impede mobility in small streams (Peterson et al. 2014) and increase vulnerability to predation (Armstrong et al. 2019), thus smaller sizes may be advantageous in small streams. These interactions between size and environment reveal the role of varying selective environments on

favoring different phenotypes. In this study, the magnitude and direction of differences in the body length depended on lineage, the return date within a season, and the sex of the salmon, and as such does not reflect consistently divergent selection between hatchery and wild pink salmon.

We observed a strong pattern of larger even-year fish and smaller odd-year pink salmon, which is widely supported by other studies, and this may be attributed to abundance related competition for resources at sea (Ruggerone et al. 2010) or ancestral effects because even and odd year pink salmon are genetically distinct (Seeb et al. 1999; Beacham et al. 2012). As expected, we detected a sexually dimorphic relationship of males larger than females within odd-year lineage for both hatchery and wild pink salmon (Quinn and Foote 1994). But unexpectedly, in even years stray hatchery females had the greatest body length early in the season, followed in average size by wild males, while hatchery males and wild females were smallest. Although patterns of larger females have been observed in lower-density species such as coho salmon (*O. kisutch*; Holtby and Healey 1990; Spidle et al. 1998), wild males were still larger than wild females which may imply a hatchery effect in the size of hatchery females. To the extent that length and timing mediate fitness through inter- and intrasexual competition on the spawning grounds and through fecundity (Van Den Berghe and Gross 1989; Essington et al. 1999; Kodama et al. 2012), this result suggests the possibility of greater hatchery fitness than wild pink salmon in even years compared to odd years when wild fish are longer, although the strength of sexual selection on wild spawning grounds may vary among years as well.

The average body length of pink salmon changed over the spawning season to a greater degree for wild fish than for hatchery fish and the direction and magnitude was considerably different between low density even-years and high density odd-years. In even years, the average length of returning fish increased throughout the season, consistent with predictions of additional

body size increases through additional time at sea (Quinn 2018). In studies of coho salmon, which spend a comparable amount of time at sea as pink salmon but spawn in lower densities, later arriving fish were female and larger (Spidle et al. 1998), although coho salmon favor different spawning habitats than pink salmon (Bjornn and Reiser 1991). In odd years we observed the opposite pattern, with the largest individuals returning earlier and length of returning fish declining over the season. This contrasts to a pink salmon study that found inconsistent relationships among length, arrival timing and density over two even and two odd years (Dickerson et al. 2002). In other salmon species, the change in body length within a season is partially due to age structuring, with the largest and oldest fish tending to return early in the run (Doctor and Quinn 2009), but this pattern is not only due to age class structure and is also seen within age classes (Shearer 1990; Molyneaux et al. 2009).

Streams that support numerically small populations of salmon are predicted to be most susceptible to moderate or even small influxes of stray fish (Bett et al. 2017). While the streams in this dataset were chosen from the index streams used in aerial escapement surveys for PWS, these streams tend to be larger than the average PWS stream. Therefore, inferences drawn from this analysis are most appropriately extended to the other index streams ($n = 214$ in 2012) but not representative of every single spawning stream in PWS (Harrison et al. 2018). Ultimately, the potential for body size-mediated interactions we explore here are likely conservative estimates, and hatchery strays may have a greater, but unknown, impact in numerically smaller systems.

Hatchery fish freshwater lifespan was two days shorter than wild fish in Paddy and Erb creeks, but the difference was potentially due to chance alone. Our ability to distinguish a difference in adult freshwater lifespan was challenged by small hatchery fish sample sizes, which limited our ability to detect differences between groups. There may be biological significance

associated with as few as two days of instream lifespan (Dickerson et al. 2005; Grant et al. 2011), particularly given that two days represents approximately 30% of the mean freshwater lifespan. Unfortunately, small hatchery sample size prevented a robust analysis of the difference between hatchery and wild instream lifespan.

Regardless of natal origin, we expected that mean instream lifespan of wild fish would be approximately 12 days long, and two days shorter in Paddy Creek than Erb Creek given previously published findings (Fried et al. 1998). Using comparable field and analysis methods, such as only using senescent fish, we found that mean instream lifespan was only seven days as opposed to 12, but there was still a two-day difference in mean stream life between the two creeks. The shorter instream life-span we documented compared to the stream life documented in the 1960s could be a consequence of environmental conditions such as stream flow (Banks 1969), changing selection via bear predation (Carlson et al. 2009; Lin et al. 2016), a genetic difference driven by hatchery influence (e.g., run timing; Tillotson et al. 2019), or a combination of these effects. The consistent two-day difference in stream life between Paddy and Erb creeks persisting from the 1990's until this study may be a function of the relationship between creek size and predation. Paddy Creek is about half the size of Erb Creek, and studies have linked higher predation rates to smaller creeks (Quinn et al. 2001; Armstrong et al. 2019). In 2018, 93% of tagged fish from Paddy Creek had evidence of pre-spawning predation compared to 52% of tagged fish in Erb Creek. The higher predation rate in Paddy Creek may be driving the two-day difference in instream lifespan between these two creeks, similar to findings in sockeye salmon (Carlson et al. 2007). Another noticeable trend was that instream lifespan of wild fish consistently decreased over the spawning run, and later arriving fish did not live as long. This

relationship is echoed in many studies of salmonids (McPhee and Quinn 1998; Hendry et al. 2003; Dickerson et al. 2005; Grant et al. 2011).

In some systems, hatchery salmonids can have higher egg retention rates in the wild than wild fish (McConnell et al. 2018), or egg retention rate may increase within a season as a function of fish density and habitat competition (Fleming and Gross 1993). Contrary to our expectations, the egg retention of hatchery fish was the same as that of wild fish and did not increase over the spawning run in fish of either origin. It is possible that the low spawning densities during both years of our tagging study, low sample sizes for hatchery and wild females, and/or high black bear predation obscured relationships. However, since egg retention was statistically indistinguishable from zero, it appears that egg retention was not a major factor affecting potential fitness differences in these creeks.

The fitness impact of stray hatchery fish on wild conspecifics is partially mediated by the extent to which heritable phenotypic traits differ between donor and recipient populations. Pink salmon hatcheries have operated in PWS since the mid 1970s. Presumably hatchery strays have been spawning in wild creeks since that time, though the numbers of hatchery strays have most likely increased with increasing hatchery production. Despite approximately 15 generations of potential introgression and phenotypic homogenization, we observed that hatchery and wild pink salmon of PWS have differences in length and instream lifespan. There are many other potentially important biotic and abiotic traits and conditions, such as hatchery fry release timing and locations, wild fry outmigration timing, spawning timing, spawning behavior, spawning location, salinity at spawning location, and stream flow, that have been documented as influencing fitness in wild and lab-reared salmon populations (e.g. Berejikian et al. 2009; Fraser

et al. 2011). All of these traits may contribute to or inhibit the reproductive success of hatchery fish in the wild and PWS remains a model system for understanding these relationships.

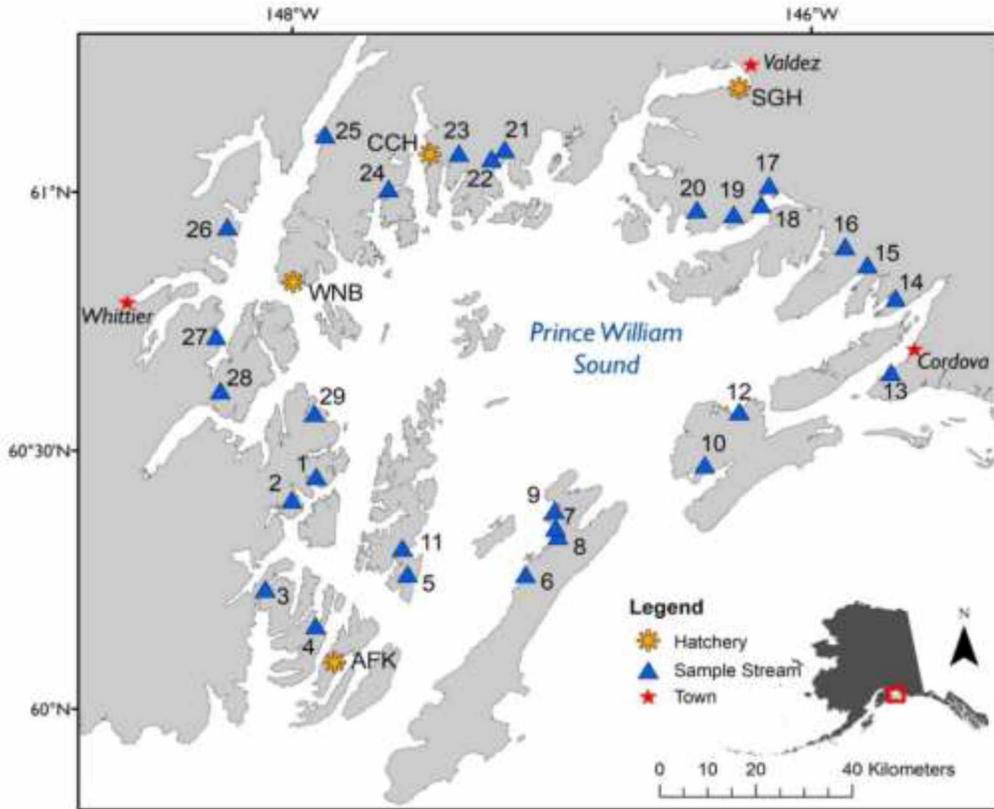


Figure 1.1: Prince William Sound, Alaska, USA. Blue triangles mark the locations of sampling efforts. Tagging took place at Paddy Creek (1) and Erb Creek (2). Paddy Creek, Erb Creek, Hogan Bay Creek (5), Gilmour Creek (8), and Stockdale Creek (9) were sampled as part of the Alaska Hatchery Research Project (AHRP), 2013 – 2018. Bainbridge Creek (3), Johnson Creek (4), Swamp Creek (6), Cabin Creek (7), Constantine Creek (10), Snug Harbor Creek (11), Double Creek (12), Hartney Creek (13), Spring Creek (14)^a, Sheep River (15), Beartrap Creek (16), Sunny River (17), Short Creek (18), Fish Creek (19), Lagoon Creek (20), Long Creek (21), Spring Creek (22)^b, Surplus Creek (23), Siwash Creek (24), Coghill River (25), Hummer Creek (26), Paulson Creek (27), West Finger Creek (28), Comstock Creek (29) were sampled by the AHRP from 2013 to 2015. Yellow asterisks mark the location of hatcheries that release pink salmon; SGH: Solomon Gulch Hatchery, CCH: Cannery Creek Hatchery, WNB: Wally Norenberg Hatchery, AFK: Armin F Koerning Hatchery.

^a Spring Creek ADF&G code 221-20-10200

^b Spring Creek ADF&G code 222-10-12170

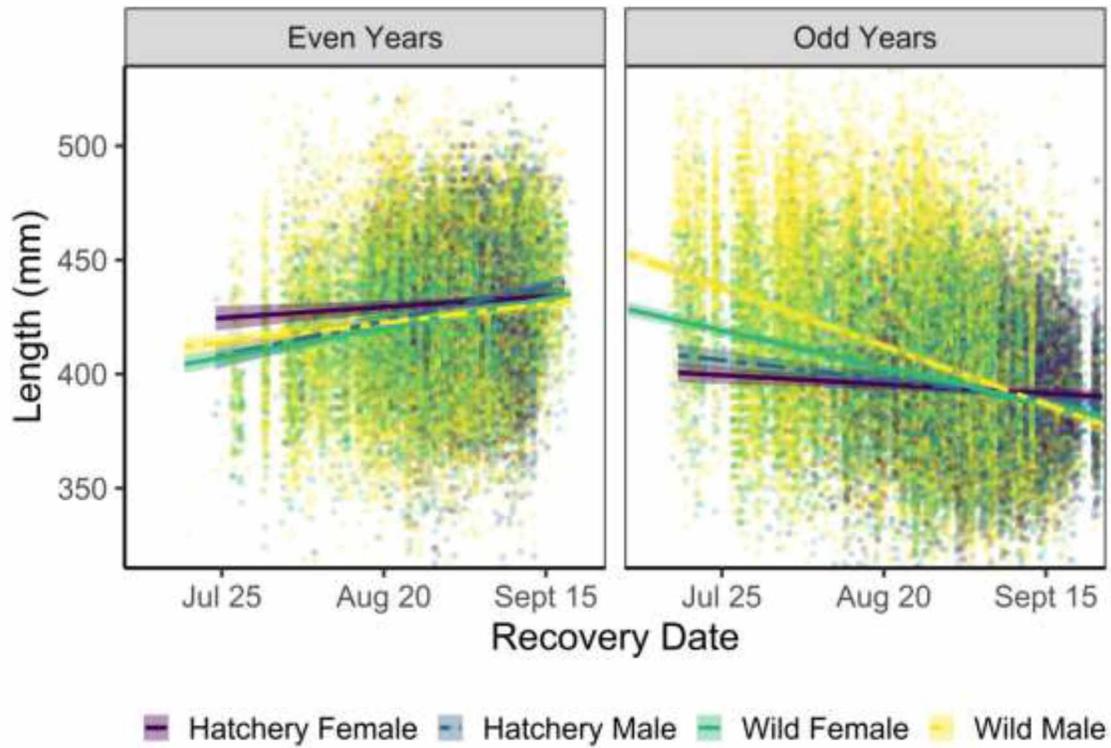


Figure 1.2: Fitted model of length (mid-eye hypural, mm) plotted against recovery date for male and female pink salmon that were identified as hatchery (dashed line) or wild (solid line) with 95% confidence intervals (shading). Data are from 2013 through 2018.

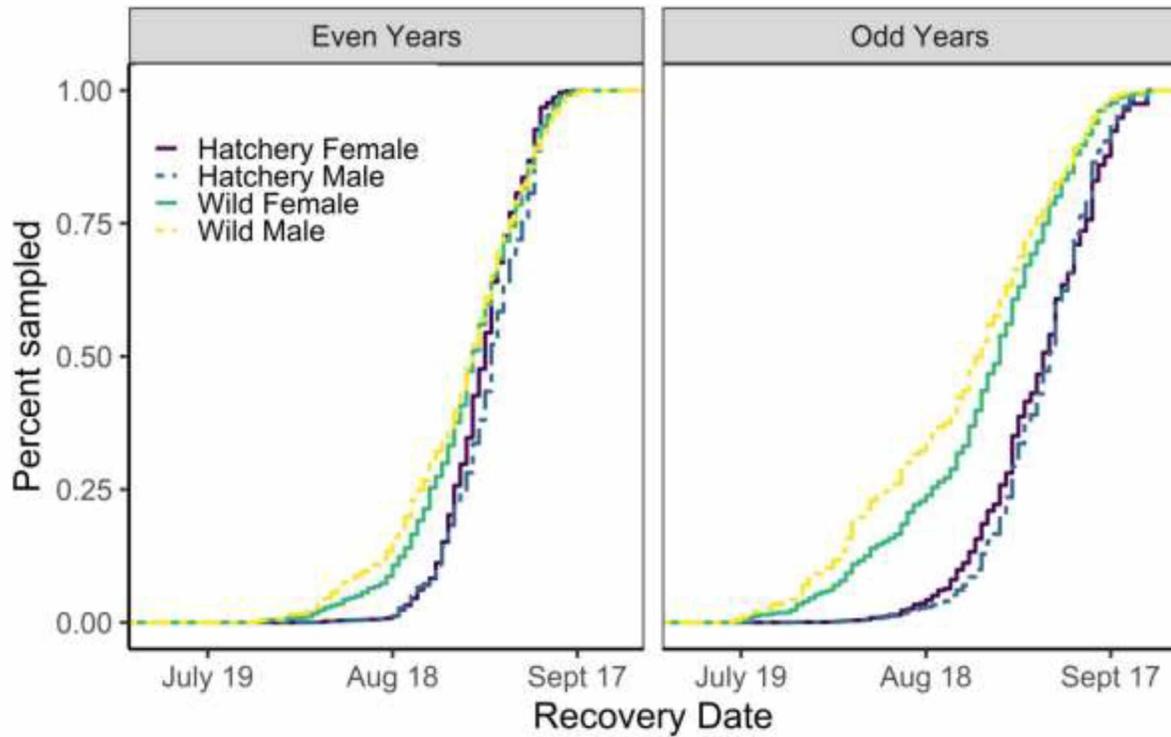


Figure 1.3: Cumulative proportion of samples collected by recovery date of male and female pink salmon that were identified as hatchery or wild from Prince William Sound creeks during the years 2013 – 2018, compiled in even and odd years. Plotted data includes 51,194 even-year samples and 60,986 odd year samples.

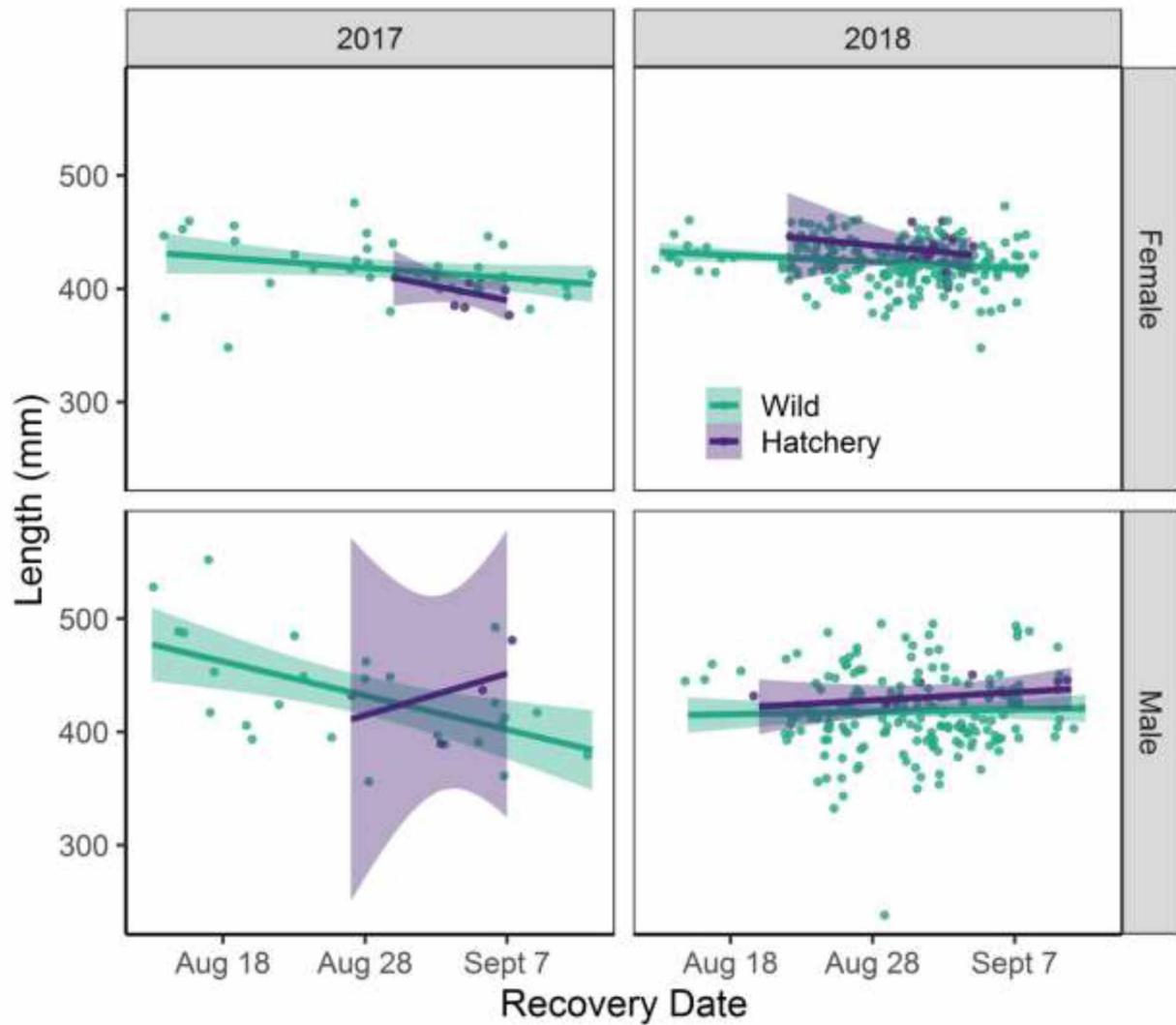


Figure 1.4: The length of tagged and recovered pink salmon by recovery date from 2017 and 2018. Regression lines with 95% confidence intervals of mid-eye hypural length (mm) plotted against the day of year of recovery for male and female pink salmon that were identified as hatchery or wild from otolith readings.

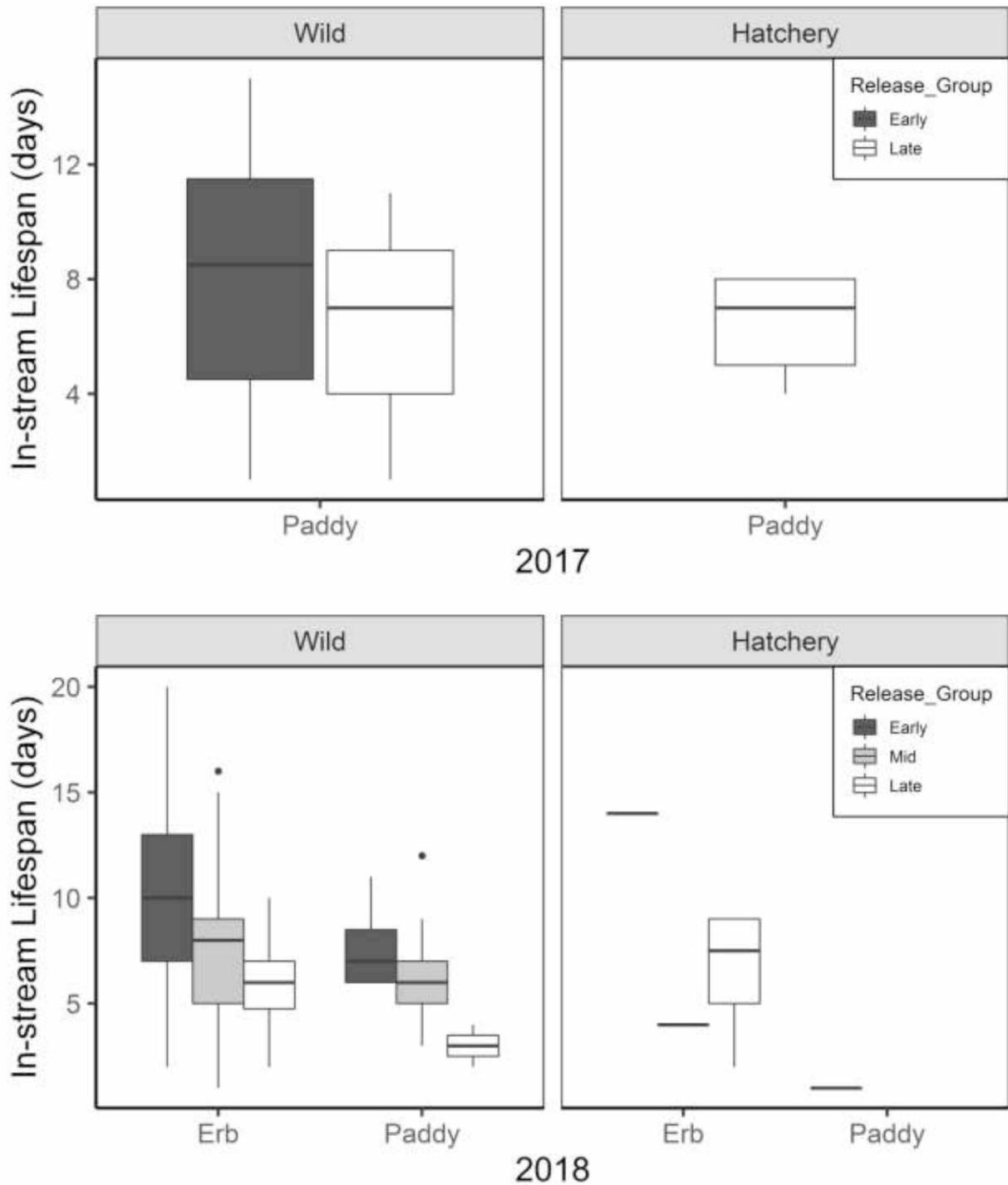


Figure 1.5: Instream lifespan in days of hatchery and wild pink salmon caught, tagged, re-sighted and recovered from Paddy Creek, 2017 (top panel) and Paddy and Erb creeks 2018 (bottom panel). Fish were excluded if they were stranded or were preyed upon.

Table 1.1 Mean mid-eye to hypural-plate body length (mm), standard deviation, and the total number of otoliths read of hatchery (H) and wild (W) origin sampled from 2013 to 2018. “na” indicates that no hatchery or wild samples were identified at that creek in that year and “--” indicates no samples were collected.

		2013	2014	2015	2016	2017	2018
Origin		mean, sd, n	mean, sd, n	mean, sd, n	mean, sd, n	mean, sd, n	mean, sd, n
Bainbridge C	H	395, 25, 25	na, na, 0	388, 22, 65	--	--	--
(3)	W	404, 30, 219	410, 28, 476	414, 36, 508	--	--	--
Beartrap R	H	437, 33, 3	419, na, 1	424, 31, 5	--	--	--
(16)	W	432, 42, 366	414, 32, 460	424, 34, 448	--	--	--
Cabin C	H	392, 20, 11	434, 25, 56	385, 22, 52	--	--	--
(7)	W	400, 27, 221	423, 25, 298	393, 28, 489	--	--	--
Coghill R	H	384, 15, 3	448, 27, 24	na, na, 0	--	--	--
(25)	W	415, 33, 139	421, 28, 222	429, 34, 461	--	--	--
Comstock C	H	396, 26, 105	418, 24, 435	378, 22, 348	--	--	--
(29)	W	394, 32, 12	414, 25, 73	379, 22, 76	--	--	--
Constantine C	H	na, na, 0	416, 33, 7	400, 9, 2	--	--	--
(10)	W	405, 30, 294	415, 25, 269	406, 32, 528	--	--	--
Double C	H	400, na, 1	408, 34, 7	467, 26, 4	--	--	--
(12)	W	414, 36, 574	423, 26, 130	435, 33, 366	--	--	--
Erb C	H	394, 24, 43	429, 23, 403	391, 22, 69	438, 18, 20	403, 22, 64	428, 19, 33
(2)	W	401, 26, 385	407, 27, 1086	405, 33, 303	433, 24, 276	417, 36, 275	419, 27, 596
Fish C	H	na, na, 0	431, 18, 16	388, 16, 11	--	--	--
(19)	W	420, 35, 312	419, 27, 414	418, 36, 577	--	--	--
Gilmour C	H	--	430, 22, 311	391, 21, 86	435, 23, 38	400, 20, 78	415, 27, 29
(8)	W	--	423, 22, 252	386, 28, 280	436, 25, 314	397, 27, 259	419, 27, 329
Hartney C	H	390, 19, 5	423, 24, 15	395, 25, 5	--	--	--
(13)	W	400, 25, 433	432, 27, 203	414, 39, 526	--	--	--
Hogan Bay C	H	405, 22, 426	440, 23, 2222	385, 23, 4791	441, 22, 2445	396, 24, 5584	420, 26, 4053
(5)	W	400, 26, 263	428, 27, 264	395, 31, 4140	437, 22, 9695	398, 32, 3263	417, 26, 5956
Hummer C	H	414, 16, 2	432, 21, 81	387, 19, 36	--	--	--
(26)	W	403, 30, 128	411, 25, 308	413, 36, 383	--	--	--

Table 1.1 continued

Johnson C	H	393, 26, 43	431, 22, 329	391, 24, 157	--	--	--
(4)	W	399, 24, 95	412, 23, 156	408, 32, 448	--	--	--
Lagoon C	H	389, 17, 6	428, 32, 23	415, 31, 16	--	--	--
(20)	W	408, 32, 467	420, 26, 390	425, 36, 545	--	--	--
Long C	H	401, 8, 3	431, 24, 71	400, 31, 30	--	--	--
(21)	W	413, 32, 89	415, 21, 88	430, 35, 400	--	--	--
Paddy C	H	410, 26, 8	430, 23, 556	384, 22, 122	442, 20, 57	409, 26, 72	422, 23, 14
(3)	W	391, 22, 70	415, 27, 338	393, 28, 256	437, 21, 256	421, 37, 254	418, 29, 235
Paulson C	H	391, 29, 16	401, 18, 3	397, 23, 63	--	--	--
(27)	W	399, 28, 262	405, 28, 455	418, 35, 473	--	--	--
Sheep R	H	na, na, 0	398, 24, 6	415, 23, 2	--	--	--
(15)	W	427, 38, 695	417, 30, 417	433, 35, 554	--	--	--
Short C	H	402, 31, 7	419, 29, 30	403, 25, 14	--	--	--
(18)	W	411, 31, 1091	415, 26, 306	417, 33, 436	--	--	--
Siwash R	H	414, 24, 16	437, 20, 151	390, 25, 118	--	--	--
(24)	W	409, 29, 138	414, 28, 302	421, 33, 463	--	--	--
Snug Harbor C	H	--	--	393, 24, 25	--	--	--
(11)	W	--	--	406, 30, 265	--	--	--
Spring C ^a	H	na, na, 0	415, 12, 5	401, 33, 14	--	--	--
14)	W	391, 28, 67	405, 24, 294	408, 32, 570	--	--	--
Spring C ^b	H	385, 33, 26	415, na, 1	373, 9, 2	--	--	--
(22)	W	400, 31, 1214	419, 22, 93	401, 32, 376	--	--	--
Stockdale C	H	395, 20, 155	434, 23, 894	385, 24, 1654	442, 22, 583	400, 25, 1043	426, 27, 219
(9)	W	392, 22, 852	420, 27, 396	388, 29, 6656	439, 25, 7208	411, 32, 9610	420, 27, 4370
Sunny R	H	na, na, 0	409, 33, 9	377, 43, 6	--	--	--
(17)	W	419, 35, 260	429, 30, 296	419, 36, 378	--	--	--
Surplus C	H	396, na, 1	427, 21, 44	383, 22, 34	--	--	--
(23)	W	419, 35, 370	411, 21, 126	433, 35, 447	--	--	--

Table 1.1 continued

Swamp C	H	397, 26, 12	436, 30, 21	384, 32, 55	--	--	--
(6)	W	397, 27, 259	428, 27, 187	429, 36, 526	--	--	--
West Finger C	H	387, 15, 7	na, na, 0	389, 22, 12	--	--	--
(28)	W	397, 24, 220	411, 26, 448	412, 36, 389	--	--	--
Year total	H	398, 23, 924	425, 24, 5721	395, 24, 7798	439, 21, 3143	402, 23, 6841	422, 24, 4348
	W	406, 30, 9495	417, 26, 8747	412, 33, 22267	436, 24, 17749	409, 33, 13661	419, 27, 11486

^a Spring Creek ADF&G code 221-20-10200

^b Spring Creek ADF&G code 222-10-12170

Table 1.2: Tagged and recovered hatchery and wild pink salmon from Paddy and Erb creeks sampled in 2017 and 2018 including the average body length (mm). The total number of tags recovered includes fish killed by black bears (*Ursus americanus*). The mean length, sd, and “n” excludes recovered individuals with evidence of predation. In 2017, one wild male tagged in Paddy Creek was recovered in Erb Creek.

	2017			2018			Creek Totals	
	Tagged	Recovered	mean length, sd, n	Tagged	Recovered	mean length, sd, n	Tagged	Recovered
Erb Creek	-	1	H 492, --, 1	499	18	H 426, 17, 6	499	35.5%
		--	W --		318	W 422, 30, 178		
Paddy Creek	200	12	H 408, 29, 11	500	7	H 445, --, 1	700	10%
		60	W 414, 32, 32		110	W 419, 26, 23		
Year Totals	200	24.5%		999	40.5%			

Table 1.3: Candidate mixed-effects models used to estimate the mid-eye-hypural length (mm) of hatchery and wild pink salmon sampled in Prince William Sound, Alaska, USA. Variables include the date a fish was sampled (Timing), the hatchery or wild origin (HW), an even or odd sample year (EO), sex (MF), and the random effect of tray nested within stream (R).

Model Equation	K	AICc	Δ_i	w_i	Log(L)
HW * EO * Timing * MF + (R)	19	1056366	0	1	-528164
HW * EO * Timing + HW * EO * MF + HW * EO * MF + EO * Timing * MF + (R)	18	1056382	16	0	-528173
HW*EO + HW*Timing + EO*Timing + HW*MF + EO*MF + Timing*MF + (R)	14	1056627	260	0	-528299
Timing * EO + Timing * HW + Timing * MF + (R)	11	1057211	844	0	-528594
HW * EO * Timing + (R)	11	1057614	1248	0	-528796
Timing * EO + HW + MF + (R)	9	1057981	1614	0	-528981
HW + EO + Timing + MF + (R)	8	1058655	2289	0	-529320
HW *EO + (R)	7	1058844	2478	0	-529415
HW + (R)	5	1060730	4364	0	-530360
+ (R) (null model)	4	1060735	4369	0	-530364

Table 1.4: Coefficients from the top model for mid-eye-hypural length (mm) of pink salmon in Prince William Sound, AK, USA sampled from 2013 to 2018. The continuous variable Timing was standardized (mean = 0, SD = 1) and all other variables are two-level factors including hatchery or wild origin (HW), an even or odd sample year (EO), and sex (MF). The intercept represents wild, even-year females.

Fixed effects	β	SE
(Intercept)	424.89	1.09
HW (Hatchery)	6.18	0.46
EO (Odd Years)	-27.71	0.55
Timing	6.20	0.52
Sex (Male)	0.54	0.28
HW (Hatchery) * EO (Odd Years)	-9.26	0.63
HW (Hatchery) * Timing	-3.93	0.75
EO (Odd Years) * Timing	-13.90	0.60
HW (Hatchery) * Sex(Male)	-2.81	0.61
EO (Odd Years) * Sex(Male)	5.38	0.38
Timing * Sex(Male)	-2.16	0.35
HW (Hatchery) * EO (Odd Years) * Timing	9.73	0.89
HW (Hatchery) * EO (Odd Years) * Sex(Male)	-2.48	0.86
HW (Hatchery) * Timing * Sex(Male)	7.25	0.96
EO (Odd Years) * Timing * Sex(Male)	-2.34	0.41
HW (Hatchery) * EO (Odd Years) * Timing * Sex(Male)	-4.83	1.15

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Chapter 2: Stable isotopes suggest foraging niche overlap between adult hatchery and wild Alaskan pink salmon during their last summer at sea²

Abstract

Intraspecific interactions are an important ecological force shaping wild animal populations, yet quantifying interactions is notoriously difficult and made more complicated in highly mobile species that are beyond observation for much of their life history. Here, we use bulk carbon ($^{13}\text{C}/^{12}\text{C}$, $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$, $\delta^{15}\text{N}$) lipid-corrected stable isotope analysis (SIA) of muscle and liver tissues to explore the potential for trophic interactions between odd-year wild and hatchery-produced pink salmon (*Oncorhynchus gorbuscha*) during the last summer of their marine life history stage. General linear modeling revealed that hatchery and wild fish broadly overlap in both carbon and nitrogen signatures, with the exception of nitrogen in the liver and muscle of fully mature pink salmon just prior to spawning. Overall, the average isotope values (\pm sd) of hatchery fish muscle tissues were -21.58 ‰ (± 0.57 ‰; $\delta^{13}\text{C}$) and 10.67 ‰ (± 0.80 ; $\delta^{15}\text{N}$) and were -21.60 ‰ (± 0.59 ; $\delta^{13}\text{C}$) and 11.29 ‰ (± 0.74 ; $\delta^{15}\text{N}$) for wild fish. Body size and trophic position were positively correlated, and although wild fish were statistically larger than hatchery fish, their greatest size differences occurred at the ends of the size continuum which suggests that average sized hatchery and wild fish may have foraged on overlapping prey items. We detected differences between the sexes in liver tissue, where males tended to have higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than females. Taken as a whole, our study helps to illuminate foraging dynamics in the most abundant Pacific salmon in an era in which over five billion hatchery pink salmon are released into the ocean to support fisheries. The broad isotopic

² McMahon, J., K. B. Gorman, and P. A. H. Westley. *In prep.* Stable isotopes suggest niche overlap between adult hatchery and wild Alaska pink salmon during their last summer at sea. Marine Ecological Progress Series.

overlap between hatchery and wild fish suggests the potential for intraspecific competitive interactions.

Introduction

Pacific salmon (*Oncorhynchus* spp.) are renowned for their wide-ranging migrations between relatively unproductive freshwater habitats and rich marine ecosystems to prey on abundant food (Gross et al. 1988). Growth potential in the ocean is staggering; some species routinely gain over 95% of their body size foraging at sea (Groot and Margolis 1991; Quinn 2018). Overlapping distributions in time and space, and the tendency for Pacific salmon to have similar generalist diets in the ocean (Davis 2003; Karpenko et al. 2007), sets the stage for inter- and intra-specific interactions (Holt et al. 2008; Kaeriyama and Qin 2014; Ruggerone and Connors 2015). Competition for prey resources is likely exacerbated by the rise of aquaculture and favorable ocean conditions that have increased yearly adult hatchery and wild pink salmon (*O. gorbuscha*) abundance in the North Pacific Ocean to over 445 million (Ruggerone and Irvine 2018). As the most numerically dominant species (Ruggerone and Irvine 2018), pink salmon abundance has been linked to declines in size and age at maturity of returning sockeye (*O. nerka*) and Chinook salmon (*O. tshawytscha*; Ruggerone and Connors 2015; Kendall et al. 2020; Oke et al. 2020), dynamics of killer whale survival and plankton abundance patterns (Batten et al. 2018; Ruggerone et al. 2019), and even decreased nesting success of seabirds with which they compete for foraging opportunities (Springer and van Vliet 2014). Despite pink salmon being an increasingly important ecological force shaping North Pacific oceanic food webs (Ruggerone et al. 2007; Kaga et al. 2013; Springer and van Vliet 2014; Batten et al. 2018), relatively little is known about the ocean trophic ecology surrounding hatchery and wild pink salmon, especially in the context of intraspecific interactions.

While ocean trophic ecology is typically approached through diet analysis of gut contents, naturally occurring stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$, $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$, $\delta^{15}\text{N}$) provide a tractable approach to compare diets of Pacific salmon (hereafter salmon) during their ocean residency because they predictably fractionate through food webs and can serve as biogeochemical tracers of dietary sources (Peterson and Fry 1987). While stable isotope analysis (SIA) has clarified some aspects of salmon biology, such as foraging patterns in the North Pacific (Johnson and Schindler 2009), others, such as life history traits known to influence success on the spawning grounds, have been inconsistently linked with trends in isotope values. For example, large body size at maturity is associated with greater fecundity, dominance, and reproductive success in salmon (Auld et al. 2019), and since salmon body size is a product of diet at sea (traceable with isotope values), larger fish have been hypothesized to forage closer to shore and at higher trophic positions (Romanuk et al. 2011). This pattern is found in trophic hierarchies of salmon species; piscivorous and coastally orientated Chinook and Coho (*O. kisutch*) salmon have higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than open ocean foraging sockeye, chum (*O. keta*), and pink salmon (Satterfield IV and Finney 2002; Johnson and Schindler 2009; Qin and Kaeriyama 2016). However, within a species, larger salmon can have higher, similar, or lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than smaller salmon (Satterfield IV and Finney 2002; Acolas et al. 2008; Johnson and Schindler 2012a, 2012b) and body size has been linked with a number of life history traits such as run timing (Johnson and Schindler 2012a; Quinn et al. 2012; Torniainen et al. 2014). Despite substantial work to understand the ecological interactions between hatchery and wild conspecifics, stable isotope analyses have not been widely used in this context (Atcheson et al. 2012; Quinn et al. 2012; Lamperth et al. 2017).

In this paper, we use stable isotope ratios of carbon and nitrogen as proxies to test the hypothesis that hatchery and wild pink salmon overlap in foraging locations and trophic positions and thus potentially compete for food during their final months at sea. To do so, we sampled homeward migrating pink salmon returning to Prince William Sound (PWS), Alaska in 2015 at two periods: as maturing adults in the ocean, and once these fish reach their spawning grounds. We use linear mixed-effects models to test whether hatchery or wild originating pink salmon are associated with variation in carbon and nitrogen isotopic values, while controlling for the effects of body size, the relative timing of migration, and the sampling locations.

Methods

Study system and tissue sampling

Prince William Sound (Figure 2.1) is located in southcentral Alaska and produces millions of wild and hatchery pink salmon. On average, from 1990 through 2015, hatchery pink salmon in this region represented 85% or approximately 32 million fish of the total pink salmon harvest including commercial fishing and hatchery cost-recovery fishing (Evenson et al. 2018). Of all Pacific salmon species, pink salmon life-history is most associated with the ocean, using freshwater habitats only for spawning and embryonic development. Juvenile fish emerge from the gravel in the spring and migrate directly to the ocean (Heard 1991). Once at sea, pink salmon grow rapidly and within their native range invariably return to spawn in either odd or even-numbered years after two years (Beamish 2018). As a consequence of this two-year life cycle, pink salmon returns can differ by many orders of magnitude between even and odd years (Radchenko et al. 2007). This occurs in PWS despite consistent annual releases of hatchery pink salmon fry that have been increasing since the 1990s. Currently, four pink salmon hatcheries annually release over 750 million pink salmon fry every spring (Wilson 2020). All hatchery

releases in PWS are thermally marked, which creates a year- and hatchery-specific pattern on otoliths (Volk et al. 1990, 1999).

Homeward migrating adult pink salmon were collected from June to August 2015 in conjunction with the Alaska Hatchery Research Project (see Knudsen et al. 2021 for additional details). Pink salmon entering PWS and caught at the ocean stations are outside the primary commercial fishing areas and thus reflect pre-harvest conditions of the stock. Pink salmon were caught at nine ocean locations along migration corridors entering PWS (Figure 2.1). Salmon were caught in a variable mesh gillnet with four panels (366 m long; each panel 91.5 m by 6–8 m deep and mesh sized 111, 121, 130 and 140 mm) from a 9.8 m commercial fishing vessel. Fishing effort was limited to one hour per site or less dependent on weather, vessel traffic, small or large catches, and marine mammal presence. A total of 2,250 pink salmon was caught in the ocean test fishery, and of those, a random subset of approximately 40 pink salmon (20 males and 20 females) was selected for SIA from the nine ocean stations in the first and second halves of each month, for a total of 241 individual fish. Of the fish selected for SIA, there were no hatchery pink salmon sampled in the first two weeks of ocean test fishing, but numbers increased as the season progressed and by the last week 53% of the pink salmon were from PWS hatcheries.

In addition to the fish caught when entering PWS, pink salmon were sampled at 11 spawning streams (Figure 2.1) that were also sampled as part of the Alaska Hatchery Research Project (AHRP; Knudsen et al. 2021). From each sampling event at each stream, approximately 40 pink salmon (20 males and 20 females) were collected with a beach seine (~ 50 m x 5 m) or dipnet for a total of 881 individuals. Stream samples were restricted to pre-spawned fish, determined by an absence of fin wear from fighting or digging in males and females. Wild

salmon tend to arrive earlier at spawning streams than straying hatchery salmon that generally arrive towards the middle and end of a stream's salmon run (Brenner et al. 2012; Knudsen et al. 2021). Thus, streams were sampled twice: once during an 'early' sampling event between July and early August, and once during a 'late' sampling event between late August and early September. Only 2% of samples from 'early' stream sampling events had thermally marked otoliths and hatchery presence increased to 16% in the 'late' stream samples.

All tissue samples were associated with a sample date, region (ocean or stream), sample location (the specific ocean or stream site), mid-eye hypural length (mm, henceforth length), and sex. An approximate 2 x 2 cm piece of liver and muscle tissue was dissected from each fish, immediately placed on ice for transport to storage facilities, and then frozen at -20°C . Sagittal otoliths were recovered and retained for otolith readings of thermal marks. Otoliths were read for hatchery or wild origin at the Cordova Otolith Lab (Fernandez & Moffitt 2016). We refer to any fish with unmarked otoliths as 'wild' but acknowledge that these fish may have hatchery ancestry, because hatchery-origin individuals can successfully spawn in the wild (Lescak et al. 2019).

Sample selection and preparation

Muscle and liver tissues for bulk carbon and nitrogen SIA were dried at 60°C to completion (weight ± 0.01 g in 24 hours). Dried samples were homogenized, aliquoted to the nearest 0.001 mg, and sent to the University of California Davis, Stable Isotope Facility for elemental analysis. Bulk SIA was conducted with a PDZ Europa 20-20 isotope ratio mass spectrometer. The carbon and nitrogen δ values of isotopes are expressed as the difference from international standards (carbon: Vienna PeeDee Belemnite, nitrogen: atmospheric nitrogen) as

$\delta X (\text{‰}) = 10^3 [R_{\text{sample}}/R_{\text{standard}} - 1]$, where X is ^{13}C or ^{15}N , and R is the ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively. Measurement precision was estimated at 0.07‰ for $\delta^{13}\text{C}$ and 0.10‰ for $\delta^{15}\text{N}$. Carbon values were mathematically lipid-corrected with Eq. 3 from Post et al. (2007) and C:N ratios from sample weight.

Statistical analysis

To assess potential differences in foraging patterns between hatchery or wild origin pink salmon in this system, we used a linear mixed-effects modeling approach (Zuur et al. 2009). Each tissue (liver or muscle) and stable isotope (carbon or nitrogen) combination was analyzed as a separate response because the tissues represent different “snapshots” of time and the stable isotopes represent either the general foraging location ($\delta^{13}\text{C}$) or the trophic position ($\delta^{15}\text{N}$) of an individual's diet. Therefore, the four responses were $\delta^{13}\text{C}$ values of liver, $\delta^{13}\text{C}$ values of muscle, $\delta^{15}\text{N}$ values of liver, and $\delta^{15}\text{N}$ values of muscle.

Explanatory variables included (1) hatchery or wild origin as determined from otolith readings; (2) the sampling region, which designates ocean-caught or stream-sampled specimens; (3) timing, whether a fish was sampled ‘early’ or ‘late’ in the 2015 season; (4) body size as length (cm); and (5) sex. Timing designations for continuously migrating ocean-caught fish were ‘early’ if caught before July 1 or ‘late’ if caught after, based on the number of fishing days in the data. Additionally, we incorporated a random intercept term for the specific ocean station or stream to account for sampling design (Bennington and Thayne 1994).

The specific objective of our analytical approach was to assess whether hatchery and wild pink salmon exhibited differences in $\delta^{13}\text{C}$ values or $\delta^{15}\text{N}$ values while accounting for differences in sampling region, timing, body size, and sex. We fit three models to all four tissue and isotope

responses and assessed the relative support for each: 1) a full model that included the hatchery/wild origin term, 2) a reduced model that omitted the origin term, and 3) a null model. The full model included a four-way interaction between origin, sampling region, timing, and length, as well as a main effect for sex. The reduced model omitted the origin term. Plausible and previously identified interactions were incorporated (Brenner et al 2012, Chapter 1). For example, in 2015, wild pink salmon were larger on average than hatchery pink salmon, male salmon were larger than females, and length of sampled, returning fish decreased over the season (Chapter 1). These two models, and a null model, were compared for each tissue and isotope response. We assessed model performance with Akaike's Information Criterion corrected for small sample size (AICc; Hurvich and Tsai 1989; Burnham and Anderson 2002). A model was considered the top model when it had a difference in AICc value ≥ 2 from any other model (Burnham and Anderson 2002). We performed our analysis in the R language environment (version 3.6.1, R Core Team 2019) with package lme4 (Bates et al. 2015).

Results

Overall, mean (\pm standard deviation, sd) hatchery and wild pink salmon $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of liver and muscle tissue did not substantially differ, except between the mean $\delta^{15}\text{N}$ values of muscle tissue from stream caught hatchery fish ($\delta^{15}\text{N} = 10.57 \pm 0.85\text{‰}$) compared to wild fish ($\delta^{15}\text{N} = 11.38 \pm 0.73\text{‰}$); Figure 2.2; Table 2.1). The mean $\delta^{13}\text{C}$ value of pink salmon liver was $-21.46 \pm 0.61\text{‰}$ and the mean muscle tissue $\delta^{13}\text{C}$ value was $-21.60 \pm 0.59\text{‰}$. Correspondingly, the mean pink salmon $\delta^{15}\text{N}$ value for liver was $10.99 \pm 0.91\text{‰}$ and $11.20 \pm 0.78\text{‰}$ for muscle.

After taking into account other sources of variation that may have obscured effects of hatchery or wild origin, wild and hatchery pink salmon did not differ in $\delta^{13}\text{C}$ values of liver or

muscle tissue (Table 2.2). For liver tissue (Figure 2.3), there was a positive relationship between $\delta^{13}\text{C}$ values and length of pink salmon for three out of four combinations of region and timing. Early arriving ocean caught pink salmon were 1‰ more positive than late ocean caught fish, but this pattern was not repeated in stream caught fish. Additionally, there was a sex effect; males had $0.29 \pm 0.03\text{‰}$ greater $\delta^{13}\text{C}$ liver values than females. For muscle tissue (Figure 2.4), the top model did not include origin and outperformed the more complex model that included origin (Table 2.2). There was a consistent positive relationship between $\delta^{13}\text{C}$ values of pink salmon muscle tissues and length for all combinations of region and timing. The muscle tissue $\delta^{13}\text{C}$ values of an average stream caught fish were 1‰ lower (suggestive of a more ‘offshore’ signature) than ocean caught fish and males were $0.07 \pm 0.03\text{‰}$ lower than females.

In contrast to carbon, both liver and muscle of wild and hatchery pink salmon differed in $\delta^{15}\text{N}$ values (Table 2.2 and Table 2.3). For wild pink salmon liver and muscle tissues there was a positive relationship between $\delta^{15}\text{N}$ values and length for all combinations of region and timing. However, for hatchery pink salmon, three out of four slopes had a negative relationship between liver $\delta^{15}\text{N}$ values and length, while hatchery pink salmon muscle $\delta^{15}\text{N}$ values exhibited a positive relationship for ocean sampled hatchery fish but not stream sampled fish (Figure 2.5). There was a sex effect seen in liver, where males had $0.51 \pm 0.04\text{‰}$ higher average $\delta^{15}\text{N}$ values than females. Liver tissue of early, ocean caught fish had roughly 2‰ lower values than all other categories (Figure 2.5; Table 2.3). In muscle tissue, the pattern of increasing $\delta^{15}\text{N}$ values by length was consistent between early and late, ocean and stream sampled fish, except for late, stream caught hatchery fish and there was very little difference between males and females (0.04 ± 0.03 sd; Figure 2.6; Table 2.3). Generally, the difference in $\delta^{15}\text{N}$ values between hatchery and wild pink salmon was greatest in late, stream sampled, large fish for both tissue types.

Discussion

In this paper we used stable isotope analyses to help illuminate the poorly known trophic ecology of abundant hatchery and wild pink salmon during the last summer of their ocean phase. Our results yielded the following salient insights: 1) no isotopic differences were detected in $\delta^{13}\text{C}$ between hatchery and wild pink salmon, even after controlling for the effects of body size and run timing, 2) only subtle differences in $\delta^{15}\text{N}$ were detected between hatchery and wild pink salmon when sampled just prior to spawning in streams but not when entering coastal waters from the open ocean, 3) body size of salmon was positively associated with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and was weakly origin-specific for $\delta^{15}\text{N}$ values and sex-specific for liver tissue. Except where specifically stated, isotopic results discussed here are from muscle tissue, as it integrates a longer time period (Sakano et al. 2005; Skinner et al. 2017) and is more comparable to other studies. Taken as a whole, we conclude that there is a high degree of isotopic overlap between hatchery and wild salmon, suggesting that hatchery and wild pink salmon in PWS likely forage on similar diets and overlap in foraging space. To the extent that food may be limiting, our results are consistent with the possibility of intra-specific competition.

We found no difference in $\delta^{13}\text{C}$ values of hatchery and wild pink salmon after controlling for other known sources of variation. Given that carbon isotopes fractionate up food webs by only 0 – 2‰ (Tieszen et al. 1983; McCutchan et al. 2003) while there is a pelagic-coastal carbon isotope gradient of about 4‰ between the Gulf of Alaska and PWS (Kline 1997; Eslinger et al. 2001), comparatively higher $\delta^{13}\text{C}$ values can be broadly interpreted as evidence of more ‘nearshore’ foraging while lower $\delta^{13}\text{C}$ values can be interpreted as more of an ‘offshore’ foraging signature (McConnaughey and McRoy 1979; Johnson and Schindler 2009). Thus, the lack of difference between hatchery and wild fish $\delta^{13}\text{C}$ values is consistent with foraging in the same general region of the Gulf of Alaska. While the low $\delta^{13}\text{C}$ values in this study are suggestive

of offshore foraging, at least in comparison to other congeneric species (Figure 2.7), the ~ 1.5 ‰ difference between pink salmon $\delta^{13}\text{C}$ values from this study and the range of values derived from a comprehensive meta-analysis (-20.4 to -21.9‰; Johnson and Schindler 2009) was greater than expected. One reason for this could be from the anomalously high sea surface temperatures in the GOA during 2015 (Di Lorenzo and Mantua 2016). Sea surface temperature is a reliable proxy for phytoplankton growth at the base of the marine food web (Richardson and Schoeman 2004) which exhibits rapid growth during high temperatures. This rapid phytoplankton growth lowers the carbon isotope fractionation rate, which would decrease observed $\delta^{13}\text{C}$ values (Tagliabue and Bopp 2008). Another contributing factor may be the multiple years and locations included in the meta-analysis, while in this study we have just one year of data from one location. Additionally, 2015 had the highest pink salmon return to PWS on record and the implied competition through abundance may have encouraged foraging on lower order prey items, which would also decrease observed $\delta^{13}\text{C}$ values (Qin and Kaeriyama 2016). These results largely serve to reinforce our understanding that pink salmon forage on a food web derived largely from pelagic primary producers (Radchenko et al. 2018).

We detected a positive association between body size and carbon isotope composition, which contrasts to previous studies on other salmon species that report the opposite trend (Johnson and Schindler 2012b; Quinn et al. 2012). This seeming contradiction is actually consistent with the known relationship between growth, size, and maturation in salmon whereby the largest and fastest growing individuals of salmon cohorts tend to mature at younger ages than slower growing, smaller individuals (Morita and Fukuwaka 2006). Pink salmon mature at the same age, and thus fast growth translates into larger sizes at maturity, whereas faster growth in species with variable ages at maturity (e.g., Chinook salmon and steelhead trout used in previous SIA studies)

tend to result in younger ages, and hence smaller sizes, at maturity. Curiously, pink salmon sampled from streams had lower $\delta^{13}\text{C}$ values than earlier arriving, ocean sampled pink salmon, which may be related to seasonal prey availability (Sturdevant et al. 2013) or subtle variation in migration routes.

In contrast to $\delta^{13}\text{C}$, hatchery and wild pink salmon differed in their relative trophic positions as inferred by $\delta^{15}\text{N}$ values. This difference appears mostly attributed to variation between hatchery and wild fish at the ends of the size continuum, but $\delta^{15}\text{N}$ values were similar for average sized fish. This pattern is likely driven by $\delta^{15}\text{N}$ values of late, stream-caught large individuals. Large wild pink salmon had muscle tissue $\delta^{15}\text{N}$ values that were almost 1.5‰ greater than large hatchery pink salmon in late stream sampled individuals, but all other timing and location categories had highly overlapping confidence intervals. This pattern, in which the largest hatchery and wild fish appear to be foraging at the most different trophic positions, was also seen in hatchery and wild steelhead returning to Forks Creek, Washington (Quinn 2012). In PWS, odd-year wild pink salmon are larger than the few stray hatchery pink salmon earlier in the season, but they are similar sized later in the season when the majority of hatchery fish are found in wild spawning streams (Chapter 1). These previously observed patterns, coupled with the difference in $\delta^{15}\text{N}$ values of large, late hatchery and wild pink salmon, suggest resource partitioning in larger hatchery and wild salmon. Although there is no SIA data for even-year pink salmon, there is a much smaller size difference of hatchery and wild pink salmon, and it is possible that there is also a smaller difference in even-year isotope values, which serve as a proxy for resource use, between hatchery and wild pink salmon.

We expect body size to positively scale with trophic position (Romanuk et al. 2011), as suggested by between-species trophic relationships in salmon (Figure 2.7). However, this is not

well supported within a salmon species, with various studies finding neutral, negative, or positive relationships between body size and trophic position for chum and sockeye salmon (Satterfield IV and Finney 2002; Johnson and Schindler 2012b, 2012a). An alternative and non-mutually exclusive interpretation of higher $\delta^{15}\text{N}$ values in wild salmon is related to their capital breeding life history, in which pink salmon stop feeding as they approach final maturation and spawning is fueled by stored energy reserves. Thus, as individuals complete spawning and approach senescence it is likely that their $\delta^{15}\text{N}$ values will increase as they functionally self-cannibalize their reserves (Hertz et al. 2015). Wild pink salmon tend to enter streams earlier than hatchery fish (Chapter 1; Brenner et al. 2012), and thus it seems likely that this underpins observed differences. Our work contributes to a small number of studies that have quantified trophic ecology with SIA between adult hatchery and wild Pacific salmon of any species including West Coast, USA steelhead trout (Atcheson et al. 2012; Quinn et al. 2012; Lamperth et al. 2017), chum salmon in Japan (Qin et al. 2013), and Baltic Sea Atlantic salmon (Torniainen et al. 2014). Taken as a whole, there appears to be a highly variable relationship between hatchery and wild isotopes and life history traits, with no consistent trends linking life history traits and origin, suggesting that results are likely to be species and context specific.

We acknowledge several inherent caveats and limitations to our study. First, we were only able to conduct the sampling during one spawning season. Given the fixed two-year age of maturity in pink salmon, our data collected in an odd-numbered year should only be generalized to odd-year lineage pink salmon. Despite using the same habitats, even and odd year lineage pink salmon are known to differ not only genetically but also phenotypically, with differences in life history traits such as run timing within a river (Oke et al. 2019). Differences between lineages are confounded by consistently different conspecific densities, with odd year lineage pink

salmon now being the dominant year of return in the North Pacific. As a result, the potential for intraspecific competition is higher in odd years when the abundance of pink salmon is higher than in even years. Related to this, a second major caveat of our study is the acknowledgment that 2015 was an extraordinary year with a record high return of pink salmon to Prince William Sound. While on one hand this chance event was fortuitous as it set the stage for potentially revealing intraspecific competition between hatchery and wild salmon as inferred by SIA, it also limits the extent to which we can generalize the results. One consequence of the large return was very high exploitation rates on hatchery pink salmon (99%; Knudsen et al. 2021). It is possible, but not known, to what extent fishery selection may underpin the observation that the average ocean caught fish was 27 mm larger than the average stream caught fish. Although purse seine fisheries are frequently thought to be much less selective on size than gill net fisheries (Kendall and Quinn 2012), future work to understand the potential for intense harvest on wild and hatchery salmon in PWS to shape life history and population demographics would be useful. A third caveat is that all hatchery fish sampled from spawning streams are strays and may represent a different demographic than homing hatchery individuals. However, we currently do not know whether strays are a random or non-random subset of the fish that home back to hatchery release locations.

Despite these caveats, our work serves to narrow the knowledge gaps of pink salmon ocean ecology and is the first to quantify their hatchery and wild isotopic signatures. Although this study was not designed to detect competition per se, our findings suggest that competition between hatchery and wild salmon is likely given the large overlap in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Of course, an understanding to what extent food resources are limiting is needed to assess competition (Kaga et al. 2013; Daly et al. 2019). Despite their apparent similarities, the annual

addition of over 650 million pink salmon fry to PWS (Wilson 2020) vastly outnumbers estimates of wild fry abundance (Boldt and Haldorson 2004), and likely has impacts on PWS ecosystems (Sturdevant et al. 2013; Amoroso et al. 2017). Pink salmon are increasingly thought to be a driver of North Pacific food web dynamics and this study contributes to a better understanding of the intraspecific complexities of pink salmon.

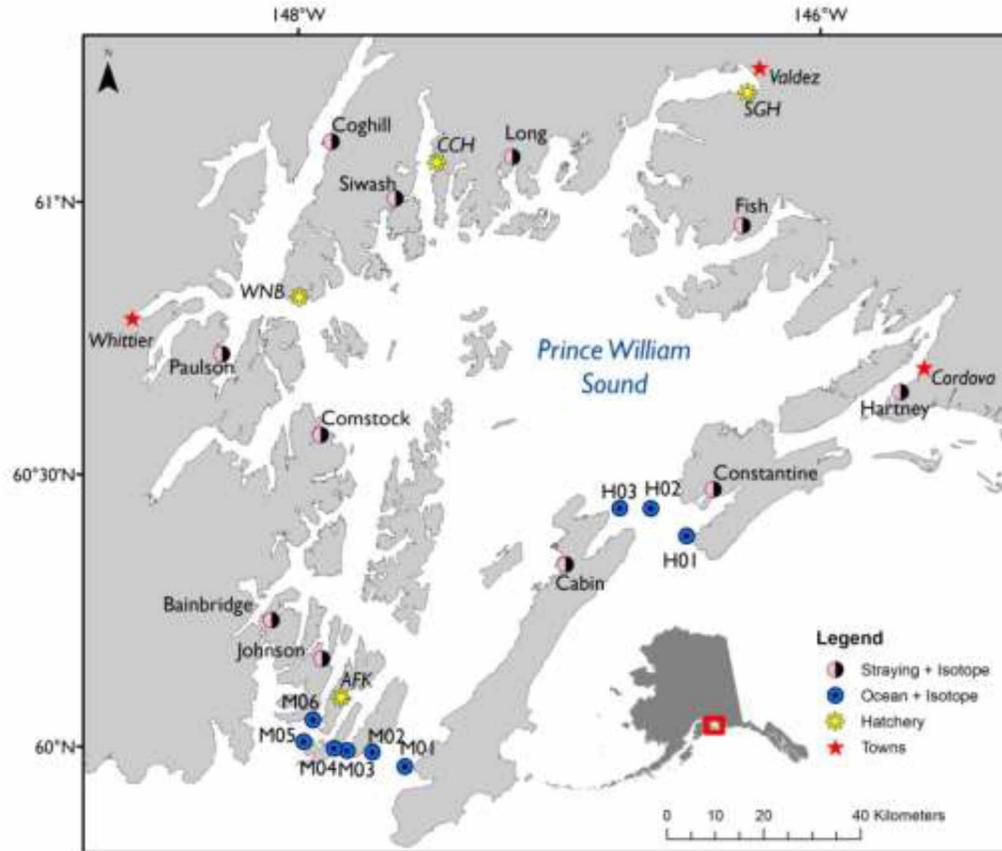


Figure 2.1 Ocean (blue circles) and stream sampling (pink and black circles) locations of pink salmon in Prince William Sound, Alaska, USA. Locations of pink salmon hatcheries are marked with yellow asterisks and towns are marked with red stars.

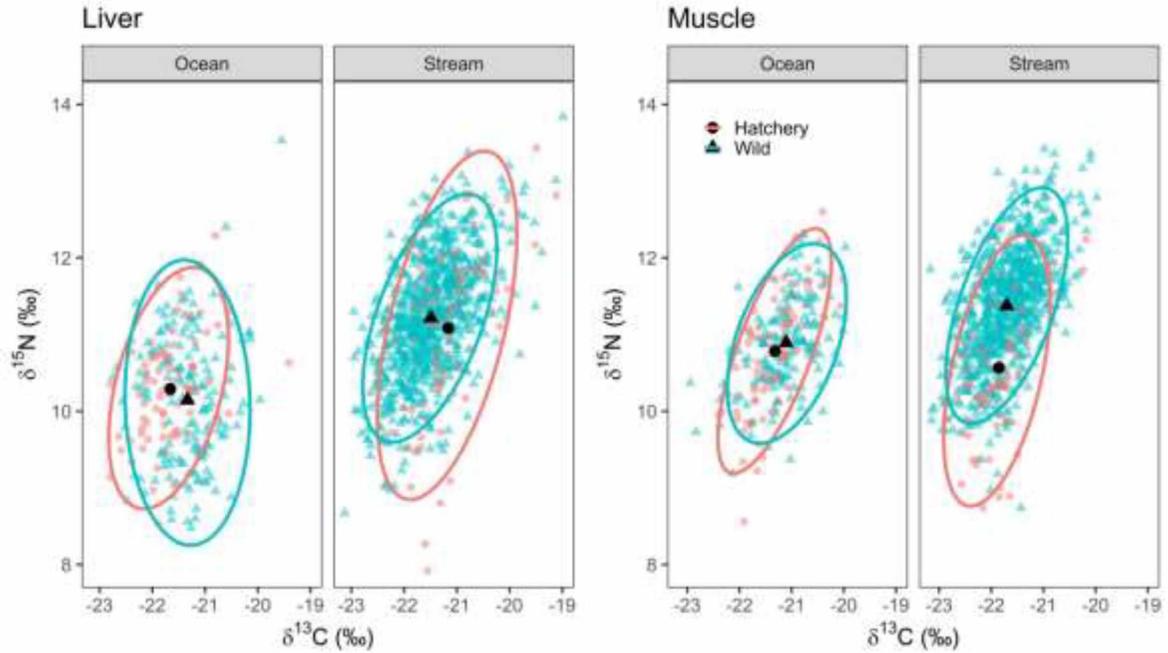


Figure 2.2 The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) from liver (A) and muscle (B) tissue of hatchery (red circles) and wild (blue triangles) pink salmon. Ellipses (95% confidence contour) are presented as a visual aid and black points represent the means of hatchery and wild samples. Data from all ocean and stream locations are included.

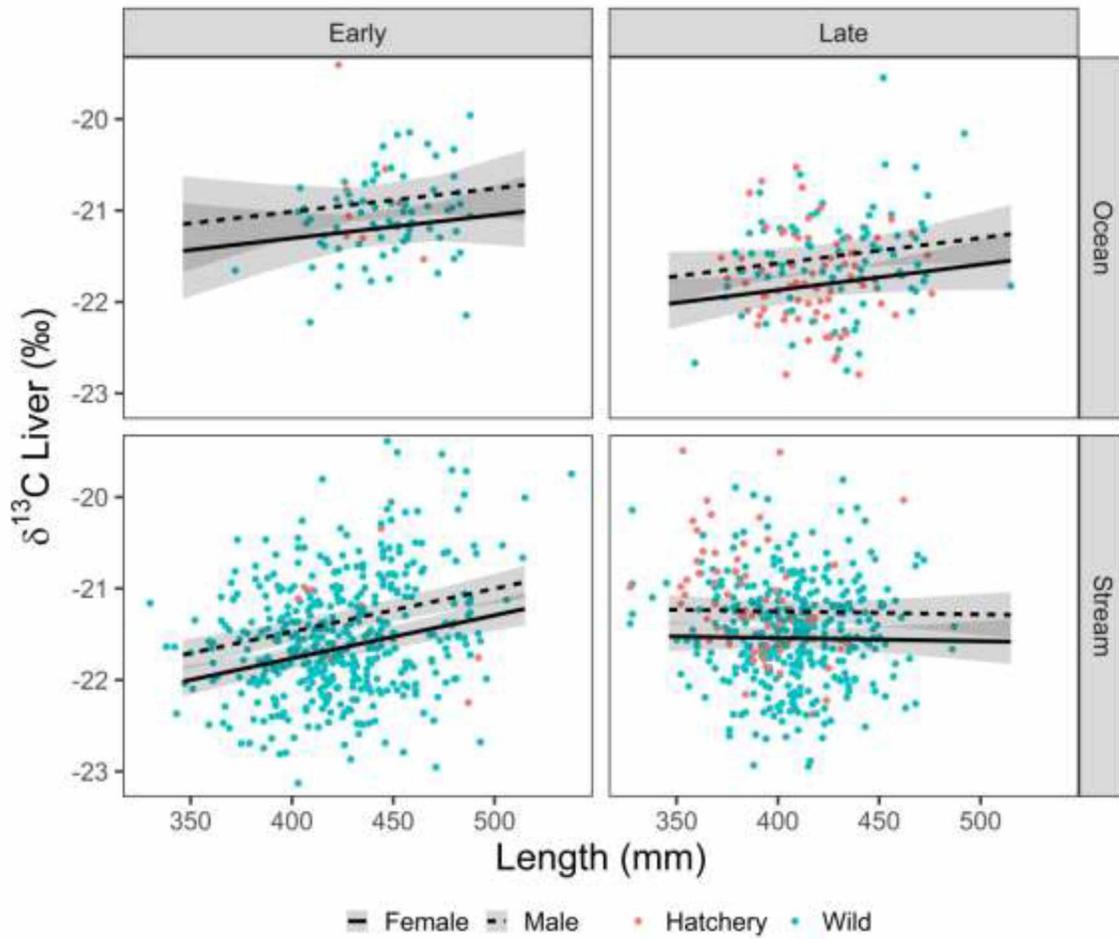


Figure 2.3 The relationship of $\delta^{13}\text{C}$ values of liver tissue to pink salmon length for early and late (as columns), ocean and stream (as rows) sampled fish. The fitted line represents the results of the top model for male and female hatchery and wild fish and shading indicates 95% confidence intervals.

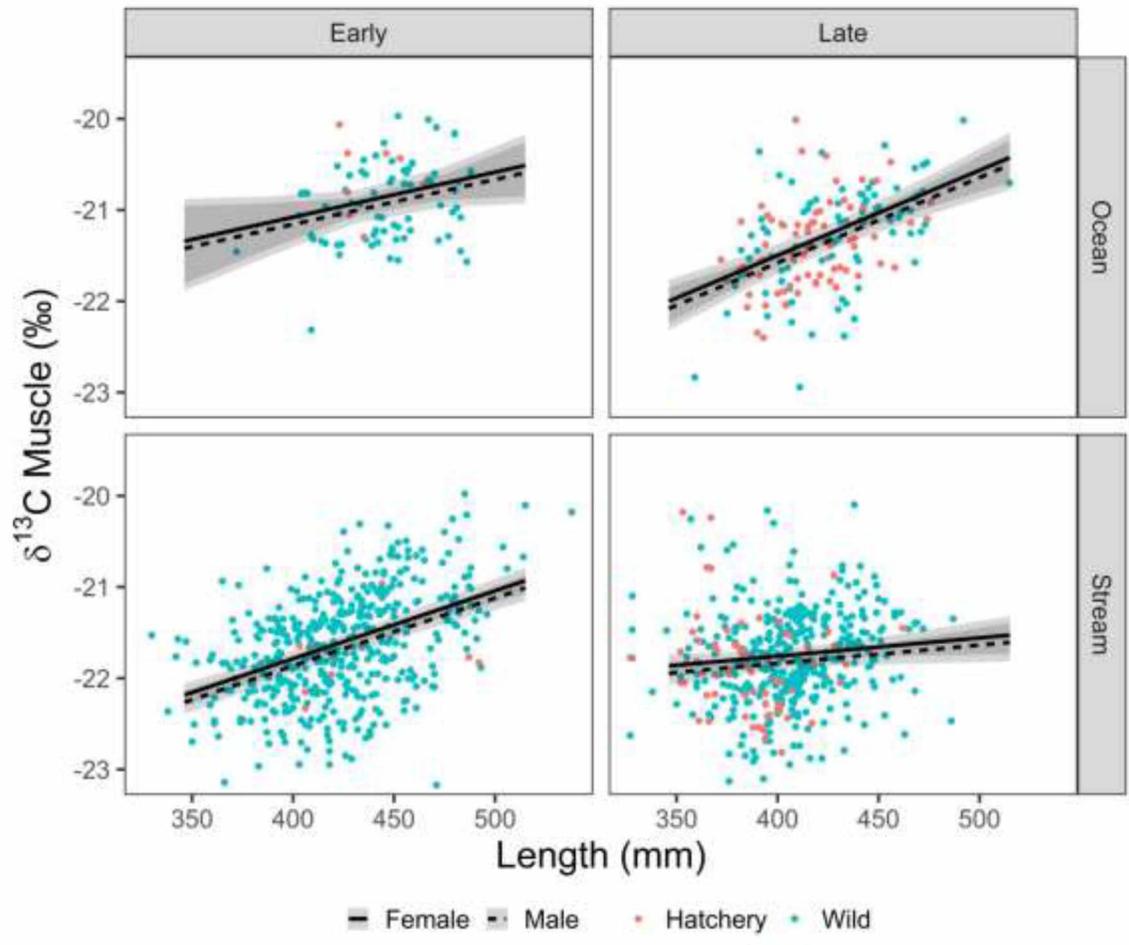


Figure 2.4 The relationship of $\delta^{13}\text{C}$ values of muscle tissue to pink salmon length for early and late (as columns), ocean and stream (as rows) sampled fish. The fitted line represents the results of the top model for male and female fish and shading indicates 95% confidence intervals.

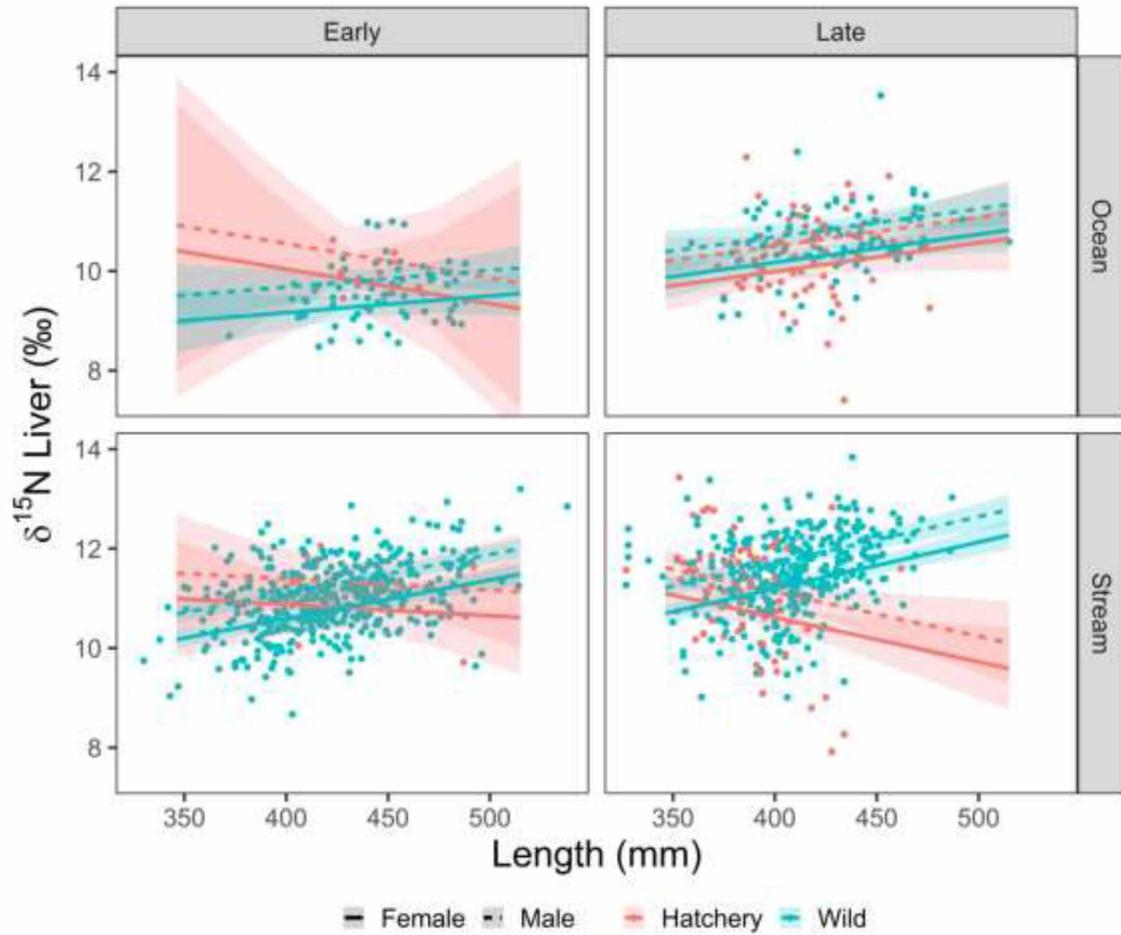


Figure 2.5 The relationship of $\delta^{15}\text{N}$ values of liver tissue to pink salmon length for early and late (as columns), ocean and stream (as rows) sampled fish. The fitted line represents the results of the top model for male and female, hatchery and wild fish, and shading indicates 95% confidence intervals.

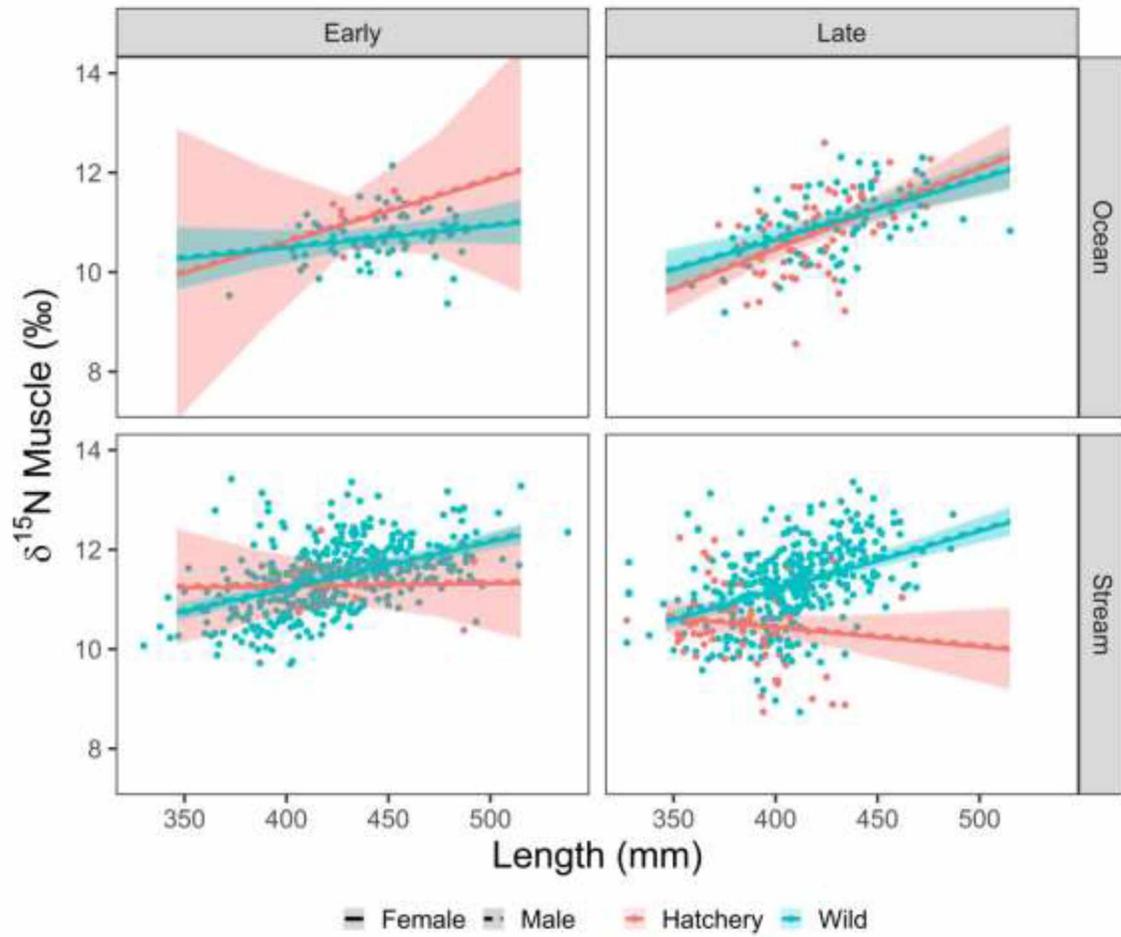


Figure 2.6 The relationship of $\delta^{15}\text{N}$ values of muscle tissue to pink salmon length for early and late (as columns), ocean and stream (as rows) sampled fish. The fitted line represents the results of the top model for male and female, hatchery and wild fish, and shading indicates 95% confidence intervals.

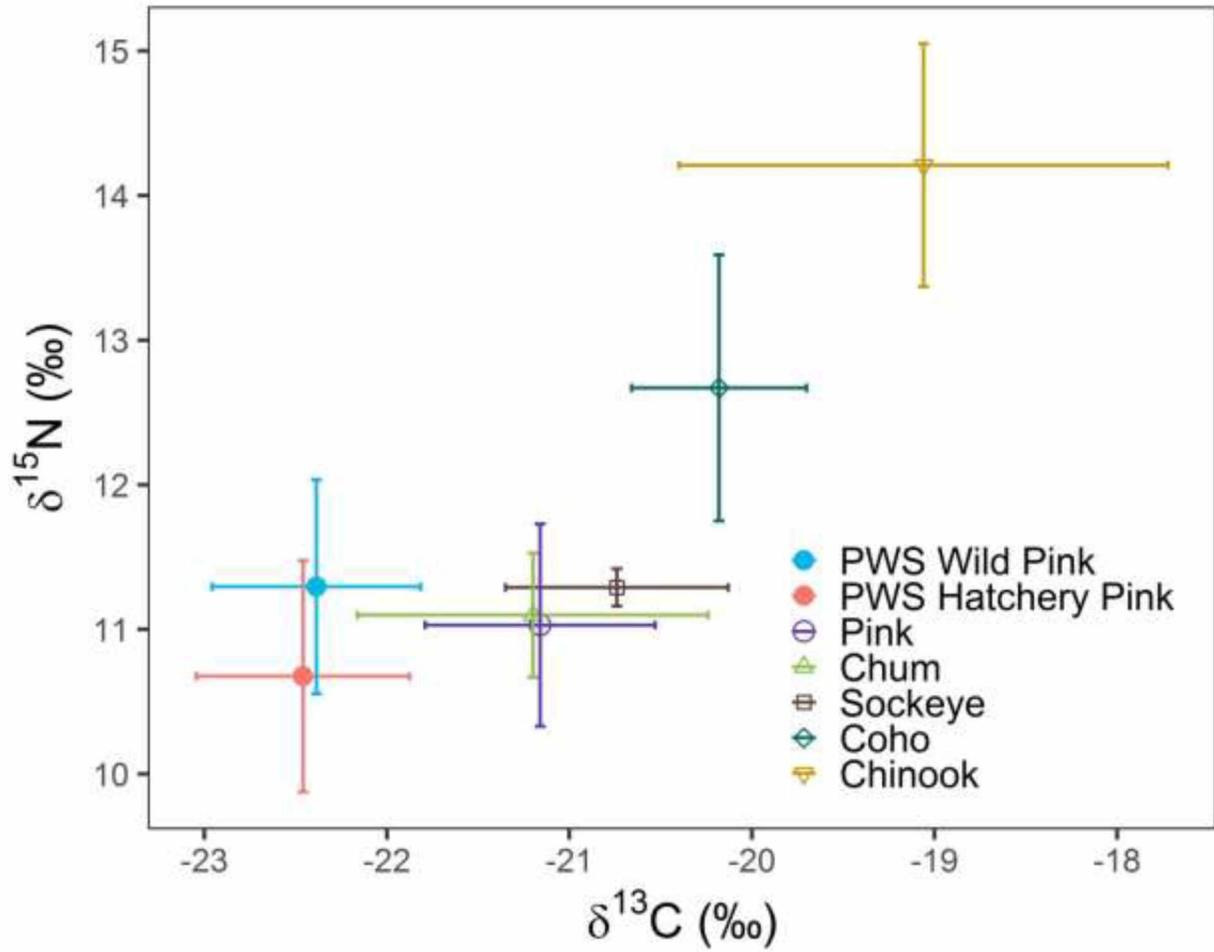


Figure 2.7 Isotope values of Prince William Sound (PWS) hatchery and wild pink salmon muscle relative to a meta-analysis of Gulf of Alaska salmon (Johnson and Schindler 2009). Error bars are one standard deviation. For this plot, PWS hatchery and wild pink salmon $\delta^{13}\text{C}$ values were lipid corrected with methods from McConnaughey and McRoy (1979) to provide an accurate comparison to Johnson and Schindler (2009).

Table 2.1 Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values (and sd) for muscle and liver tissues from ocean and stream sampled, hatchery and wild pink salmon of Prince William Sound, Alaska, USA.

Region	Origin	Sample size	Tissue and stable isotope			
			Muscle		Liver	
			$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Ocean	Hatchery	83	-21.66 (0.56)	10.29 (0.77)	-21.32 (0.51)	10.78 (0.74)
	Wild	156	-21.34 (0.56)	10.15 (0.85)	-21.10 (0.57)	10.89 (0.66)
Stream	Hatchery	79	-21.16 (0.64)	11.08 (1.08)	-21.85 (0.50)	10.57 (0.85)
	Wild	791	-21.49 (0.61)	11.22 (0.77)	-21.70 (0.55)	11.38 (0.73)

Table 2.2 Candidate mixed-effects model sets for all combinations of isotope and tissue responses. The full model “With origin” includes the interactions of origin (hatchery vs. wild) as well as location, timing, and condition. The model “Without origin” excludes origin, but includes all aforementioned covariates. The null model is the intercept only model.

Response	Covariates	K	AICc	Δ_i	W_i	Log(L)
$\delta^{13}\text{C}$ Liver	Without origin	11	1859.8	0.0	0.5	-918.8
	With origin	19	1859.8	0.0	0.5	-910.6
	Null	3	2023.5	163.7	0.0	-1008.8
$\delta^{13}\text{C}$ Muscle	Without origin	11	1613.0	0.0	0.8	-795.4
	With origin	19	1615.2	2.2	0.2	-788.2
	Null	3	1836.0	223.0	0.0	-915.0
$\delta^{15}\text{N}$ Liver	With origin	19	2228.9	0.0	1.0	-1095.1
	Without origin	11	2265.3	36.4	0.0	-1121.5
	Null	3	2663.7	434.7	0.0	-1328.8
$\delta^{15}\text{N}$ Muscle	With origin	19	2199.3	0.0	1.0	-1080.3
	Without origin	11	2247.0	47.7	0.0	-1112.4
	Null	3	2470.4	271.1	0.0	-1232.2

Table 2.3 Fixed effect coefficient estimates and standard errors from the top model of each of the isotope-by-tissue response. Each of the top models includes region, length, timing, and origin except the top models for $\delta^{13}\text{C}$ muscle and liver, which do not include the origin coefficient. The reference category is an early sampled, ocean caught and hatchery origin fish. All models included the random term of “location” which was the specific ocean or stream sampling site.

	Response: $\delta^{13}\text{C}$ Liver		$\delta^{13}\text{C}$ Muscle		$\delta^{15}\text{N}$ Liver		$\delta^{15}\text{N}$ Muscle	
	Top Model: Without origin		Without origin		With origin		With origin	
	β	se	β	se	β	se	β	se
Intercept	-21.26	0.11	-20.99	0.09	9.92	0.41	10.83	0.40
Region(Stream)	-0.42	0.12	-0.66	0.10	0.92	0.47	0.45	0.46
Length	0.08	0.08	0.16	0.07	-0.23	0.53	0.40	0.52
Timing (Late)	-0.56	0.11	-0.34	0.09	0.17	0.41	-0.08	0.41
Origin(Wild)	--	--	--	--	-0.69	0.42	-0.26	0.42
Sex (Male)	0.29	0.03	-0.08	0.03	0.51	0.04	0.04	0.04
Region * Length	0.07	0.09	0.08	0.08	0.15	0.57	-0.38	0.56
Region * Timing	0.70	0.11	0.27	0.10	-0.55	0.49	-0.83	0.48
Length * Timing	0.01	0.10	0.14	0.09	0.41	0.54	0.12	0.53
Region * Origin	--	--	--	--	0.58	0.48	0.37	0.47
Length * Origin	--	--	--	--	0.33	0.54	-0.26	0.53
Timing * Origin	--	--	--	--	0.87	0.44	0.38	0.43
Region * Length * Timing	-0.17	0.11	-0.32	0.10	-0.63	0.59	-0.27	0.58
Region * Length * Origin	--	--	--	--	-0.01	0.58	0.55	0.57
Region * Timing * Origin	--	--	--	--	0.13	0.51	0.53	0.51
Length * Timing * Origin	--	--	--	--	-0.34	0.55	0.13	0.55
Region * Length * Timing * Origin	--	--	--	--	0.61	0.60	0.09	0.60

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Conclusions

This thesis sought to elucidate some of the potential ecological mechanisms that may yield differential reproductive success between hatchery and wild Pacific salmon. This study was conducted with the highly abundant pink salmon of Prince William Sound, Alaska (PWS), with the following goals: 1) quantify differences in fitness-related life-history traits associated with stray hatchery origin or homing wild fish sampled in wild spawning streams; and 2) explore whether broad-scale differences in ocean foraging contributed to differences in length. The main findings of this study are as follows:

- **Body size of pink salmon is highly variable and differs between lineages.** Length differences between hatchery and wild pink salmon were driven by a combination of lineage, return timing, and sex. Odd-year wild fish were larger earlier, arrived earlier, and males were larger than females. To the extent that length mediates reproductive success, these findings implied that wild fish had greater reproductive potential than hatchery fish in odd years. The opposite trends were generally found in even year fish. Even year fish were smaller earlier and hatchery females were largest on average, but hatchery fish still arrived about a week later than wild fish. To the extent that length mediates reproductive success, hatchery fish may have greater reproductive potential in even years than in odd years.
- **Instream lifespan between hatchery and wild fish was similar.** Instream lifespan of hatchery fish was two days shorter than wild fish. Although not statistically significantly different, this difference may be biologically significant.
- **Instream lifespan differed markedly between wild fish in spatially adjacent streams of different sizes.** Predation risk is a well-known driver of salmon life history evolution,

and consistent with this, salmon from a high risk site lived 2 days less on average than wild fish from a lower risk site. This is highly suggestive of local adaptation to predation pressure and is worthy of future examination.

- **The egg retention of hatchery and wild pink salmon was not different in the two years measured.** In contrast to other studies egg retention rates were extremely low for both hatchery and wild pink salmon.
- **Hatchery and wild pink salmon were spatially integrated during foraging.** As inferred by $\delta^{13}\text{C}$ values, hatchery and wild pink salmon were foraging in statistically indistinguishable locations in 2015.
- **Average sized hatchery and wild pink salmon had similar trophic positions.** Large and small hatchery and wild pink salmon were foraging at inversely related trophic positions, but these were broadly overlapping for mean fish lengths, suggesting shared trophic niches for the majority of fish in 2015.
- **Larger fish forage ‘closer’ to shore and at higher trophic positions, with exceptions.** Length positively scaled with foraging location ($\delta^{13}\text{C}$) for hatchery and wild pink salmon. Length also positively scaled with trophic position ($\delta^{15}\text{N}$) of wild pink salmon, but was inconsistently related to trophic position for hatchery pink salmon.

Observed differences in life-history traits and implications for management

Prince William Sound, Alaska harbors the largest pink salmon hatchery program in the world, annually releasing over 650 million juvenile pink salmon (Wilson 2020). On average, 32 million hatchery fish return to PWS (Evenson et al. 2018), and recipient stray rates in wild streams ranges from 0.5 to 0.15 % (Knudsen et al. 2021). The number of straying hatchery pink salmon into wild spawning grounds is above the suggested straying threshold of 2% set by the

PWS comprehensive Salmon Management Plan (ADF&G Staff 1994), and at or above other 5–10 % thresholds suggested by genetic modeling and analysis (Ford 2002; Moberg et al. 2005). Salmon hatcheries in PWS are intended to bolster returns of harvestable pink salmon while maintaining harvestable wild runs (McGee 2005) and minimizing interactions between hatchery and wild fish (Helle 1976), but the extent to which strays occur in wild spawning streams has raised concerns surrounding wild pink salmon ecological and genetic integrity (Brenner et al. 2012).

Research conducted in other systems indicates that a wide variety of life-history traits have the potential to influence reproductive success of hatchery and wild salmon spawning in the wild, but some of the most notable, and interrelated, are body length, arrival timing, instream lifespan, and egg retention (McPhee and Quinn 1998; Dickerson et al. 2002, 2005; Grant et al. 2011; McConnell et al. 2018). We add our observations of reduced hatchery fish body length in high abundance years compared to wild fish, but we found the opposite pattern in even years; this pattern may be due to the high abundance of pink salmon competing for at sea resources during odd years and differential success of hatchery and wild foraging tactics. This hypothesis is only partially supported by our odd-year analysis of foraging niche, in which hatchery and wild pink salmon exhibited similar stable carbon isotope signatures that indicate foraging in similar areas but may be partitioning prey resources (stable nitrogen isotope values) based on body size (or behavior). Additionally, we found weak evidence that hatchery pink salmon had shorter instream lifespans and no evidence that hatchery fish have higher egg retention, unlike some other studies of egg retention in hatchery fish spawning in the wild (McConnell et al. 2018).

Ultimately, this work identified life-history differences between hatchery and wild pink salmon in Alaska that have the potential to influence interactions between hatchery and wild salmon. It must be noted that there were very few hatchery fish sampled for the instream lifespan and egg retention analyses because, by chance, there were few stray hatchery fish in the years sampled. Additionally, the work on foraging niche is only derived from 2015, which was anomalous for its record-breaking pink salmon return (Haught et al. 2017) and high sea surface temperatures (Di Lorenzo and Mantua 2016), and thus may poorly reflect foraging patterns in other years and not represent average baseline carbon and nitrogen isotope values (MacKenzie et al. 2011). Additional tagging efforts to document instream lifespan, egg retention, and other pertinent life-history traits in creeks spanning a range of hatchery stray rates is a logical next step in clarifying and continuing investigations of the mechanisms linked to differential reproductive success of hatchery and wild pink salmon in the wild. A complementary approach currently being addressed (Lescak et al. 2019), is comprehensive genotyping to compare hatchery and wild reproductive success. Results from Lescak et al. (2019) suggest reduced hatchery fitness for later arriving and smaller males but no difference in reproductive success between hatchery and wild females in an even year. Taken together, the melding of empirically sampled ecological data with modern advances in genomics stand to greatly increase our understanding of hatchery and wild salmon in the Prince William Sound ecosystem.

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